Long term dynamics of the vegetation at the subalpine-alpine ecocline during the Holocene : comparative study in the Aletsch region, Val d'Arpette and Furka Pass (Valais, Switzerland)

CARNELLI, Adriana Luisa

Abstract

Le présent travail a comme objectif l'étude de la dynamique de la végétation subalpine-alpine durant l'Holocène dans les Alpes. Une approche multidisciplinaire a été utilisée (pédoanthracologie, analyse des phytolites, études des sols, palynologique, des macrorestes végétaux, de la végétation et dendrocronologique). La zone d'étude est située dans le canton du Valais (47°N, Suisse). Les investigations paléobotaniques entreprises ont mis en évidence que dans les sites étudiés, la limite maximale atteinte par les arbres (> 2 m) durant l'Holocène était située autour de 2500-2550 m. En accord avec cette reconstruction, la limite supérieure de l'arbre était située 250-300 m au-dessus de sa limite potentielle actuelle (2250-2300 m). En outre, cette étude a permis de comparer les résultats provenant de diverses méthodes paléoécologiques. Parmi celles-ci, l'étude de la silice biogénique dans les sols a été utilisée pour la première fois dans les Alpes.

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UNIVERSITÉ DE GENÈVE
Institut F.-A. Forel
UNIVERSITÉ DE BERNE
Institut of Plant Science

FACULTÉ DES SCIENCES
Professeur W. Wildi
Professeur B. Ammann

Long Term Dynamics of the Vegetation at the Subalpine-Alpine Ecocline during the Holocene: Comparative Study in the Aletsch Region, Val D'Arpette, and Furka Pass (Valais, Switzerland)

THÈSE

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par
Adriana L. CARNELLI
(Italie)

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1. Cadre et buts de la recherche

L’écocline subalpin-alpin représente une zone complexe de transition bioclimatique entre la forêt dense et la pelouse alpine. Cette zone est sensible à divers processus écologiques qui dépendent soit du climat, soit de l'influence humaine. Elle a une très grande importance écologique et socio-économique. Le présent travail a comme objectif l’étude de la dynamique de la végétation de l’écocline subalpin-alpin durant l'Holocène et le passé dans les Alpes.

Une approche multidisciplinaire a été utilisée en associant deux méthodes d'investigation principales (pédoanthracologie et analyse des phytolites) et cinq approches complémentaires (études des sols, palynologique, des macrorestes végétaux, de la végétation et dendrocronologique). A travers la combinaison des résultats fournis par ces méthodes, notre travail se propose de donner des réponses sur l'écologie passée et présente de la végétation alpine et, surtout, sur la naturalité et l'extension en altitude de l’étage alpin en relation avec l'extension de la limite de la forêt dans le passé, notamment l’altitude maximale atteinte par celle-ci. En particulier, il s'agit de vérifier aussi si l’étage alpin est naturellement dépourvu d'arbres ou si les phanérophytes y étaient présentes une fois et qu’elles auraient disparu à la suite des activités humaines. Ce dernier point est important pour comprendre si la végétation de cet étage est proche de l’équilibre naturel en fonction du climat et des facteurs écologiques.

En outre, notre étude a permis de comparer les résultats provenant de diverses méthodes paléoécologiques. Parmi celles-ci, l'étude de la silice biogénique dans les sols a été, à notre connaissance, utilisée pour la première fois dans les Alpes.

2. Zone d'étude et échantillonnage

La zone d'étude est située dans le canton du Valais (47°N, Suisse) qui correspond au cours supérieur du Rhône dans les Alpes centro-occidentales. Quatre sites ont été sélectionnés, tous sur roche acide: 1) le *Val d'Arpette* situé à la limite Est du massif du Mt. Blanc, 2) la région de *Belalp* dans la partie sud du Massif de l'Aar (région d'Aletsch, 3) le lieu-dit *"Hindererhinertüre"* en bordure même du Glacier d'Aletsch (rive gauche hydrologiquement parlant), 5) la région de *"Tälli"* à proximité du col de la Furka. L'échantillonnage a été réalisé à l'étage alpin sous forme de cinq transects altitudinaux compris entre 2300 et 2850 m, dont deux à Belalp, le transect *Belalp-Hofathorn* (BA-HO) et le transect *Belalp-Lengi Egga* (BA-LE), et un transect dans chacun des trois autres sites: le transect Arpette (AR), le transect glacier d'Aletsch (HT) et le transect Furka (FK). Les points d'échantillonnage, deux à quatre selon le transect, sont espacés l'un de l'autre par une différence altitudinale de ± 200 m à l'exception du transect BA-LE où l'interval est de ± 100 m. A chaque point d'échantillonnage, un profil de sol a été creusé en situation aussi plane que possible, c'est-à-dire le moins possible exposée à l'érosion active. D'une manière générale, la limite supérieure potentielle actuelle de la forêt est située vers 2200-2250 m à Arpette et à Belalp et vers 2100 m à la Furka. Respectivement, la limite supérieur potentielle de l'arbre est située vers 2250-2300 m à Arpette et à Belalp et vers 2200 m à la Furka.

3. Synthèse des résultats

Deux types de résultats ont été obtenus:

1. Des résultats méthodologiques, qui sont à mettre en relation avec l'étude de la silice biogénique dans les plantes et dans les sols; de nouvelles approches méthodologiques ont été testées dans le but d'appliquer ces résultats à la reconstruction de la limite de la forêt.

2. Des résultats qui ont trait aux évidences paléoécologiques utilisées pour reconstruire la limite de la forêt.

Recherches méthodologiques

L'étude de la silice biogénique d'origine végétale dans les écosystèmes alpins est à ses premiers débuts et beaucoup d'aspects méthodologiques doivent encore faire l'objet d'une évaluation. Nous avons donc premièrement réalisé une collection de référence. Pour y parvenir, il a été nécessaire d'extraire la silice biogénique des tissus (feuilles et bois) de 28 espèces dominantes et/ou communes aux étages subalpin et alpin (voir ci-après). Deuxièmement, le contenu et la production de silice biogénique de même que la fréquence des morphotypes et leur composition chimique ont été évalués sur le matériel de référence. Troisièmement, la silice biogénique dans les sols actuels a été analysée pour déterminer l'origine des assemblages de phytolites observés et mettre ces données en relation avec celles provenant du matériel de référence.

Les espèces suivantes ont été étudiées (collection de référence): *Abies alba* Miller, *Alchemilla pentaphylla* L., *Alnus viridis* (Chaix) DC, *Arctostaphylos uva-ursi* Spreng., *Calamagrostis villosa* (Chaix.) Gmelin, *Calluna vulgaris* L., *Carex curvula* All., *Carex sempervirens* Vill., *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher, *Festuca halleri* All., *Festuca melanopsis* Foggi, Rossi & Signorini (= *F. puccinellii* auct.), *Festuca scabriculmis* subsp. *luedii* Markgraf-Dannenberg, *Geum montanum* L., *Juniperus nana* Willd., *Larix decidua* Miller, *Leontodon helveticus* Merat, *Loiseleuria procumbens* Desf., *Nardus stricta* L., *Picea abies* (L.) Karsten, *Pinus cembra* L., *Pinus mugo* Turra, *Poa alpina* L., *Rhododendron ferrugineum* L., *Salix helvetica* Vill., *Vaccinium myrtillus* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., *Veronica bellidioides* L.

Silice biogénique dans les plantes subalpines-alpines

A l'exception de *Leontodon helveticus* et de *Veronica bellidioides,* toutes les espèces prises en considération contiennent de la silice biogénique. Les plus fortes teneurs s'observent chez les graminées et les cypéracées, comme par exemple *Calamagrostis villosa* (5.9%), *Carex sempervirens* (2.29%), *Festuca scabriculmis* (2.41%). A l'opposé, les herbacées non graminoïdes ne contiennent que très peu de silice biogénique, de l'ordre de 0.1 à 0.2%, de même que les éricacées (exception. *Calluna vulgaris:* 0.68%). Chez les conifères, la teneur est variable, de l'ordre de 0.1% *(Pinus mugo, P. cembra),* elle peut atteindre 1% (*Larix decidua:* 1.09% dans les aiguilles, 0.54% dans le bois; *Picea abies:* 0.85% dans les aiguilles, 0.16% dans le bois).

A l'aide des mesures de la silice biogénique contenue dans les espèces de la collection de référence, il a été possible d'estimer la production de silice biogénique des principales communautés végétales alpines et subalpines sur sol acide, dans le but d'évaluer l'apport potentiel annuel dans les sols après la minéralisation de la nécromasse. Cette estimation a été calculée en tenant compte de la productivité du groupement végétal, de la durée de la saison de végétation et de la contribution en biomasse relative des espèces dominantes dans le groupement en question. La comparaison entre les apports estimés des différentes communautés végétales a permis de mettre en évidence l'importance des pelouses subalpines dans le cycle biogéochimique de la silice. Il résulte que, dans l'écosystème subalpin, la production annuelle moyenne de silice biogénique des pelouses (9.4 g m^2 y^{-1}) est à peu près d'un ordre de magnitude supérieure à celle des landes à éricacées mésophiles (0.45-0.48 g m^2 y^{-1}), des aulnaies vertes et des formations arbustives (0.46-0.51 g m^2 y^{-1}), de la litière des forêts de conifères (1.6 g m^2 y^{-1}) ainsi que des pelouses de l'étage alpin supérieur (1.2 g m^2 y^{-1}).

L'intérêt de la silice biogénique dans les études paléoécologiques est forcément associé à l'ubiquité des espèces et à leur disponibilité dans les archives paléoécologiques que sont les sols et les tourbes: l'évaluation quantitative de la silice biogénique permet de conclure que l'analyse de la silice biogénique dans les sols subalpins-alpins est à même de fournir de précieuses indications écologiques.

Morphologie des phytolithes

La silice amorphe (opale) se dépose dans les plantes sous forme de remplissages cellulaires ou de dépôts intracellulaires qui, suite à la décomposition de la matière végétale, sont délivrés sous forme de silice particulaire, les phytolithes, dans les sols et dans les sédiments. L'observation au microscope optique et électronique de la silice biogénique extraite des tissus des plantes appartenant au matériel de référence a permis d'établir une typologie des phytolithes et, également, de quantifier leur fréquence. On a réalisé ainsi un atlas des différents types observés. Les monocotylédones ont produit des phytolithes bien silicifiés et idiomorphes, principalement d'origine épidermale ("short cells" ou "trapezoids" des graminées et "cones" des cypéracées). Les phytolithes des éricacées proviennent surtout des cellules épidermiques, des complexes stomatiques et des vaisseaux. Au contraire, chez les conifères, les dépôts silicifiés se font surtout dans les tissus de transfusion et dans les cellules endodermales. Nous avons testé le pouvoir diagnostique des phytolithes par des analyses statistiques multivariées. Il résulte que, en tenant compte des fréquences, les monocotylédones (graminées et cypéracées) forment un groupe qui se différencie nettement vis-à-vis des autres espèces (éricacées, *Alnus viridis* et conifères). Par contre, au sein du deuxième groupe, éricacées, *Alnus* et conifères ne sont pas toujours nettement séparés de façon univoque. En effet, *Alnus viridis, Pinus cembra* et *Juniperus nana* peuvent parfois être rattachés aux éricacées. Parmi les phytolithes des espèces examinées on peut donc potentiellement distinguer entre monocotylédones et espèces ligneuses. Toutefois, l'approche strictement morphologique est limitée du fait que certaines cellules silicifiées peuvent prendre une forme similaire dans les tissus d'une même plante ou d'espèces différentes.

L'aluminium dans la silice biogénique des plantes subalpines et alpines

L'approche morphologique présentant des limites dans l'utilisation des phytolithes, une approche complémentaire a été testée en analysant la composition chimique des phytolithes. Celle-ci a été mesurée grâce à une méthode semiquantitative par microanalyse aux rayons X sur le matériel de la collection de référence. Il est alors ressorti que de l'aluminium peut être présent dans le réticule de silice opaline de certains phytolithes. Parmi les espèces analysées, cette présence d'aluminium s'est avérérée être un précieux indicateur permettant alors de distinguer les espèces ligneuses des espèces non ligneuses. En effet, jusqu'à 97% des phytolithes de conifères et d'éricacées testés sont caractérisés par la présence d'aluminium dans la silice biogénique. Au contraire, les phytolithes de graminées et de cypéracées ne contiennent presque pas d'aluminium (au maximum dans 10% des phytolites testés).

Cette méthode constitue un apport nouveau dans la recherche sur les phytolithes. Combinée avec l'approche morphologique, cette méthode peut améliorer le potentiel diagnostique taxonomique des phytholithes. En effet, cette méthode permet de surmonter les difficultés liées à la répétitivité des formes de certains phytolithes et aussi d'identifier les phytolithes qui, ayant subi des processus taphonomiques dans les sols, ne correspondent plus aux morphotypes du matériel de référence de l'espèce. Sur la base de ces résultats, on peut affirmer que l'aluminium pourra être utilisé comme marqueur de la silice biogénique des conifères dans les études sur les changements de la végétation qui intéressent les conifères et les herbacées, par exemple dans les écosystèmes alpins, boréaux et méditerranéens. De manière plus générale, la teneur en aluminium peut trouver des applications dans les reconstructions paléoécologiques qui s'intéressent au passage d'une végétation ligneuse à une végétation herbacée, par exemple dans les cas forêt-steppe ou forêt-savanne. En outre, la composition chimique des phytolithes est importante pour mieux comprendre leur durée de vie dans les sols, les phytolithes riches en aluminium étant plus résistants à la dissolution.

La formation des assemblages de phytholithes dans les sols

Le but principal de l'étude des phytholithes est de fournir une base pour l'interprétation de leurs assemblages fossiles dans les sols où la silice biogénique subit des processus de migration et de dissolution. Ces processus étant différents entre les horizons supérieurs holorganiques (O) et organo-minéraux (A) d'une part, et entre les horizons minéraux plus profonds d'autre part.

Notre étude a mis en évidence que les assemblages de phytholithes dans les horizons holorganiques supérieurs sont dominés par les processus de déposition. Au contraire, déjà dans les horizons organo-minéraux sous-jacents, ce sont les processus de migration et de dissolution qui sont dominants. Ainsi, les assemblages de phytolithes dans les horizons O reflètent la végétation actuelle in situ et les assemblages dans l'horizon A correspondent à un processus où le temps est intervenu.

Dans les conditions actuelles, les horizons supérieurs du sol enregistrent rapidement les apports en silice biogénique des plantes. Les parties supérieures des sols sous une prairie subalpine productive à *Festuca scabriculmis* et *Carex sempervirens* contiennent jusqu'à 16% de silice biogénique. Par contre, les horizons organiques sous des prairies alpines moins productives à *Carex curvula* ne contiennent que jusqu'à 3.9% de silice biogénique. La présence de phytolithes riches en aluminium dans les horizons supérieurs est généralement plus élevée aux point d'échantillonnage les plus bas, très probablement parce les éricacées et les conifères qui les produisent en majeure partie sont présents de manière éparse à ces altitudes. Le contenu total en silice, la fréquence des phytolithes riches en aluminium et le pourcentage des morphotypes mesurés et estimés suggèrent que la formation des assemblages de phytolithes dans les pelouses subalpines et alpines est dominée par un mécanisme d'héritage *in situ*. Toutefois, un export de biomasse par le pâturage et par les avalanches pourrait aussi intervenir et jouer un rôle dans une rédistribution des phytolithes.

La comparaison entre l'apport théorique et les fréquences observées a mis en évidence le rôle dominant des processus taphonomiques déjà dans la partie sommitale du sol. En effet, si la fréquence des “ short cells ” bien silicifiées est prévisible sur la base de la productivité de la communauté végétale, ce n'est pas du tout le cas pour les morphotypes plus fragiles ou plus faiblement silicifiés comme les "cônes" des cypéracées. Ici, l'apport théorique est un mauvais indicateur car les processus taphonomiques sont dominants.

Comme le laissait supposer déjà les morphotypes de la collection de référence, les assemblages de phytolithes dans le sol ne permettent pas de faire une distinction entre les pelouses subalpines et les pelouses alpines. En effet, d'une part les graminées présentes dans ces écosystèmes appartiennent toutes à la même sous-famille des *Pooideae* et sont donc toutes caractérisées par des " short cells " du même type; d'autre part, les "cônes", phytolithes diagnostiques des cypéracées, sont faiblement préservés dans les sols.

Les recherches effectuées ont donc aidé à comprendre les processus qui règlent la formation des assemblages de phytolithes dans les sols. Il en résulte aussi que, pour améliorer les interprétations des données fossiles, on souligne l'importance qu'il y a de connaître le signal donné par la végétation actuelle.

Résultats paléoécologiques

Etude des sols subalpins et alpins

L'étude des sols a permis d'établir la limite supérieure des podzols dans les sites étudiés. On ne trouve plus de véritable PODZOSOLS au-dessus de 2'550 m. Au-delà, on entre dans le domaine des sols ocreux (ALOCRISOLS) dont la géochimie est dominée par l'aluminium. La raison de ce brusque changement nous paraît relever des conditions mêmes de la podzolisation, processus lié à un substrat acide, un climat froid et humide permettant la chéluviation (dans le cas particulier la période de fonte de la neige où ce phénomène est maximal) et à une végétation acidifiante. Or, si l'on raisonne pour un transect donné, il apparaît que la roche et le type de climat général sont constants. La seule variable permettant d'expliquer la transition PODZOSOL-ALOCRISOL est la végétation. Or, tous les sols étudiés se situent actuellement sous prairie acidophile, que ce soient des sols podzolisés, ocreux ou bruns. Ce genre de végétation, bien que pouvant produire une litière quelque peu acidifiante et engendrer une certaine podzolisation, ne peut cependant en aucun cas mener à des stades aussi aboutis que le PODZOSOL MEUBLE, solum typique des forêt de conifères. Les descriptions des sols tendraient donc à prouver que les PODZOSOLS se sont formés sous forêt ou du moins sous une végétation à éricacées et, par conséquent, qu'à une époque passée, la végétation ligneuse s'est étendue bien au-delà de sa limite actuelle.

La silice biogénique dans les sols

La limite supérieure de la forêt durant l'Holocène a été déterminée sur la base du type de sol, du contenu en silice biogénique ainsi que de la fréquence en phytholithes riches en aluminium. Dans les PODZOSOLS, une faible quantité de silice biogénique et une haute fréquence de phytholithes riches en aluminium ont été detectées. Dans les ALOCRISOLS, la quantité de silice biogénique est plus élevée et la fréquence de phytolithes riches en aluminium est plus basse. Ces évidences ont été interprétées comme un indice de la présence d'une forêt de conifères ou d'une végétation à éricacées dans le passé pouvant produire l'humus acide nécessaire à la podzolisation tout un fournissant une faible quantité de silice biogénique mais un pourcentage élevé de phytholithes riches en aluminium. Par contre, on peut conclure que les pelouses alpines fournissant simultanément peu de silice biogénique que de phytolithes riches en aluminium étaient dominantes et bien développées dans l'étage alpin.

Par ailleurs, le contenu en silice biogénique dans les différents horizons des profils de sol a pu être mis en relation avec les fluctuations climatiques de la deuxième moitié de l'Holocène, ouvrant la porte à d'intéressantes interprétations. Toutefois, au stade actuel, il manque des données précises sur les processus de dissolution de la silice biogénique et sur la masse volumique des différents horizons des sols pour vérifier le bien-fondé des hypothèses avancées.

Pédoanthrachologie

L'analyse des charbons dans les sols, ou pédoanthracologie, a fourni des données bien localisées dans l'espace qui ont permis de reconstruire avec une bonne précision les fluctuations de la limite supérieure de la forêt. L’anthracomasse, c’est-à-dire la quantité de charbons par quantité de sol, varie en fonction de l'altitude. Il est ainsi possible de reconnaître trois zones en fonction de l’altitude:

1) jusqu'à 2400 m, l’anthracomasse est caractérisée par des valeurs supérieures à 2 mg kg^{-1}, allant jusqu'à 19 mg kg^{-1};
2) entre 2400 et 2570 m, l’anthracomasse est comprise entre 0.11 et 1.57 mg kg^{-1};
3) au-delà de 2550-2600 m, l’anthracomasse est négligeable voire nulle, c’est-à-dire que les charbons sont très rares voire absents.

Les limites des trois sections altitudinales distinguées varient entre les sites en fonction de la pente, de la continentalité hygrique ou de la proximité du glacier (cas de HT). Ces ordres de grandeur se retrouvent également dans des études antérieures dans les Alpes du sud de la France. Nous en avons déduit que la zone inférieure jusqu’à 2400 m correspond à une zone forestière dont la limite supérieure correspond à l’altitude maximale atteinte par la forêt dans le passé. Les charbons datés par la méthode ^{14}C indiquent que cette zone a été éclaircie à plusieurs reprises par des incendies au cours du Subboréal (4300-2600 BP) à Belalp, ainsi qu’au cours du Subatlantique (1300-2300 BP) à la Furka (FK) et au bord du glacier d’Aletsch (HT). Entre 2400 et 2600 m, on trouve une zone de transition, l’écocline subalpin-alpin (ou kampfzone) dont la limite supérieure correspond à l’altitude maximale atteinte par les arbres. Enfin, la zone supérieure au-dessus de 2600 m correspond à l’étage alpin, asylvatique, où des arbres isolés inférieurs à 2 m de haut ont pu néanmoins se développer dans des endroits favorables particuliers, très rocheux et raides, comme on peut encore l'observer aujourd'hui sur les pentes sud du Val d'Arpette.

Nous avons déduit de ces résultats que la limite supérieure maximale atteinte par la forêt durant l'Holocène était environ 100-200 m plus haut qu'actuellement, soit 2400 ± 100 m, en fonction des particularités stationnelles locales, et donc, respectivement, que la limite supérieure de l'arbre a pu atteindre 2500 ± 100 m à Belalp, soit 250 ± 100 m au-dessus de la limite potentielle actuelle, 2400-2500 m dans le Val d'Arpette, 2400-2450 m dans la partie supérieure du glacier d'Aletsch (HT) ainsi qu'à la Furka.

Palynologie et analyse des macrorestes végétaux

Les données sur les macrofossiles et les pollens suggèrent qu'à Lengi Egga (2557 m), les pelouses alpines étaient dominantes tout au long de l'Holocène. Ainsi qu'en témoignent les pourcentages de pollens, plusieurs épisodes du recul de la forêt sont survenus au cours de cette période. La plus grande diminution des pollens d'arbres est probablement due aux activités humaines car, dans la région, l'Age du Bronze commence autour de 2300 BC (3850 BP uncal.). Toutefois, cette diminution correspond simultanément à une diminution de la température dans les Alpes du nord et sur l'Atlantique septentrional (4000 BP). Plus tard, on observe aussi une corrélation avec le Petit-Age glaciaire (1400, 1800 AD). Il faut remarquer cependant que ces diminutions de température ne sont pas enregistrées directement par les pollens de la végétation alpine de Lengi Egga mais par ceux des espèces arborescentes de plus basse altitude.

En comparant ces résultats avec ceux provenent d'autres d'études polliniques et de macrorestes en Valais, tel qu'à Gouillé Rion, situé à la limite actuelle des arbres (2343 m), et à Gouillé Loéré, situé au-dessus de la limite actuelle des arbres (2503 m), on peut envisager que, durant l'Holocène, la limite supérieure maximale atteinte par la forêt était 120-180 m au-dessus de sa limite potentielle actuelle (Tinner and Theurillat, unpublished).

Dendrochronologie

Les observations dendrochronologiques effectuées sur les pentes sud du Val d'Arpette ont montré que *Pinus cembra* peut croître dans l'étage alpin jusqu'à plus de 2800 m et y atteindre 100 à 200 ans sous forme de krumholz, cela à une époque où la température moyenne annuelle était inférieure de plus de 1° C à celle actuelle. Ces données soutiennent fortement l'hypothèse que, dans les conditions d'une température moyenne annuelle environ 1° C plus élevé que la température actuelle et sous un climat probablement plus continental, la limite supérieure de l'arbre pouvait se trouver 250 m plus haut qu'à présent, voire même 300 m plus haut localement.

4. Conclusions

Les investigations paléobotaniques (charbons, pollens, macrorestes) entreprises dans l'écocline subalpin-alpin ont mis en évidence que, dans les sites étudiés, la limite maximale atteinte par les arbres (> 2 m) durant l'Holocène était située autour de 2500-2550 m. En accord avec cette reconstruction, on peut donc conclure que la limite supérieure de l'arbre était située 250-300 m au-dessus de sa limite potentielle actuelle (2250-2300 m). On peut alors déduire que, si les autres facteurs climatiques étaient les mêmes que aujourd'hui, les températures étaient environ 1.4-1.7° (-1.8°) C plus élevées. Toutefois, le climat pendant l'Holocène moyen semble avoir été plus continental, et donc la différence de température a pu être moindre.

Les investigations méthodologiques sur la silice biogénique ont mis en évidence que:

1. L'apport annuel de silice biogénique dans les pelouses subalpines était d'un ordre de magnitude supérieur par rapport à l'apport des pelouses alpines, des landes et des forêts de conifères subalpines supérieures.

2. Les phytolithes de monocotylédones peuvent être séparées morphologiquement de celles des éricacées et des conifères.
3. Les phytolithes riches en aluminium sont caractéristiques d'espèces ligneuses (éricacées et conifères).
4. Le contenu en silice biogénique et la fréquence des phytolithes de monocotylédones dans les pelouses subalpines et alpines actuelles montrent que les assemblages de phytolithes dans les sols subalpins et alpins sont le résultat d'une décomposition *in situ* de la végétation suivie de processus de dissolution.

Du fait que, durant les phases de l'Holocène où les conditions thermiques étaient les plus favorables, la température moyenne de l'air n'était probablement que 0.8-1.2° (-1.8°) C plus élevée qu'aujourd'hui et que la limite supérieure de l'arbre se trouvait 250-300 m au-dessus de la limite potentielle actuelle, on peut s'attendre à ce que les effets des changements climatiques prédits (1.47-5.87° C; IPCC) pour les 50-100 prochaines années produisent un déplacement en altitude bien plus important de la limite supérieure de l'arbre, ainsi que des espèces en général. Cela conduira très vraisemblablement à des extinctions locales et régionales de plusieurs espèces alpines.

ABSTRACT

The uppermost limit matched during the Holocene by the treeline was detected by means of soil study, pedoantrachology, pollen, plant macrorests, vegetation analysis and dendrochronology.

Biogenic silica was extracted from the above ground tissues of subalpine and alpine plants. The investigations carried out on plant biogenic silica showed that the annual biogenic silica input from subalpine grasslands is one order of magnitude higher than in alpine grasslands, heathlands and conifer forests; the study of phytolith typologies evidenced that phytoliths have the potential to identify monocotyledons, *Ericaceae* and conifers. A new methodology to detect woody species phytoliths on the basis of the presence of aluminium was proposed.

Fifteen soil profiles along five altitudinal transects in the Central Swiss Alps were investigated: soil, biogenic silica (phytolith) and soil charcoal analysis were performed.

On the basis of the palaeoecological evidences gathered, the palaeotreeline was situated at about 2500-2550 m a.s.l. in the study area. According to the present reconstruction, the treeline was up to 300 meters higher than its present potential limit. Such elevation would support the hypothesis that temperature could be about 1.8C° higher than present if the other climatic factors were the same than present.

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CHAPTER 1: INTRODUCTION

1.1 The subalpine-alpine ecocline

The subalpine-alpine ecocline is a complex, biologically very important, bioclimatic transition zone between dense forest and alpine meadows which is sensitive to various ecological processes controlled by climate and human impact. It is, therefore, of great ecological and socio-economical significance (Theurillat *et al.*, 1998).

Where edaphic and orographic factors abruptly prevent the growth of trees, the contact between forest and alpine meadows is a sharp boundary of ecotone type. In the European Alps, in contrast, this transition is generally due to climatic reasons, and the change of vegetation type is gradual and give origin to a transitional belt (the subalpine-alpine ecocline) that consists of a zone of growth of scattered, often stunted, trees (microphanerophytes 2-8 m tall), shrubs and graminoid vegetation. The subalpine-alpine ecocline is also called kampfzone, krummholz zone, treeline, tree limit or Baumgrenze. In natural conditions, the kampfzone has an altitudinal extension that may vary in response to local factors such as topography and site exposure [(50)100-150 m] (e.g.: Ozenda, 1985; Favarger, 1995; Burga and Perret, 2001). However, in the European Alps, the subalpine-alpine ecocline rarely occurs in natural conditions, since its extension has often been broadened by human activities (e.g. Wick and Tinner, 1997)

1.2 Functional and ecological explanations for treelines

Above a certain altitude, in the European Alps, the closed forested area shifts to a more open canopy zone and then into a treeless vegetation where only shrubs, forbs and graminoid species grow, creating a striking vegetation boundary (e.g.: Brockmann-Jerosch, 1919; Stevens *et al.*, 1971; Troll, 1973; Tranquillini, 1979; Larcher and Bauer, 1981; Wardle, 1983; Tallis, 1991; Slayter and Noble, 1992; Holtmeier, 1994; Eggenberg, 1995; Körner, 1999). This phenomenon is due to regular decrease of air temperature in the atmosphere with elevation: in the Alps the is about 0.558 K per 100 m differences. The decrease of temperature determines the zonation of the vegetation in altitudinal belts (named from bottom to top: colline, montane, subalpine, alpine, and nival). The altitudinal extension of each of these belts differs according to species composition and latitude (bioclimatic zones), the extension of each belt in the European Alps is of about 700 m. The subalpine belt is the upper forest belt dominated in the Alps by conifers. The elevation at which the transition between subalpine and alpine belts occurs, is variable, depending on different regional and local factors. On a global scale, treeline elevation seems to be correlated with a lower thermal threshold of mean summer seasonal values of air temperature between 5.5 and 7.5°C and to soil temperature of about 7°C (Körner, 1999). The correlation between air temperature and altitudinal limit of the forest is valid at any latitude, and has been used for a functional explanation of treelines. Plant species need a minimum temperature for the production of biosynthetised compounds necessary for cellular growth and for the development and differentiation of new functional tissues. The production of new tissues would be, therefore, mainly reduced by the sink inhibition due to low temperatures (Körner, 1999). Trees experience growth limitations at a lower altitude than shrubs and forbs, because, unlike graminoids species, rosette forbs and dwarf shrubs, trees cannot benefit from radiant canopy warming during the day, nor from stored warmth in the topsoil during the night (Paulsen, 2000).

Meso- and micro-climatic factors, together with the ecophysiology and phenotypic plasticity of tree species, locally influence the altitude matched by the forest. Relevant factors are:

1) precipitation regime determines the degree of oceanicity or continentality, which in turns, influence forest elevation. It was shown that in the European Alps, the present distribution of the forest is higher in areas with a more continental and/or arid climate (Eggenberg, 1995; Pache *et al.*, 1996). This phenomenon is linked to ecological requirements of dominant tree taxa in the Alps. Indeed, harsh continental climatic conditions do not impede the expansion of both *Pinus cembra* and *Larix decidua*, the two dominant species in subalpine forests in the Central Alps. These species, in contrast, hardly bear oceanic conditions;
2) the occurrence of the “Massenerhebungseffect” (mountain mass elevation effect) (Brockmann-Jerosch, 1919), thanks to which the treeline is higher in areas surrounded by

large massifs, than in isolated mountains. This phenomenon is explained by the fact that inner ranges receive less precipitation, less cloud cover, are protected against strong winds, and profit from solar reflection from surrounding mountains, compared to front ranges. Thanks to more sunshine and less moisture, treelines can climb higher in inner mountain ranges;

3) the decrease of solar radiation with increasing latitude: in the northern hemisphere, in the temperate zone, an increase of about 100 km of latitude North corresponds to a negative temperature gradient that leads to about 100 m of lowering of treeline position .

In temperate regions trees growing at higher altitude suffer from frost damage, late frost desiccation, mechanical damage due to avalanches and wind. Locally, the presence of permafrost impedes tree growth, and periglacial phenomena (gelifluction, cryoturbation) affect the altitude of the treeline, resulting in loss of biomass, and limitation of seed production and developmental processes (Tranquillini, 1979). These stress factors are not considered critical for established trees that can show a high phenotypic plasticity and can survive as krummholtz (stunted individuals), but are known to reduce the probability for re-growth of young trees and to prevent tree recruitment at higher altitude.

1.3 Past treeline fluctuations

The close relationship between treeline position and climatic factors, mainly temperature, makes palaeotreelines a suitable proxy for inferring past climatic conditions (Payette *et al.*, 1989; Tinner and Ammann, 2001). The correlation between climate and treeline position is very complex, and forests respond relatively slowly to climatic changes because the established closed canopy produces a favourable self-sustaining microclimate. In addition, plant phenotypic plasticity may act as a buffer (Hättenschwiler and Körner, 1995; Lavoie and Payette, 1996). The complexity of orographic setting and frequency of exposure to extreme climatic events, tend to blur climatically driven changes, that are, therefore better and more easily recognised on a subcontinental scale and by comparison of independent proxies (Ammann *et al.*, 2000).

A reconstruction of past ecological and climatic conditions should rely on interdisciplinary studies: for instance palaeoecological records from four Swiss sites (two lakes on the Swiss Plateau and two at the timberline in the Alps) showed eight synchronous pre-Roman cold phases (at 9600-9200, 8600-8150, 7550-6900, 6600-6200, 5340-4900, 4600-4400, 3500-3200 and 2600-2350 radiocarbon years BP) (Haas *et al.*, 1998). These early- and mid-Holocene cold phases are recorded as well by the Greenland ice cores, glacier advances in the Swiss and Austrian Alps and dendro-densitometry on subfossil wood, suggesting that a correlation can be made between regional and northern hemispheric climatic oscillations (full references in: Haas *et al.*, 1998).

The amplitude of Holocene climatic variability can be inferred on the basis of glaciological studies and lacustrine level variations. Mountain glaciers are sensitive indicators of changes in precipitation and temperature, that are recorded by changes in extension (Denton and Karlén, 1973; Patzelt, 1977; Röthlisberger *et al.*, 1980; Gamper and Suter, 1982; Holzhauser, 2002).

At present, however, no quantitative timberline-based temperature reconstruction is available for the Alps. A first problem to produce a quantitative temperature reconstruction lays on the fact that today treelines cannot be taken as reference since they have been artificially lowered (even by 200-300 meters), and therefore do not express natural conditions. A qualitative estimate of treeline temperature requirements is based only on single trees surviving at high altitude, indicating a potential altitudinal limit of tree growth. In addition, for a reliable reconstruction, continuous and well dated records from today back to the Late Glacial in sites at, above, and below present treelines are required (Tinner and Ammann, 2001). Tinner and Amman (2001) integrate palaeoecological data from pollen and plant macrorests in two mires in the Swiss Alps (Gouille Rion and Lengi Egga; see also Chapter 7), Swiss glacier length variations (Maisch *et al.*, 1999), chironomid studies (Heiri, 2001), and lake level changes in the Swiss Plateau (Magny and Richoz, 1998; Magny and Schoellammer, 1999), to propose a climatic reconstruction that considers both temperature and precipitation during the Holocene. According to this reconstruction, the maximum altitude of treeline was about 120-180 m higher than today in the warmest phases of the Holocene (9000-8200; 7000-6400; and 5000-4000 cal yr BP) and temperature might have been about 0.8-1.2°C higher than today. Between 10500 and 3900 cal yr BP treeline was always situated above the present one.

Comparison of palaeobotanical reconstructions of timberline fluctuations with glaciological evidences and lake level variations may enhance the understanding of the relative importance of temperature and precipitation. Treelines, glaciers and lake levels show consistent variations. For instance, evidences of extension of glaciers smaller than today were detected in the Swiss Central Alps (Hormes *et al.*, 2001). In this work radiocarbon dated macro- and mega-fossils of glacially deformed wood, collected in front of six glaciers, provide evidence of eight phases of glacier recession (9910-9550, 9010-7980, 7250-6500, 6170-5950, 5290-3873, 3640-3360, 2740-2620 and, 1530-1170 cal years BP); among them the most pronounced minima (9000-8200; 7000-6400; 5000-4000 cal years BP) are synchronous with uppermost timberline positions (Tinner and Ammann, 2001), and minimum lake levels in the Swiss Jura and on the Swiss Plateau (Magny and Richoz, 1998; Magny and Schoellammer, 1999).

These evidences confirm that high Holocene timberline position reflects warm and dry conditions. Early Holocene was in general more continental, with warm and dry summers and cold winters. A transition to more oceanic conditions occurred in Central and Northern Europe at 8200 cal yr BP (Tinner and Lotter, 2001), however this transition was not synchronous and due to their orographic setting, the continental climate mode has persisted in some valleys of the central Alps (e.g. the Valais).

1.4 Human prehistoric populations in the Valais and neighbouring regions

For millennia the Alps have experienced the pressure of human activities, and the effect of farming, forestry and mining, even in remote areas, have caused changes in landscape physiognomy and species distribution. Archeological findings, though scattered, can provide a better understanding of the various phases of human colonisation of the Alps and can help in disentangling the effects of climatic changes from the impact of human activities.

Human frequentation of the Alps in prehistoric times can be reconstructed on the basis of both direct archeological evidences and indirect ones (such as cultural affinities among populations settled on opposite sides of the alpine range). Main steps of prehistoric human colonisation of the Central Swiss Alps and contiguous mountain regions (Northern and Southern Alps) are summarised as follows (for a review see (Bezinge and Curdy, 1994; Curdy *et al.*, 1999).

Palaeolithic - No archeological evidences of human presence is available for this period for the Valais. The Würm glaciation (about 100,000-10,000 cal. years BP) probably impeded the access of man to the alpine zone, and, in addition, probably cancelled possible traces of human presence. Only at about 40,000 BP, a warmer interstadial allows a first colonisation of the alpine range by populations of the Middle Paleolithic (two caves in the Simmenthal BE), but during the Upper Paleolithic, the harsh climatic conditions, prevented any further settlement in mountain ranges.

Starting from 15,000 BC, glaciers are confined to the lateral valleys of the Rhône. No traces of human presence are available in mountain areas until 13,500 BC. At this time the very first traces of human presence from the Upper Palaeolithic are found in neighbouring regions (on the Swiss Plateau, and at the easternmost limit of Lac Leman, at Villeneuve, VD).

Mesolithic (9000-5500 BC) - Mesolithic findings are few, mainly concentrated in the Prealps (Simmental BE) between 900 and 1900 m; in the high Rhône valley one lowland site was found not far from the Lake Leman (Vionnaz VS). Probably, human frequentation was limited to the montane belt, as testified by findings in shelters below rocks, and was only seasonal. In the Southern Alps, in contrast, these seasonal camping sites seem to occur at higher elevation, in the alpine belt (Cianciavero Alpe Veglia, Novara, Italy). No evidences of colonisation of central Valais during the Mesolithic are available, possibly the area was not suitable because the very steep lateral valleys did not supply a hunting area of easy access. In Sion (VS), the first evidences of settlements date to the end of the Mesolithic (the first half of the 6th millennium).

The final epoch of the Mesolithic culture corresponds to the Boreal and first half of the Atlantic period. Mesolithic societies had a considerable impact on vegetation, with a lowering of the timberline, as testified by palaeobotanical records in the Southern Alps at Lago Basso (Splügen Pass) (Fedele and Wick, 1998).

Neolithic (5500-2200 BC) - All along the Neolithic age the most important settlements and burial sites in the Valais region were located in the lowland. Higher altitude sites were frequented only starting from Middle and Upper Neolithic. During this period, the montane belt seems to be neglected, and preference is shown for the alpine passes and the exploitation of the alpine grasslands. Since the arrival of Neolithic populations of herders and farmers coming from the Italian side of the Alps, livestock played a major role (80-90%) in the economy of Central Swiss Alps. This activity was mainly based on small ruminants (sheep and goats), and involved a complementary exploitation of lowland (farming and grazing) and alpine sites (grazing).

The Neolithic is conventionally divided in three periods:

- Lower Neolithic (5500-4800 BC) is represented by five settlements in Sion; although no findings at high elevation were discovered exchanges through the alpine passes between the Valais and Northern-Italian Neolithic civilisation (e.g. the civilisation of the "Isolino di Varese") can be inferred on the basis of cultural affinities between these cultures (such as similar patterns for pottery or carved stelae).
- Middle Neolithic (4800-3200 BC) is the period most rich in sites (24 settlements and 22 necropoles or isolated burials); worth remembering is a ritual site with menhirs arranged on a line present in Sion.
- Upper Neolithic (3200-2200 BC) is described by fewer sites (11 settlements and 24 necropoles and burials); in contrasts, isolated findings are more frequent than in former periods and occur mainly at high elevation.

Bronze Age (2200-800 BC) – The amount of sites dating to the Bronze Age in the Swiss Central Alps is remarkable (159 among settlements and necropolis, plus 800 isolated findings). The Rhône valley was rather densely inhabited, while areas at higher elevation were only seldom frequented. All burial sites are located below 1000 m a.s.l.. Between 1000 and 2000 m a.s.l. findings are rare, and above 2000 m a.s.l. only five isolated findings were recovered, mainly in proximity of alpine passes. If the assumption is made that the necropolis are situated in proximity of permanent settlements, an occupation of the lower montane belt can be argued. It can be speculated that the higher elevation sites were mainly linked to the exploitation of grasslands for livestock, the search for minerals for metallurgy (copper), and the control of paths towards alpine passes. Since Bronze Age transhumance became important for cattle-breeding. Palaeobotanical records show that the impact on vegetation by lowering of the timberline became strong starting from Bronze Age (Haas *et al.*, 1998).

Iron Age (800-15 BC) – Iron Age is represented in the Rhône valley by 116 sites. Concerning the altitude of settlements, the occupation in this period shows some peculiarities compared to previous ages: settlements are mainly in the colline belt (78%), and even in the montane belt (11%). Necropolis locations confirm a preference for the montane and subalpine belts. At higher elevation the situation is similar to the one of the Bronze Age, with findings in correspondence of herder shelters. Rare findings in proximity of alpine passes are interpreted as votive deposits. The location of settlements in the mountain belt, put the basis for a vertical control of the territory, and facilitated the setting of a vertical transhumance of livestock, on which traditional farming in alpine areas is based.

1.5 Aim of the study

The aim of this study is to investigate in four test areas the dynamics of the vegetation at the upper subalpine and alpine belts (i.e. from timberline above treeline) during the Holocene and the recent past. This study is characterised by a multidisciplinary approach: it combines two main methods of investigation (pedoanthracology and phytolith analysis), plus four additional ones (soil, pollen, plant macrorests, vegetation and dendrochronological analysis). This study is aimed at answering key questions on past and present ecology of alpine vegetation, such as the naturality and the altitudinal extension of the alpine belt in relation to past altitudinal extension of treeline. In particular, whether the alpine belt is naturally devoided of trees or, whether phanerophytes were once present in the alpine belt and disappeared as a consequence of human activities and/or changed climatic conditions. The assessment of the uppermost elevation attained by the treeline should lead to understand whether present equilibrium between climate and ecological factors at the subalpine-alpine ecocline is close to the natural one, and to predict future responses of subalpine-alpine vegetation to the forecasted changed climatic conditions.

In addition, the project should provide a comparison of methods, some of them never tested in the Alps (e.g. the study of biogenic silica). Indeed, in dry terrestrial enviroments the study of soil, soil-biogenic silica and soil charcoal allows a potentially illimited availability of sampling site that is denied to methods linked to the presence of “wet-spots” that are very scattered or missing in alpine ecosystems.

Interdisciplinarity in palaeoecological studies is called for by main authors and it is strongly desirable for studies in ecoclinal conditions in order to enhance, as much as possible, the spatial resolution.

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CHAPTER 2: SITE DESCRIPTIONS AND METHODS OF INVESTIGATIONS

2.1 Site location

The study area is located in the Swiss Central Alps, in the upper Rhone river valley (46°N), in the Canton of Valais (CH). Four sites were selected in close proximity to areas in which long-term research projects on responses of the subalpine-alpine ecosystems to global climatic changes are on going (Theurillat, 1996; Körner, 1997). In each site the sampling was performed along altitudinal transects (Table 2.1, Figure 2.1). The transects consist of three to four points, and are located in the alpine belt, between 2300 and 2850 m a.s.l.. Slope, aspect and bedrock were kept homogeneous in all the sampling points. Rather flat areas, not subject to active erosion were selected. Parent rock material is acidic in all the sites. The sites are:

1) *Val d'Arpette*

Transect Arpette (AR, Figure 2.2.): it is located in the territory of the commune of Orsières, on the hydrological left of Rhône river, South-West from Martigny, near Champex, at the eastern limit of the Mt. Blanc massif. In Val d'Arpette, the slope is very steep, between 30° and 40° on average. Bedrock consists of granite. The transect is situated on the S-slope of the Clochers d'Arpette (2810 m a.s.l.), between 2375 and 2720 m a.s.l.. One transect of three points was sampled: AR1, AR2, and AR3 (Table 2.1).

2) *Belalp*

\- *Transect Belalp-Hofathorn* (BA-HO, Figure 2.3): it is in the territory of the village of Naters, above the village of Blatten, North-West of Brig, in the Aletsch Glacier Region, at the Southern limit of the Aar massif. The transect is situated on the S-E slope of Hofathorn (2845 m a.s.l.), the slope is very regular, between 25° and 30° on average. Bedrock consists of gneiss. Four points were sampled between 2358 and 2830 m a.s.l.

- *Transect Belalp-Lengi Egga* (BA-LE, Figure 2.4): is on the S-E slope of Mt. Sparrhorn (3020 m a.s.l.). Bedrock consists of gneiss. The three sampling points are located between 2305 and 2550 m a.s.l.. The site at highest elevation (BA-LE 5) is only a few meters away from the peat bog Lengi Egga. This site was selected to allow a close comparison between the data of pollen and plant macrorests sampled in the mire and data of soil, phytolith, and charcoal analysis.

3) *Aletsch Glacier-Hindererhinertüre*

Transect Aletsch (HT, Figure 2.5): it is in the commune of Fieschertal, on the hydrological left side of the Aletsch Glacier, along a S-W slope at the basis of Mt. Gross Wannenhorn (3905 m a.s.l.). Bedrock consists of gneiss. Two sites were sampled at 2580 and 2710 m a.s.l., plus two additional ones (HT3 and HT4) in proximity of HT2.

5) *Furka Pass*

Transect Furka (FK): it is the easternmost transect, it is located in proximity of the Furka Pass, in the territory of Oberalp, on the S-W slope of Tällistock (2861 m a.s.l). Bedrock consists of gneiss. The three sampling points of the transect are located between 2403 and 2785 m a.s.l..

Figure 2.1 Location of study area (dashed line marks upper Rhône river catchment area).

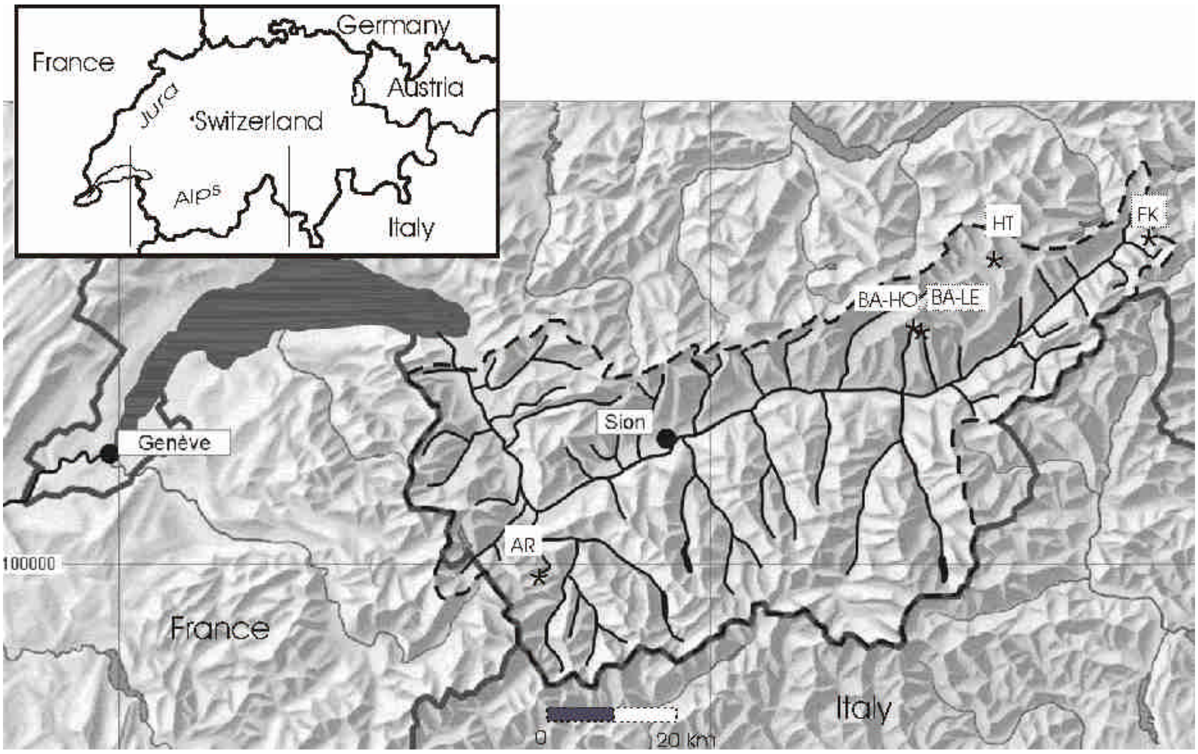


Table 2.1 Samplig sites: acronyms, elevation, location, slope, aspect and topography for the five transects.

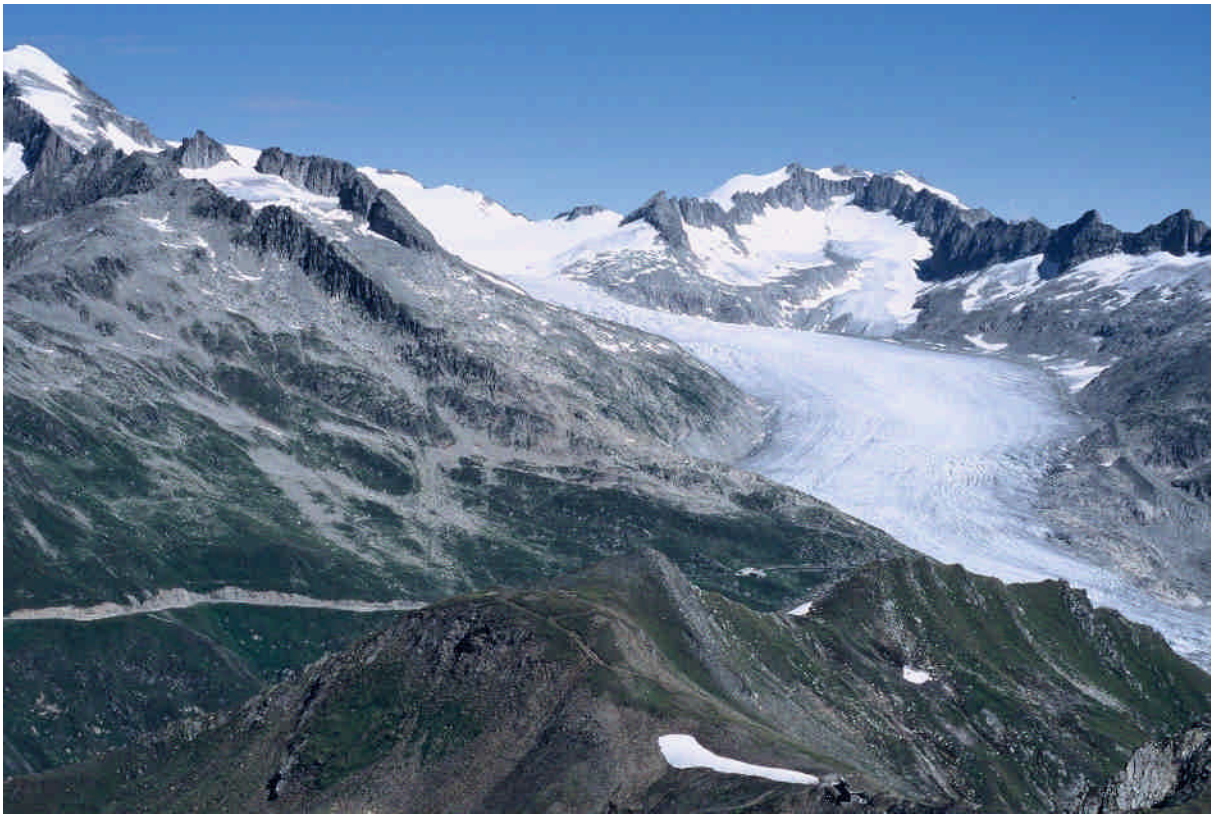
Site	Altitude m a.s.l.	Swiss Coord.	Slope degrees	Aspect	Topography
Val d'Arpette					
AR1	2375	571.725/ 97.513	33	S	Small saddle
AR2	2565	571.725/ 97.513	33	S	Flat area
AR3	2720	571.125/ 97.713	32	S	Flat area
Belalp- Hofathorn					
BA-HO1	2358	639.325/135.400	18	E-SE	Small saddle
BA-HO2	2570	639.050/134.750	3	84° N	Flat area
BA-HO3	2665	639.825/135.450	15	235°N	Flat area
BA-HO4	2830	638.650/135.900	20	98° N	Slope near the crest
Belalp- Lengi Egga					
BA-LE7	2305	641.300/137.188	20	171°N	Flat area
BA-LE6	2451	641.325/137.563	12	189°N	Flat area
BA-LE5	2550	641.113/138.113	12	148°N	Flat area
Aletsch Glacier- Hindererhinertüre					
HT1	2580	649.325/ 147.,275	12	197°N	Saddle, solifluction terrace
HT2	2710	649.375/ 147.385	0	SW	Large saddle
HT3	2740		-	-	-
HT4	2710		-	-	-
Furka Pass					
FK1	2403	672.735/ 154.980	12	134°N	Flat area
FK2	2618	673.310/ 155.790	2	231°N	Flat area
FK3	2785	673.700/ 156.290	16	243°N	Slope near the crest

Figure 2.2 Val d’Arpette

Figure 2.3. Belalp-Hofathorn

Figure 2.4 Belalp-Lengi-Egga

Figure 2.5 Aletsch Glacier- Hindererhinertüre



2.2 Climate

The alpine orographic barrier is a weather divide. The northern Alps are under the influence of moist and oceanic winds of prevailing western circulation, causing abundant precipitation all year around, with maximum in winter and summer. In the upper Rhone valley, the dual shelterig effect of the southern and northen ranges results in dry conditions. In the Valais, the degree of continentality increases eastward, from Martigny to Visp (with decreasing of precipitation and increasing of annual temperature ranges), then it decreases slightly from Visp to Furka Pass.

Meteoreological data for the years 1993-1998 are available for Val d'Arpette and Belalp (Schlüssel, 1999). Average daily temperature was, in this period, 4.2°C at Val d'Arpette, and 3.2°C at Belalp. At the same altitude Val d'Arpette is 0.45K warmer than Belalp.

In the same period annual precipitation was 1524 mm m^{-2} in Val d'Arpette (Gams Index of hygric continentality is 70.1) and, 908 mm m^{-2} at Belalp (Gams Index of hygric continentality is 124.2). The precipitation increases linerarly with altitude at Belalp with a max at 2400 m (not the highest elevation, possibly as consequence of the crest-effect). In Val d'Arpette the precipitation increases only slightly with altitude on the southern facing slope. As a consequence of southern exposition and steeper slopes, snow cover melts earlier and faster at Val d'Arpette (April - May), than at Belalp (May-June).

Soil temperatures at Belalp were recordered in the year 1999 (2400m a.s.l., 10 cm depth): soil temperatures were comprised between 5°C and 15°C during the growing season (June - September), between 5°C and 0°C in October-November and, were about 0°C for the rest of the year (Alpnet data, C. Körner).

Aletsch transect is located in proximity of Belalp, however climatic conditions are affected by the close proximity of glacier, resulting in a slight increase of continentality. At Furka, snowmelt is in late June; mid Summer air temperatures vary between 7°C and 10°C. The growing season is 10-14 weeks long, but night frosts occur at any time; the onset of severe frosts is in early September. Precipitation peaks in summer, with annual sum of about 1500 mm m^{-2} (Gams Index of hygric continentality is 95.5) (Körner *et al.*, 1997).

2.3 Present vegetation description

All the grasslands in the sampling sites belong to the class *Juncetea trifidi* Hadac 1946. For the descriptions of the vegetation thisstady follows Theurillat *et al.* (1995) for the classification in higher units, and Schlüssel (1999) for the plant communities, unless otherwise indicated (see Chapter 4.1).

AR1 belongs to the alliance *Festucion variae* (order *Festucetalia spadiceae* Barbero 1970) and corresponds to a *"Festucetum scabriculmis callunetosum"* community.

BA-HO4 pertains to *an "Agrostietum schraderianae"* community of the alliance *Agrostion schraderianae* Grabherr in Grabherr et Mucina 1993 (order *Caricetalia curvulae* Braun-Blanquet in Braun-Blanquet et Jenny 1926). It is a cool alpine sward dominated by the clonal grass *Agrostis schraderiana* in moist conditions.

All the other sites corresponds to plant communities belonging to the alliance *Caricion curvulae* Braun-Blanquet in Braun-Blanquet et Jenny 1926 (order *Caricetalia curvulae*).

BA-OH1, BA-LE6, BA-LE7 correspond to a *"Trifolio-Caricetum sempervirentis"*. BA-LE5, FK1 to a transition between the *Nardion* and the *Caricion curvulae* alliances and which could be attributed to the *Carici-Nardetum* Oberdorfer 1959. AR2 and AR3 alpine grasslands form an undescribed community on steep slopes: co-dominant species are *Festuca nigrescens, Geum montanum,* plus mainly *Agrostis schraderiana, Carex sempervirens, Nardus stricta* and *Deschampsia flexuosa,* which replaces the *Festuca varia* swards in cooler conditions with a longer snow cover. It is species-rich and characterized by the regular presence of subalpine dwarf shrubs and even small *Pinus cembra.*

BA-OH2, FK2, FK3 corresponds to the *Caricetum curvulae* Rübel 1911 s.l., the typical alpine sward developed on gentle slope (dominance of *Carex curvula*), in rather dry conditions (presence of *Veronica bellidioides*) and with a long snow cover, especially in FK3 (presence of *Salix herbacea* and *Alchemilla pentaphyllea*). BA-LE5, is similar but, dominated by matgrass (*Nardus stricta*), very likely as a consequence of long lasting pasturing activities on gentle slopes.

2.4 Methods of investigations

Soil profiles were dug at regular altitudinal intervals from above 2300 m (i.e. about 100 m higher then present treeline) up to the crests (about 2800 m).

A key point of the study here presented is a multidisciplinary approach: seven methods of investigation were employed to reconstruct past vegetation scenario at the treeline: soil, biogenic silica (phytolith), charcoal, pollen, plant macrorests, vegetation analysis and, dendrochronology. The results of the two first methodologies are fully described in the present work, while pollen and plant macrorest data and dendrochronological data are described in Tinner and Theurillat (in press) and Theurillat *et al.* (unpublished), respectively. The combination of several proxy-data should allow a more accurate reconstruction of the treeline fluctuaction during the Holocene in the study area.

2.4.1 Soil analysis

Soils were investigated under the perspective of exploiting their potential as archives of charcoals and phytoliths (Chapter 3, ANNEXE A). Soil analysis focussed on two main points: firstly, the characterisation of soil profiles, with the aim of individuating the driving mechanisms in soil formation. Secondly, the identification of colluvial activity and description of subsequent remixing phenomena in the profile that could affect the distribution of palaeobotanical proxies. Soil mixing processes, must be taken into account when interpreting the distribution of phytoliths and charcoals in the profile. Thirdly, soil description in combination with soil charcoal study, was employed to reconstruct the upper limit of the treeline in Chapter 6.

2.4.2 Biogenic silica analysis

Biogenic silica was analysed both from plant material (Chapter 4) and, from soil samples (Chapter 5).

Biogenic silica in plants

Subalpine-alpine species were screened for biogenic silica content and frequency of phytolith typologies, and of aluminium phytoliths.

1) Biogenic silica content of dominant or very common alpine plant species was assessed by dry-ashing (Chapter 4.1). The annual input of biogenic silica at the scale of the plant community was then estimated using plant productivity, average relative biomass among typical alpine plant communities, and length of the growing season. By assessing the theoretical production of biogenic silica by main alpine and subalpine plant communities, data allowing comparison and modelling were made available.

2) Phytolith typologies were studied from biogenic silica extracted. Phytoliths were mounted on permanent slides and analysed at the optical microscope (Chapter 4.2). A fraction of the same residue was mounted on stubs for observation at the scanning electron microscope. Phytolith morphotypes were inventoried for each species and counted to assess the relative frequency of typologies. An atlas of photographs of some of the most characteristic and/or common typologies was prepared also for future studies. Frequency of typologies for each species (wood and leaf tissues separately) was analysed by means of descriptive multivariate statistics, to test the possibility of identifying plant taxa on the basis of occurrence and frequency of morphotypes.

3) The diagnostic power of the occurrence of aluminium in the opaline reticule was demonstrated (Chapter 4.3). Being phytoliths the cast of plant cells from different istological origin, the case of phytoliths with similar shapes occurring in different plant species is common. An approach complementary to the morphological one was attempted here for the first time: it was tested if redundant morphotypes could be identifiable on the basis of the occurrence of aluminium in the opal silica reticule. The measurements were performed by means of a scanning microscope with a pointing system (Carnelli *et al.*, 2002).

Biogenic silica in soil

Quantitative analysis of biogenic silica, and the occurrence of phytolith morphotypes in soil were then addressed. This study was attempted on alpine soils for the first time, and was carried out as follows:

1) Modern analogs of phytolith assemblages (Chapter 5.1) in top-soil were investigate to test if the assemblages of phytoliths in the topmost soil reflect the composition of the plant stand, and to understand the processes leading to the formation of fossil phytoliths assemblages.
to taking into account: biogenic silica quantity, phytolith morphotypes and aluminium phytolith frequencies. In addition, the theoretical input of phytoliths at each site was estimated and compared with the measured one.

2) Biogenic silica in soil was then studied in three steps in order to assess its concentration in soil, its chemical composition and the frequency of phytolith morphotypes.

a) The total biogenic silica content in soils was assessed (Chapter 5.2). For this purpose, soil samples were taken at each soil horizons, and, for deeper horizons each few centimeters. Moreover, extra samples were collected whenever soil characteristics (color, texture) showed that a discontinuity might be present. Dried soil samples were sieved at 1 mm to discard roots and gravel; biogenic silica was extracted from about 5 g of sieved soil by successive wet oxidation and floatation in heavy liquid. All the floating fraction was collected to calculate biogenic silica percent weight on dry soil basis.

b) The percentage of aluminium phytoliths was determined by examining a fraction of the extracted biogenic silica at SEM microscope equipped with a pointing system (Carnelli *et al.*, 2002). Phytolith frequency was also assessed by examinig the extracted soil biogenic silica at the optic microscope. Phytoliths mounted on permanent slides were counted.

c) Percentage content in soil samples of idiomorphic phytoliths from monocotyledon species were then plotted and correlated with log of soil biogenic silica and frequency of aluminium phytoliths[1].

2.4.3 Charcoal analysis

The sudy of charcoals in soil (Chapter 6) was performed on 17 sites, following the pedoanthracological methodology of Thinon (1992). Sampling was performed in layers of about 30 cm of thicknesss, and subsamples of 7 to 15 kg of dry soil were taken for each layer. The extraction was performed by floatation, followed by wet sieving, densimetric sorting by water flow and manual sorting under a binocular microscope. Only charcoal particles larger than 400µ were extracted[2]. Charcoals were observed under an incident light microscope with differential interference contrast and identified with reference to literature and to the charred wood reference collection of the Institut Méditerranéen d'Ecologie et de Paléoécologie of the University of Saint-Jêrome in Marseille (France). Seven samples were dated by AMS ^{14}C (Ångström Laboratory, Division of Ion Physics, Uppsala, Sweden).

2.4.4 Pollen and plant macrorest analysis

In Chapter 7 are discussed the results of pollen and plant macrorest analysis carried out on a core from the peat bog Lengi Egga. Lengi Egga is a mire of about 170 m diameter situated at 2557 m a.s.l., in the Belalp area (close to BA-LE5). The mire mean diameter is about 170 m, it is subdivided by a perennial streamlet, the basin is formed by late glacial moraine ramparts, and consists of gneiss. A modified Livingston piston corer was used to take two cores with a diameter of about 8 cm. The maximum depth reached was 191 cm. Plant macrorests and pollen extraction and identification were performed

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[1] 10,276 phytoliths in plant and 145,092 phytoliths in soil samples were observed and counted by the author at the optic microscope, i.e. a total of 155,638!

[2] An idea of the rate of recovery is given by the fact that it was necessary to collect and process a total of 312 kg of soil to extract only about 1.55 g of charcoals

(Tinner and Theurillat, unpublished; Tinner and Ammann, 2001). Chronology was assessed by radiocarbon dated plant macrorests.

The analysis were carried out by Dr. Willy Tinner (Annexe B) (University of Bern, Institute of Plant Science, Section of Paleoecology, Altenbergrain 21, Bern, Switzerland). The chronology was assessed by radiocarbon AMS dated plant macrorests at the University of Utrecht.

2.4.5 Vegetation analysis

Vegetation relevés were performed by J.-P. Theurillat at the same location of the soil profiles sampled for charcoal and biogenic silica analysis on a standard surface of 4 m^2 (2x2; cover estimate according to Barkman *et al.*, 1964). Plant species cover (percentage) were used to estimate the relative species biomass Chapter 5.1. These values, were among the parameters needed to estimate the theoretical fall-out of phytoliths in Chapter 5.1.

2.4.6 Dendrochronological analysis

Dedroconological analysis was performed by J.-P. Theurillat, P. Cherubini, D. Lavieri, and O. U. Bräker at the Swiss Federal Institute for Forest, Snow and Lanscape Research (WSL), CH-8903 Birmensdorf, Switzerland. The south oriented slope of Val d'Arpette was studied along a transect between 1800 m and 2700 m a.s.l. at the location "Clochers d'Arpette" (2815 m a.sl.). The age of trees was assessed, at different elevations below and above the timberline, and ring-width growth patterns were studied, to understand the role played by climate on both germination processes and growth dynamics. Finally, biomass allocation on young individuals at the upper subalpine and at the alpine belts was investigated to check whether investment, differs between these two cohorts. For comparison, some individuals of mountain pine (*Pinus mugo* subsp. *rotundata* (Link) Janchen & Neumayer) both in its erect form and prostrate form were also cored, as well as a few Norway spruces (*Picea abies* (L.) Karsten).

To determine the age and age structure of *Pinus cembra*, the dominant trees, a total of 57 individuals, were cored in 1998 at different elevations along the transect in five 100 m altitudinal sections: (a) 1800 m a.s.l. (1800-1890), (b) 2000 m (1990-2090), (c) 2200 m (2160-2220), (d) 2300 m (2300-

2350), (e) 2500 m (2520-2570). The dominant sampling strategy may produce a bias, but in the present case, the bias is very likely to be negligible since near the timberline (around 2000 m a.s.l.) one can safely assume that the biggest trees are the oldest. The trees were cored with an *increment* borer in a radial direction, (a) at 1,3 m with two cores at a right angle, and (b) as near as possible to the base of the trunk. Each of the 5 mm cores obtained was analysed microscopically (after being air dried and polished in order to determine the age of the tree).

Special care was devoted to the analysis of the first years of growth in order to assess whether the trees grew regularly from the beginning or if there was some lagging, especially at the subalpine-alpine ecocline (a) during the 20th century and (b) in the last two decades. Trees were excavated and roots and the base of the trunc were taken. Tree growth was analysed on cross sections in order to find the first year: (a) in 10 individuals, 7 of them dead, collected in 1999 between 2200 and 2470 m a.s.l., (b) in 14 small individuals collected entirely in 1999, with 9 individuals (29-50 cm) growing between 2280 and 2300 m a.s.l. and 5 individuals (29-36 cm) growing between 2670 and 2695 m. In (a) the stems were cut in 2 cm long pieces near the collar, and then in 5 cm pieces. In (b) the stems were cut in 5 cm long pieces.

For *Pinus mugo* subsp. *rotundata,* 14 erected individuals were cored between 2000 and 2070 m a.s.l. and 11 prostrated individuals between 1980 and 2050 m a.s.l.. For *Picea abies* 4 individuals were cored between 2290 and 2320 m a.s.l.. (Results are fully discussed in (Theurillat *et al*., unpublished) and briefly addressed in Chapter 8).

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CHAPTER 3: SUBALPINE AND ALPINE SOILS

3.1 Introduction

Soil formation is a complex process in which mineral and organic processes, solid, liquid and gas processes, and biological, chemical and physical processes, are integrated (e.g Duchaufour, 1998). The time scale of this process can vary in a very wide range: soil formation in subalpine and alpine climatic conditions requires several thousand of years to lead to a fully developed soil "type". Well developed alpine podzosols in the Austrian Alps date to the beginning of the Holocene (Veit and Höfner, 1993). However, many soil processes can also act faster: mineralisation of organic matter, for intance, start few weeks after deposition and podzolised soil layers can form in few centuries (Theurillat et al., 1998; Gobat et al., 1998). In addition, other geomorphological processes are active on a shorter time scale: for instance, colluvial movement allows constant rejuvenation of the soil by adding calcium, which prevents acidification, and maintain a coarse structure that promotes rapid water transit. The main soil types that occur on acidic siliceous rock in subalpine and alpine environment are listed in Table 3.1.

Podzolisation is a phenomenon triggered by taïga-type climate, bedrock composition and vegetation (Duchaufour, 1998). Podzolisation occurs only in acidic conditions and involves the formation of organometallic compounds (chelates) migrating from O or A horizons, to the spodic horizons BP, where they precipitate as organic molecules (BPh) and metal oxides (BPs). During snow melt, the conditions for migrations are particularly favourable. On steep slopes, podzolisation may be slowed down by the constant erosion of organic layers.

The rate of organic matter turnover gives indication of the biological activity of soils. At high altitude litter break down is delayed as a consequence of low temperature and a strong solar radiation that reduces microbial activity. The full structural decomposition of leaves may take 2 years in high alpine forbs, 5 years in sedges and 10 years or more in evergreen dwarf shrubs, while at low altitude leaf litter is mostly recycled within a year (Körner, 1999). The content of silica in soil developed from rocks poor in weatherable minerals mainly depends on vegetation and humus-type.

Three humus types with decreasing biological activity occur in the study sites: *mull*, with strong earthworm activity leading to a rapid incorporation of organic matter, *moder*, in which this phenomenon is slowed down by the absence of anecitic earthworm and with limited fungal activity; and *mor* in which soil fauna is less abundant, fungal activity peaks and organic matter accumulates in thick black layers. Soil holorganic horizons (O) contain up to 30% dry weight organic matter (O.M.). According to the degree of decomposition of the O.M. the horizons are distinguished in OL (litter slightly decomposed), OF (intermediately decomposed litter consisting of fragments of leaves and fine O.M.), and OH (highly decomposed, more than 70% fine O.M.) (Gobat et al., 1998). The horizon A is the topmost mineral horizon, in here, the majority of O.M. is humified, partially mineralised and complexed with clays.

Investigation of soil dynamics in the study area are very few (Paternoster, 1981; Spaltenstein, 1984; Keller, 1991; Fierz and Gobat, 1996). In the present study two aspects were privileged. First, the potential of soil of supplying information on the palaeoecological conditions (climate and vegetation) in which they were formed in which they were formed in comparison with present conditions.Second, the careful description of soil profiles to detect biological and geomorphological processes that may affect the distribution of charcoals and phytoliths in situ or ex situ, with the aim of allowing an accurate interpretation of these proxies in soil. Indeed, soil mixing processes that lead to truncated soil, buried horizon and palaeohorizons are frequent in alpine soils (Gobat et al., 1998). The study of alpine soils have to take into account geomorphological determinants of alpine soil formation; cryogenic processes are very active in these systems. At a very early stage of soil formation, the coarse matrix is redistributed principally by landslides and glacial deposits. According to the geomorphological setting, other processes supply fine matrix, such as on site erosion of parent rock, gravitational processes along the slope, sedimentation by water and snow avalanches. Eolic sedimentation supply the finer fraction, mainly from glacial silt, that allows plant colonisation at very early stages of soil formation. A study in the Austrian Hohen Tauern mountains (Gruber, 1980), estimated a range of deposition from 0.01 to

1.45 mm of eolian dusts per year; taking the minimum rate, the deposition of fine substrate during the postglacial would have been about 10 centimeter.

Subalpine-alpine soils are subjected to freezing phenomena, following both diurnal and seasonal cycles. As a consequence of ice needle formation, top soil and vegetation are heaved and the substrate becomes periodically loose. During spring defrost and in combination with moisture loading, these movements may lead to secondary processes such as soil creeping (solifluction). On slopes, the upper soil layers migrate downwards, leading to the formation of pockets and to revolution of the creeping front. Solifluction leads to a systematic mixing of soil strata and the formation of buried A-horizons.

Table 3.1 Subalpine and alpine soil types occurring on acidic bedrock (from Theurillat et al., 1998, p.237).

Soil type (Baize and Girard 1992)	Soil type (Duchafour 1977)	Soil type (Soil Taxonomy 1977)	Horizons (Baize and Girard 1992)	pH range (average)	Dominant process	Humus forms	Example of vegetation
Rankosol	Ranker	Lithic Humitropept	OL-OF-A-R	3.5-5.0	Weak humus-clay aggregation	Moder	*Caricion curvulae*
Neoluvisol	Sol brun lessivé	Typic Hapludalf	OL-OF-A-E-BT	4.5-5.5	Clay leaching	Mull, moder	*Nardion strictae*
Alocrisol	Sol brun acide	Typic Dystrochrept	OL-OF-A-S-C	4.0-5.5	Brunification Weak pozolization	Mull, moder	*Oxytropido-Elynion* *Festucion variae*
Podzosol	Podzsol humo-ferrugineux	Humic Cryorthord	OL-OF-OH-A-E-BPh-BPs-C	3.0-5.0	Cheluviation	Moder, mor	*Rhododendro-Vaccinion*

3.2 Methods

Soil descriptions and analyses were carried out by Gäelle Vadi (Institut de Botanique, Université de Neuchâtel, rue Emile-Argand 11, CH-2007 Neuchâtel, Switzerland).

Soil types were described in the field during summers 1998 and 1999, according to Baize and Jabiol (1995)and Baize (2000). Soil pH for each horizon was first measured with a field pH-meter (Hellige); and later again in the lab by means of an electrode pH-meter (Metrhom) in distilled water, and in KCl (1:2.5). Organic carbon content, and saturation rate were also determined when necessary for horizon identification. A full description of soil methodology can be found in ANNEXE A.

3.3 Results

The soils investigated belong to three major types: PODZOSOL, ALOCRISOL, and BRUNISOL (Table 3.2). Soil profile sketches can be found in Chapter 6.

In all the sites, soil active acidity (pH H_20) was on average 5: the highest acidity occurred in the top mineral-organic horizons and decreased slightly in the deepest horizons. Organic carbon content and saturation rate are available in Annexe A. The range of soil pH in this study (4.5 to 5.5) is considered to be favourable to the preservation of biogenic silica (Iler, 1979).

Table 3.2 Soil types and locations.

Site	Altitude m a.s.l.	Soil type	Coord.	Slope % degrees	Aspect	Topography
Val d'Arpette						
AR1	2375	PODZOSOL OCRIQUE colluvial,	571.725/ 97.513	33	S	Small saddle
AR2	2565	ALOCRISOL colluvial leached	571.725/ 97.513	33	S	Flat area
AR3	2720	BRUNISOL oligosature leptique	571.125/ 97.713	32	S	Flat area
Belalp- Hofathorn						
BA-HO1	2358	PODZOSOL MEUBLE	639.325/135.400	18	E-SE	Small saddle
BA-HO2	2570	PODZOSOL OCRIQUE	639.050/134.750	3	E 84°	Flat area
BA-HO3	2665	ALOCRISOL TYPIQUE brun	639.825/135.450	15	235°N	Flat area
BA-HO4	2830	ALOCRISOL TYPIQUE brun	638.650/135.900	20	E 98°	Slope near the crest
Belalp- Lengi Egga						
BA-LE7	2305	PODZOSOL MEUBLE superposed buried soil	641.300/137.188	20	171°N	Flat area
BA-LE6	2451	PODZOSOL MEUBLE	641.325/137.563	12	189°N	Flat area
BA-LE5	2550	PODZOSOL MEUBLE	641.113/138.113	12	148°N	Proximity of flat area
Aletsch Glacier						
HT1	2580	ALOCRISOL TYPIQUE brun	649.325/ 147.,275	12	197°N	Saddle, solifluction terrace
HT2	2710	ALOCRISOL TYPIQUE on BRUNISOL truncated	649.375/ 147.385	0	-	Large saddle
Furka Pass						
FK1	2403	PODZOSOL meuble	672.735/ 154.980	12	134°N	Flat area at the base of a slope
FK2	2618	ALOCRISOL	673.310/ 155.790	2	231°N	Flat
FK3	2785	ALOCRISOL	673.700/ 156.290	16	243°N	Slope near the crest

Val d'Arpette soils show a marked decrease of the podzolic activity with increasing altitude: PODZOSOL OCRIQUE (AR1, 2375 m a.s.l.), ALOCRISOL TYPIQUE (AR2, 2565 m a.s.l.) and BRUNISOL OLIGOSATURÉ (AR3, 2720 m a.s.l.). Humus are of moder type in the first two soils and mull in the latter. Structure is little developed in all soils and texture is silty-sandy for AR1 and sandy for AR2 and AR3. Roots occur preferentially in the top centimeters. Stones at the bottom of the profile show surface-weathering. The pedogenesis in Arpette is strongly influenced by colluvial activity, leading in AR1 to the formation of a sequence of chaotic horizons and several pockets. For instance, the ochre pocket [C2] (see Annexe A) may be the residue of a podzolic illuvial horizon. The organic acids deposited on the stone surfaces in the spodic layer and the soil chemical features (low pH and high content in humified organic matter), both evidence strong podzolic activity.

In AR2, high Al concentration attested the presence of a Sal horizon. Pockets yielding a concentration of organic carbon, similar to typical BPh podzosol horizons present in C, are the result of the colluvial activity. The presence of black deposits of organic acids on stones testify of the occurrence of past podzolic activity. AR3 soil is less developed and traces of any podzolic activity are absent. The blocky structure in the S horizon is typical of the brunification process. Low pH rate indicates that the soil is hardly desaturated.

In the transect *Belalp-Hofathorn* (Figure 3.1) the soils at lower altitude were a PODZOSOL MEUBLE (BA-HO1, 2358 m a.s.l.) and a PODZOSOL OCRIQUE (BA-HO2, 2570 m a.s.l.). The two other soils at higher elevation were described as ALOCRISOLS TYPIQUES (BA-HO3, 2660 m a.s.l.; BA-HO4, 2830 m a.s.l.). In here, soils do not show colluvial activity.

Humus is of moder type along the whole transect. The four soils have similar morphological features: sandy-silty textured and poorly developed structure with sandy layers at bottom of the profile. Stones occur in the illuvial zone of the PODZOSOLS (BP horizon) and in the aluminous layers of the ALOCRISOLS (Sal), rocks are less weathered with increasing depth.

In the *transect Belalp-Lengi Egga* the soil profiles BA-LE5 (2550 m a.s.l.) and BA-LE6 (2451 m a.s.l.) are similar to the PODZOSOLS in Belalp-Hofathorn transect. Soil structure is not well developed, texture is silty-sandy in BA-LE5 and sandy in BA-LE6. Roots occurred mostly in the spodic layers (especially BPh), stones were present until about 30 cm depth and appear less weathered with increasing depth. The humus type is dysmoder in BA-LE6, and dysmoder with discontinous hemimoder in BA-LE5. BA-LE7 (2305 m a.s.l.) soil is developed on a palaeosoil. This is confirmed by numerous coloured spots (black, brown, ochre yellow and red), the stable polyhedral structure and the absence of stones in this horizon (although the horizon is placed between a gravel-rich upper-layer and the underlying unweathered bedrock). In the remaining soil horizons the structure is not stable, and texture is silty-sandy.

Figure 3.1 Soil profiles at Belalp-Hofathorn. From left: BA-HO1 (PODZOSOL MEUBLE), BA-HO2 (PODZOSOL OCHRIQUE), BA-HO4 (ALOCRISOL TYPIQUE).

In the *Aletsch transect* soils are ALOCRISOLS TYPIQUES. The soil profile HT2 (2710 m a.s.l) lays on the residue of a less developed palaeosoil (BRUNISOL OLIGOSATURÉ). Roots are present in the upper 15 cm of the profile, although fine roots reach a depth of 60 cm in HT1 (2580 m). Soil structure is unstable: granular in the organo-mineral layer (A), polyhedral in the intermediate horizons (S), particular in C. Particle size goes from silty-sandy to sandy in the deepest layer. Stones and gravel occur underneath the organo-mineral horizon, more frequently towards the bottom of the profile. In HT1 the stones at the bottom of the profile were strongly weathered.

At *Furka*, soil and humus type change consistently with increasing elevation: signs of past podzolization are present only in the low altitude soil at 2403 m a.s.l. (FK1, PODZOSOL MEUBLE), and absent at 2618 m and 2785 m a.s.l. (FK2 and FK3, ALOCRISOLS TYPIQUES). Humus types are: mor in FK1 and mull in FK2 and FK3. The soil profile FK1 has a well developed soil structure, while FK2 et FK3 show unstable aggregation. Roots dominated the organo-mineral layers (A) though they were also present in the deeper horizons; stones are strongly weathered in the three sites: for instance in FK2 and FK3 even big fragments of parent-rock can be easily broken, and rock blocks are pierced by roots.

All the PODZOSOLS studied contained moder-type humus, whereas, the ALOCRISOLS yielded preferentially mull-type (Table 3.2). Exceptions were BA-LE7 and FK1, PODZOSOLS that contained dysmull (i.e. mull with slow biological activity) and mor, respectively.

3.4 Discussion

The present study brings a contribution to the knowledge of alpine and sub-alpine soil dynamics. In soils at Belalp-Hofathorn signs of past podzolic activity were detected up to 2550 m a.s.l.. Soils of the Belalp-Lengi Egga transect show evidences of podzolic activity between 2451 m and 2550 m a.s.l.. In the Aletsch transect the podzolization is absent even in the lower altitude site (2580 m a.s.l.), and the pedogenesis is dominated by aluminium transfer. At Furka, soil and humus type change consistently with increasing elevation: signs of past podzolization are present in the soil at 2403 m a.s.l., and absent at 2618 m and 2785 m a.s.l..

A strict correlation between soil-type and altitude was detected in all the sites. Indeed, the upper limit of the podzolic activity is located in a narrow altitudinal belt comprised between 2500 m (at Furka and in Val d'Arpette) and 2550 m (at Belalp), while at higher elevation the dominant soil types were ALOCRISOLS.

Evidences of podzolic activity are to be interpreted as the result of fossil soil processes in all the sites, as the present vegetation of subalpine and alpine grasslands is not able to produce a biomass sufficient to lead to a full podzolisation. The input of organic compounds from the decomposition of conifer and ericoids shrub litter is known to be determinant for initiating the podzolisation processes.

In all the altitudinal transects here examined parent rock composition is constant and the climatic requirements for podzolic activity (low mean annual temperatures and heavy snow fall in winter) occur in all the sites. Arctic conditions may trigger podzolisation even if acidificant litter is missing on badly buffered poor substrate (i.e. quartz-rich) (Stutzer, 1999). However, only plant communities supplying acidic litter and with high net primary production (i.e. conifer woodlands and heathlands) can lead to fully developed PODZOSOL MEUBLES soil type (Duchaufour, 1998), while the present vegetation of alpine meadows is unable to drive the pedogenesis to this stage.

Since neither the present vegetation, nor the climatic conditions explain the pedologic discontinuity between PODZOSOLS and ALOCRISOLS, it can be argued that these soils were formed under different vegetation types: i.e. PODZOSOLS under a vegetation of subalpine tundra or conifer forest, and ALOCRISOLS under alpine meadows. Therefore, the upper limit of the podzolic activity is to be interpret as an evidence of the past vegetation border.

The uppermost limit of podzolisation in the study areas is never higher than 2500 to 2550 m a.s.l.. Therefore it can be inferred on the basis of pedological considerations, that rather closed woody species community (shrubs or trees) have vegetated up to this elevation. It is argued, therefore, that this limit corresponds to the uppermost altitude attained by the treeline. At higher elevation, the podzolic activity in soils blurs, giving origin to weakly podzolized soil types, i.e. PODZOSOLS OCRIQUES and ALOCRISOLS (Duchaufour, 1998). Since in favourable climatic conditions weak podzolisation may occur in soils under less acidificant humus types, this belt of weakly podzolic activity may develop in presence of heaths and isolated krummholtz of conifers.

In the sites close to the Aletsch Glacier, podzolisation do not occur at all. It can be argued that harsher mesoclimatic conditions impeded the formation of a woody species cover sufficient to trigger podzolization.

These results are in agreement with soil study carried out in the Central Valais (Tinner et al., 1996), in which in transects between 1780 and 2600 m a.s.l., the upper limit of podzolic activity was detected at 2450 m.

3.5 Conclusions

Soils are highly conservative media in which mineral and organic processes are brought together. Vegetation and climate play a major role in soil determination and their fingerprints should be a reliable evidence of palaeoecological conditions of the soil formation. In the five transects studied, the uppermost limit of podzolic activity is situated in a narrow belt between 2500 m a.s.l. (in Val d'Arpette and at Furka) and 2550 m (at Belalp). This limit probably traces the uppermost altitude attained by the treeline during the Holocene.

Soil study is an invaluable proxy for tracing past vegetation dynamics, because of virtually unlimited availability, and high spatial precision, that no other proxy can supply. The description of soil morphology allows the detection of soil mixing phenomena, palaeohorizons and colluvial activity that may affect the distribution palaeobotanical proxies in soil.

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CHAPTER 4: BIOGENIC SILICA IN PLANTS AT THE SUBALPINE-ALPINE ECOCLINE

In this chapter is addressed the study of biogenic silica in plant species, plant communities at the subalpine and alpine ecocline. Data are presented in three sections: Chapter 4.1, Chapter 4.2 and Chapter 4.3[1].

Chapter 4.1 is concerned with the analysis of biogenic silica in plants. Firstly, the biogenica silica content in the above ground tissues of dominant or very common subalpine and alpine plant species was assessed, and the annual production of plant community in which they occur was estimated. Secondly, phytolith typologies were observed, described and inventoried at the optic and scanning microscope to test their taxonomical potential (4.2). Thirdly, the composition of biogenic silica was analysed by X-rays microanalysis (4.3).

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[1] Each subsection of the Chapter 4 was written under a format suitable for five indipendent publications in scientific peered reviews, this leading inevitably to some repetitions

4.1 BIOGENIC SILICA PRODUCTION IN SELECTED ALPINE PLANT SPECIES AND PLANT COMMUNITIES *

A. L. Carnelli[1], M. Madella[2] and J.-P. Theurillat[3]

[1] Institut F. A. Forel, Université de Genève, 10 route de Suisse, CH-1290 Versoix, Switzerland; [2] The Cambridge Phytolith Project, The McDonald Institute for Archeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, U.K.; [3] Centre Alpien de Phytogéographie, Fondation J.-M. Aubert, CH-1938 Champex and Conservatoire et Jardin botaniques de la Ville de Genève, 1 ch. de l'Impératrice, CH-1292 Chambésy Switzerland

[1] For correspondence: e-mail carnelli@terre.unige.ch

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4.1.1 Abstract

The biogenic silica extracted from samples of 28 alpine plant species belonging to 23 genera and 9 families collected in the Swiss Alps (Valais) accounted for between 0.01 and 5.9% of the dry biomass of leaves and wood. Silica content and plant contribution to the soil biogenic silica pool, varied widely among taxa. Plant net productivity and biogenic silica production from the study and from the literature have been taken into account to predict the input different subalpine and alpine plant communities make to soil-borne phytolith assemblages, and their contribution to the silicon biocycle.

Key words: silicon, productivity, phytoliths, subalpine, alpine, grasslands, heaths, forests, *Gramineae*, *Cyperaceae*, *Ericaceae*, *Coniferae*.

4.1.2 Introduction

Silicon (Si) in the soil is available for uptake by plants as monosilicic acid originating from the dissolution of crystalline silicate and weathering of biogenic silica. Biological membranes are permeable to silicon (Epstein, 1999). Silicon is absorbed by the roots of vascular plants, transported into the shoots by the transpiration stream, and eventually deposited in the plant tissues as hydrated opal-A (Jones and Handreck, 1967; 1969).

Opal silica deposition can be intracellular (all or part of the cell lumen is in-filled with opal silica) or extracellular (filling intercellular spaces, or forming an external layer on epidermal cells). A considerable proportion of opal silica is laid down after the secondary wall of the cell has been formed and it is believed that opal silica deposition in the lumen is inhibited until senescence has occurred (Blackman, 1969). The opal silica content of plants increases in ageing tissues where it can accumulate in concentrations of up to five times that in the young tissues (Hodson *et al.*, 1996; Wyttenbach *et al.*, 1991; Hodson and Sangster, 1998). After deposition in plant tissues, opal silica is not remobilized and is not available for retranslocation to other parts of the plant (Raven, 1983).

The physiological role of silicon in vascular plants is still an open subject; silicon may act as an essential or a beneficial element depending on the species (Hodson and Evans, 1995; Raven, 1983; Yeo *et al.*, 1999). Silicon-deficiency symptoms are shown by rice (*Oryza sativa* L.) and horsetail (*Equisetum arvense* L.) when grown in silicon-free medium (Epstein, 1999). Evidence of the role of silicon in alleviating aluminium (Al) toxicity has been found for several species (e.g. *Sorghum bicolor* (L.) Moench, *Hordeum vulgare* L., *Zea mays* L. ssp. *mexicana* and *Glycine max* Merr; Hodson and Evans, 1995). Silicon may act at the level of the bulk soil solution, reducing aluminium bioavailability by the formation of aluminosilicate (AS) and hydroxyaluminosilicate (HAS) complexes, and there may be co-precipitation of AS and HAS in plant tissues (Cocker *et al.*, 1998). The co-deposition of Al and Si, recently documented in the needles of four species of conifers, has been interpreted as a mechanism for sequestering aluminium (Hodson and Sangster, 1999). The codeposition of silicon and heavy metals in plant tissues can function as a detoxifying mechanism in species that are heavy metal resistant e.g. *Silene cucubalus* (Wibel) *ssp. humilis.*, *Thlaspi coerulescens* J. et C. Presl, *Viola calaminaria* (D.C.) Lej. and *Minuartia verna* L. ssp. *hercynica* (Willk.) (Bringezu *et al.*, 1999; Neumann *et al.*, 1997). The active uptake of silicon has been demonstrated in sugar cane, horsetail, wheat and rice (Raven, 1983), though in other species, such as oat and barley, the content of silicon in the plant can be accounted entirely in terms of supply in the transportation stream, suggesting a passive transport mechanism. In some *Leguminosae* (*Fabaceae*) there seem to be active and passive mechanisms to exclude silicon (Jones and Handreck, 1969). The deposition of opal silica in plant tissues also plays structural and protective roles, at much lower energy cost than using lignin or polysaccarides (Raven, 1983). Opal silica improves plant resistance to mechanical stress and pathogens, and reduces palatability to herbivores (Raven, 1983).

After plant death and the decay of the organic matter, or as a consequence of plant burning, single silicified cells and fragments of silicified tissues are released into the environment as distinct elements. The single silicified elements are called "phytoliths", "silica bodies" or "silicophytoliths", with sizes ranging from a few to several tens of micrometers. The fragments of silicified tissue are called “silica skeletons”. The accumulation and persistence of these microfossils in both terrestrial and aquatic palaeoenvironments makes them a suitable tool for the reconstruction of past environments and human activities (e.g. Barboni *et al.*, 1999; Fredlund and Tieszen, 1997; Bozarth, 1993; Madella, 2000; Miller-Rosen, 1993; Pearsall, 1994; Piperno, 1988). However, for the application of this methodology to the reconstruction of long-term vegetation dynamics, more information on production, deposition and taphonomy of biogenic silica are necessary. Detailed information on contrasting vegetation types is needed to facilitate the assessment of the contribution of different taxa to the soil-borne phytolith assemblages, and their role in the biogeochemical cycle of the silicon.

Phytolith analysis can be a valuable tool in the study of the vegetation history in the Alps. Measurement of the altitudinal fluctuations of the treeline in the Alps during the Holocene is paramount for the reconstruction of past environments and the prediction of future vegetation responses to climatic changes. At present, altitudinal fluctuations of the treeline in the Alps are reconstructed using pollen and plant macrofossil analyses. According to these data, the forested subalpine zone, and its transition to the alpine zone, attained the highest elevation during the Atlantic climatic optimum (5000 to 6000 radiocarbon years BP). It is estimated that during this period the treeline was up to 300m higher than the present potential level (in the continental part of the Alps, such as the central Swiss Alps, this means that forest was present up to about 2500m a.s.l.). However, an accurate estimate of the upper limit attained by the treeline at high altitude has been hampered by the scarcity of suitable "environmental archives", such as peat bogs. Alpine soils are nonetheless important palaeoecological archives, and their potential can be tapped by the study of phytolith assemblages as indicators of past vegetation. However, no quantitative data on biogenic silica production of herbaceous species occurring in the Alpine vegetation belt are available, and only a few works have been published on silica production in woody species occurring naturally in the Alps (Klein and Geis, 1978; Wyttenbach *et al*., 1991; Hodson *et al*., 1996). In the present research, the content of opal biogenic silica from dominant or widespread species occurring in alpine grasslands, heaths, and coniferous forests on acidic bedrock has been assessed. The plant silica content has then been used to estimate the amount of biogenic silica added to the soil per year by the most common plant communities occurring in the subalpine and alpine vegetation belts. These data are important for quantifying the biogeochemical cycle of silicon and the related weathering processes in alpine ecosystems, and in the interpretation of fossil phytolith records in the Alps.

4.1.3 Methods

4.1.3.1 Site descriptions

The plant material was collected from three sites in the Valais region of the Swiss Alps (Val d'Arpette, Furka Pass, and Bel Alp-Aletsch glacier region). In the study area, the soil types formed on acidic parent rock (gneiss) follow an altitudinal zonation: podzols are located between 2300m a.s.l. and 2550m a.s.l, while at higher altitude weak podzolization has resulted in alocrisols and brunisols (AFES, 1998). The main vegetation types occurring in the sampling area belong to the subalpine vegetation belt (the highest belt where forest can survive, located approximately between 1600 and 2300m a.s.l. in the study sites) and the alpine belt (between the treeline and the snow line i.e. 2300 - 3000m a.s.l.). The potential vegetation of the subalpine belt is dominated by Boreal type coniferous forests with *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus mugo*; heaths with ericoid species (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. uliginosum, V. vitis-idaea, Arctostaphylos uva-ursi, Calluna vulgaris*); shrubs with *Alnus viridis* and *Salix herbacea*, as well as subalpine swards dominated mainly by *Carex sempervirens* and *Nardus stricta*. The alpine vegetation belt is usually divided into a lower belt potentially dominated by dwarf shrub heaths with *Loiseleuria procumbens*, *Empetrum nigrum* subsp. *hermaphroditum* and *Vaccinium uliginosum*, and an upper belt dominated by swards of *Carex curvula.*

4.1.3.2 Collection of plant material and silica extraction

Samples of 28 alpine species were collected at the three sampling sites during August 1997 and August 1998. As this period of the year corresponds to the end of the growing season, the specimens were representative of the total annual silicon deposition in the plant tissues. The species, the sampling sites and the altitude at which they were collected are listed in Table 4.1.1. All the collected species are perennials. The woody taxa are evergreen with the exception of *Larix decidua*, *Vaccinium myrtillus* and *V. vitis-idaea.* The species selected are those most commonly occurring in the subalpine plant and alpine plant communities on siliceous bedrock. A composite sample was collected from the above-ground tissues of several randomly selected plants from each species, regardless of plant age. For herbaceous species, the whole above ground plant was sampled. For low and dwarf bushes, whole branches were collected. For tree species, young branches of 20-50mm in diameter were cut and collected. Leaves and stems of herbaceous plants were analysed together. In woody species, leaves and branches were analysed separately, in order to quantify the opal silica content of the different plant tissues. For *Calluna vulgaris,* composite samples of leaves and young branches were analysed, as it was impractical to separate the needle-like leaves from the young branches. Three replicated extractions of the opal silica for each plant sample were made. The plant samples were washed several times in a solution of water and detergent (commercial washing-up liquid) and rinsed with de-ionised water. Mineral matter was removed by placing the samples in an ultrasound bath overnight (NEY, Ultrasonik 104X). The samples were then rinsed with de-ionised water, dried for 48 hrs at 60°C, and weighed. They were then placed in porcelain crucibles individually sealed with aluminium foil and reduced to ash in a muffle furnace at 420°C (at this temperature opal silica does not change to other forms of silica; Piperno, 1988, Runge, 1998). The samples were burned for between 4 and 12 hours until the ash appeared whitish. The ash was then weighed. Subsequently, any remaining organic matter was digested with concentrated HNO_3 (65%) and oxalates and carbonates were eliminated using a solution of HCl 3.5 N. The residues were washed with de-ionised water and centrifuged at 1000 r.p.m. for 3 minutes, and the supernatant discarded (this step was repeated three times). The remaining biogenic silica residue was oven dried at 60° C for 48 hours and then weighed. The extracted biogenic silica was expressed as percentage of the original plant dry weight.

4.1.3.3 Light microscopy

Permanent microscope slides of the residues extracted from each plant sample were mounted with Eukitt (refractive index 1.5 at 20 °C) and observed under a microscope equipped with phase contrast optics and polarised illumination at a magnification of x504. An estimate of the purity of the biogenic silica extracted was obtained by counting the number of optically isotropic and anisotropic particles in three microscope fields (Table 4.1.2). Since oxalates and carbonates had been removed, optically anisotropic particles were considered to be crystalline silica, alkali feldspar or micas (the most common minerals in the soil and parent rock). The weight of the extracted silica was corrected by subtracting the percentage of anisotropic particles[2], allowing for the different densities of the anisotropic and isotropic particles. The average density of the anisotropic particles is 2.65 Mg /m^3 (average density of surface soil mineral) and the density of biogenic silica is 2.35 Mg /m^3 (Brady, 1990). The mean volume of the particles of opaline silica and crystalline silica was assumed to be, on average, approximately the same.

TABLE 4.1.1. *Sampled species, plant parts, locations and altitudes*

Species	plant part	altitude (m a.s.l.)	Family
Abies alba Miller	L,W	2050	*Pinaceace*
Alchemilla pentaphylla L. [b]	L	2830	*Rosaceae*
Alnus viridis (Chaix) DC	L, W	2000	*Betulaceae*
Arctostaphylos uva-ursi Spreng.	L,W	2420	*Ericaceae*
Calamagrostis villosa (Chaix.) Gmelin.	L, C	1900	*Gramineae*
Calluna vulgaris L.	L, W	2420	*Ericaceae*
Carex curvula All.	L, C	2470	*Cyperaceae*
Carex sempervirens Vill.	L, C	2300	*Cyperaceae*
Empetrum nigrum subsp. *hermaphroditum* (Hagerup) Böcher	L, W	2000	*Ericaceae*
Festuca halleri All.	L, C	2730	*Gramineae*
Festuca puccinellii Parl.	L, C	2090	*Gramineae*
Festuca scabriculmis (Hackel.) Richter	L, C	2300	*Gramineae*
Geum montanum L. [b]	L	2830	*Rosaceae*
Juniperus nana Willd.	L, W	1930	*Pinaceace*
Larix decidua Miller	L, W	2050	*Pinaceace*
Leontodon helveticus Merat [a]	L	2795	*Asteraceae*
Loiseleuria procumbens Desf.	L, W	2370	*Ericaceae*

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[2] It can be argued that anisotropic particles were minerals adhering to the surface of the plants, not removed by the cleaning process. The species which contained the highest percentages of these impurities (*C. vulgaris*, *L. procumbens* and *E. nigrum*) all have very small leaves, either revoluted or embricated, where impurities can accumulate.

Nardus stricta L.	L	2300	*Gramineae*
Picea abies (L.) Karsten	L, W	2050	*Pinaceace*
Pinus cembra L.	L, W	2050	*Pinaceace*
Pinus mugo Turra	L, W	2050	*Pinaceace*
Poa alpina L. [a]	L	2795	*Gramineae*
Rhododendron ferrugineum Linn.	L, W	2050	*Ericaceae*
Salix herbacea L. [a]	L	2795	*Salicaceae*
Vaccinium myrtillus L.	L, W	2180	*Ericaceae*
Vaccinium uliginosum L.	W	1780	*Ericaceae*
Vaccinium vitis-idaea L.	L, W	1980	*Ericaceae*
Veronica bellidioides L. [a]	L	2795	*Scrophulariaceae*

Provenence: all samples were collected at Val d'Arpette except: [a] Furka Pass, [b] Bel Alp-Aletsch Glacier,
L= leaves, C= culms, W= woody branches

4.1.3.4 Estimate of the biogenic silica input into the soil

Since some of the species studied are dominant in widely distributed subalpine and alpine plant communities, it was decided to estimate the contribution of these plant communities to the biogenic silica budget in the soil. For grassland, heath and shrub communities the potential annual input of silica into the soil (g m^{-2} y^{-1}) was calculated by taking the product of (i) the rate of new biomass formation per day reported from, or estimated according to the literature [Above-ground Primary Productivity (APP) in g m^{-2} d^{-1}]; (ii) the mean length of the growing season (days); and (iii) the percentage of biogenic silica in the tissues of the species of the plant community (Table 4.1.3). The latter was calculated by taking into account the mean abundance of the species and, for heaths only, the different production of biogenic silica in herbaceous and woody tissues[3].(More details in ANNEXE B).

As it was not possible to find data for *Festuca scabriculmis*, its APP was assumed to be of the same order as *F. varia*, because *F. scabriculmis* belongs to the aggregate of species and grows in similar ecological conditions. Similarly, the APP of *Calamagrostis villosa*, *Carex sempervirens* and *Nardus*

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[2] The relative abundance of a species (**a**) is defined as $\mathbf{a = A/A_{tot}}$ (where A_{tot} is the sum of the cever percentages). In order to take into account the biomass of the species, the values for the ratio between biomass of herbaceous tissues (**h**) and woody tissues (**w**) were taken from the published literature. The relative biogenic silica production for the herbaceous tissues of a species (**H**) is $\mathbf{H = a \cdot ph \cdot BS\%_{corr}}$ (where $\mathbf{ph = h/(h+w)}$ and $\mathbf{BS\%_{corr}}$ is the silica content for the herbaceous tissues as in Table 2). The relative biogenic silica production for woody tissues for a species (**W**) is $\mathbf{W = a \cdot pw \cdot BS\%_{corr}}$ (where $\mathbf{pw = w/(h+w)}$ and $\mathbf{BS\%_{corr}}$ is the silica content in the woody tissues as in Table 2). The total production of biogenic silica of a given community ($\mathbf{BS_{(H,W)}}$) was calculated as the sum of all the contributions from the herbaceous and woody tissues of each species ($\mathbf{BS_{(H,W)} = H_{tot} + W_{tot}}$).

stricta were estimated using the mean productivity of subalpine grasslands and subalpine meadows. The annual silica input to the soil by conifers was calculated using data for the annual deposition of needles from the literature listed in Table 4.1.3. The silica input by conifer stands has been underestimated because the contribution of conifers' wood was not taken into account.

4.1.4 Results

Results are summarised in Table 4.1.2 and Fig. 4.1.1.

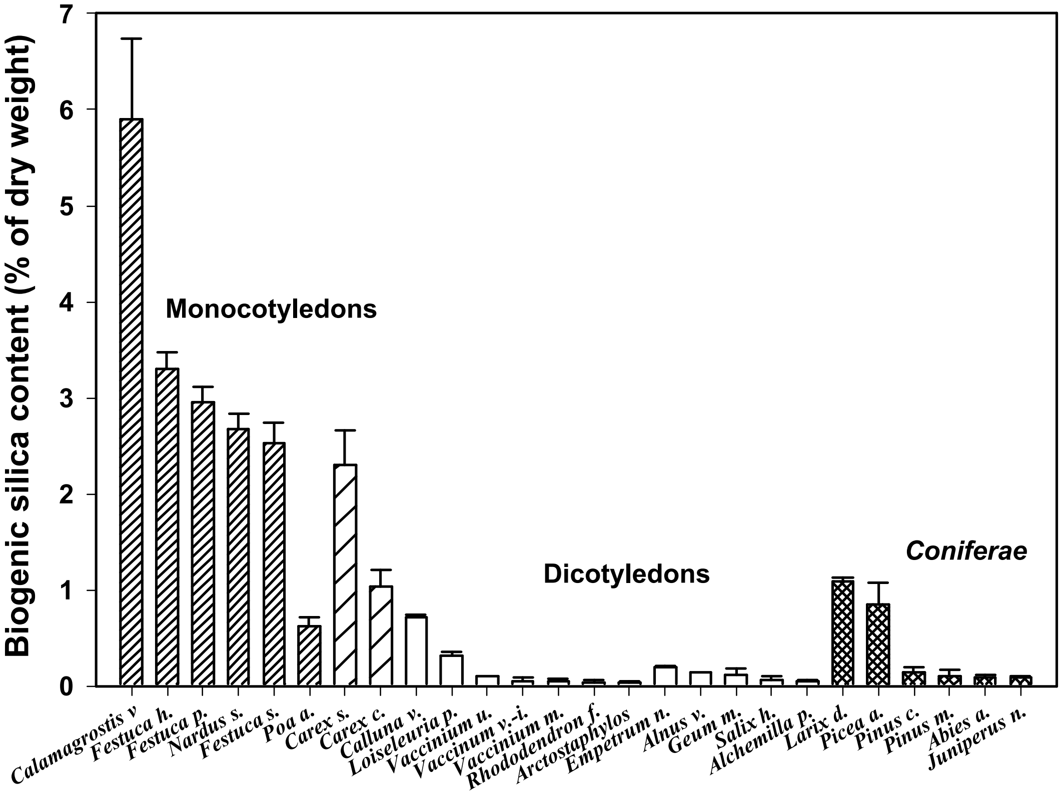
4.1.4.1 Monocotyledons

Grasses yielded the highest opal percentages. The highest content of biogenic silica was found in *Calamagrostis villosa* (5.9%), and the lowest in *Poa alpina* (0.61%), the mean value for the analysed plants for this family being 3%. The biogenic silica content of the two species of the genus *Carex* analysed was 2.29% in *C. sempervirens* and 0.96% in *C. curvula.*

4A.1.4.2 Dicotyledons

The mean content of biogenic silica in the leaves and wood of the analysed dicotyledons (0.1%) was much lower than that for monocotyledons. Among the six species of the *Ericaceae* family the highest percentage of silica extracted was from the leaves of *Calluna vulgaris* (0.68%), whereas the leaves of *Loiseleuria procumbens* contained 0.24%. The leaves of the three *Vaccinium* species, *Rhododendron ferrugineum* and *Arctostaphylos uva-ursi* all contained quantities of biogenic silica ranging from 0.04% to 0.03%. The wood samples of the *Ericaceae* had in general lower contents of opal silica ranging from 0.01% to 0.21%, with the highest value in *A. uva-ursi*. The other woody dicotyledons analysed were *Empetrum nigrum,* which gave similar values for both leaves (0.16%) and wood (0.11%), *Alnus viridis* (with values of 0.13% in leaves and 0.04 % in wood) and *Salix herbacea*. The latter accumulated higher quantities of silica in the wood (0.43%) than in the leaves (0.04%). The biogenic silica in *Alchemilla pentaphylla* was 0.04% and in *Geum montanum* 0.11%. In two herbaceous dicotyledons (*Veronica bellidioides* and *Leontodon helveticus*) the amount of plant material processed did not give a detectable silica residue.

Figure. 4.1.1 Biogenic silica content of non-woody tissues of plants collected from subalpine and alpine zones in the Swiss Alps. The vertical bars indicate s.d..



4.1.4.3 Conifers

Larix decidua and *Picea abies* produced the highest quantity of biogenic silica in the needles, at 1.09% and 0.85% respectively. Needles of *Pinus cembra*, *P. mugo*, *Abies alba* and *Juniperus nana*, all yielded about 0.1% of opal silica. The content of opal in the conifer wood ranged from 0.02% in *P. cembra* to 0.54% in *L. decidua.* On average the biogenic silica extracted from the conifer specimens (needles and wood) was 0.3%.

4.1.4.4 Estimate of biogenic silica input into the soil

The estimated annual biogenic silica productions of the subalpine and alpine plant communities were summarised in Table 4.1.3 with the relevant bibliography.

Table 4.1.2. Ash content (% of dry weight), biogenic silica content (% of dry weight, with s. d.), content of optically-isotropic particles in the final ash (% of particles) and biogenic silica content corrected for optically-isotropic particles (% of dry weight) of species growing in the Swiss Alps. The data are mean of three determinations.

	LEAVES					**WOOD**				
Species	**Ash %**	**B. S. %**	**s. d.**	**O. I. %**	**B. S. $\%_{corr}$**	**Ash %**	**B. S. %**	**s. d.**	**O. I. %**	**B. S. $\%_{corr}$**
Monocotyledons [a]										
Calamagrostis villosa	8.96	5.90	0.8410	100	5.9					
Carex curvula	-	1.03	0.1769	93	0.96					
Carex sempervirens	4.78	2.31	0.3540	99	2.29					
Festuca halleri	-	3.30	0.1706	99	3.27					
Festuca puccinellii	5.59	2.96	0.1596	100	2.96					
Festuca scabriculmis	-	2.52	0.2215	96	2.41					
Nardus stricta	4.39	2.67	0.1578	96	2.56					
Poa alpina	-	0.62	0.0838	98	0.61					
Dicotyledons										
Alchemilla pentaphylla	-	0.05	0.0119	80	0.04					
Alnus viridis	4.44	0.13	-	100	0.13	2.89	0.04	0.0358	100	0.04
Arctostaphylos uva-ursi	0.25	0.04	0.0095	70	0.03	2.59	0.25	0.0129	85	0.21
Calluna vulgaris [b]	-	0.72	0.0247	95	0.68					
Empetrum nigrum	3.05	0.19	0.0112	84	0.16	1.40	0.11	0.0111	-	0.11
Geum montanum	-	0.11	0.0724	96	0.11					
Leontodon helveticus	-	0.00	0.0000	-	0					
Loiseleuria procumbens	2.63	0.32	0.0378	75	0.24	1.17	0.10	0.0599	77	0.08
Rhododendron ferrugineum	2.79	0.04	0.0192	89	0.04	1.76	0.02	0.0114	73	0.01
Salix herbacea	-	0.06	0.0464	75	0.04	-	0.50	0.1810	87	0.43
Vaccinium myrtillus	-	0.04	0.0370	97	0.04	2.42	0.04	0.0105	77	0.03
Vaccinium uliginosum	4.92	0.10	-	-	0.1	1.51	0.08	0.0168	100	0.08
Vaccinium vitis-idaea	2.83	0.04	0.0434	67	0.03	2.46	0.03	0.0171	84	0.03
Veronica bellidioides	-	0.00	0.0000	-	0					
Coniferae										
Abies alba	5.78	0.08	0.0308	77	0.06					
Juniperus nana	3.44	0.08	0.0220	83	0.07	7.04	0.15	0.0595	-	0.15
Larix decidua	-	1.09	0.0420	100	1.09	2.10	0.59	0.1620	91	0.54

Picea abies	3.56	0.85	0.2297	100	0.85	2.25	0.18	0.0385	91	0.16
Pinus cembra	2.61	0.13	0.0540	88	0.11	2.13	0.02	0.0054	84	0.02
Pinus mugo	-	0.10	0.0708	95	0.09	1.80	0.07	0.0430	81	0.06

(a) For monocotyledons plants leaves and culms are analysed toghether ; (b) herbaceous stems and leaves.

Table 4.1.3. Estimated biogenic silica input to the soils of the main subalpine and alpine plant communities on siliceous substrate in the Alps.

Type of vegetation	**Growing season (days)**	**Above ground productivity (g d. w. m^{-2} d^{-1})**	**Biogenic silica content (% on dry weight basis)**	**Predicted biogenic silica input (g m^{-2} y^{-1})**
Grasslands				
Carex curvula cryophilous alpine sward	100 *a*	1.3 *b*	0.96	1.2
Festuca scabriculmis subsp. *luedii* thermophilous low alpine sward	130 *a*	3.3 *d*~	2.41	10.3
Carex sempervirens mesophilous upper subalpine sward	130 *a*	3.3 ~	2.29	9.8
Nardus stricta mesophilous subalpine sward	140 *a*	2.0 *e*, *f*~	2.56	7.2
Heaths				
Loiseleuria procumbens cryophilous low alpine dwarf shrub heath	110 *a*	0.8 *c*	0.22 #	0.19
Vaccinium uliginosus- Empetrum nigrum cryophilous upper subalpine dwarf shrub heath	130 *a*	2.3 *c*	0.15 §, #	0.45
Rhododendron ferrugineum-Vaccinium myrtillus mesophilous subalpine heath	140 *a*	3.8 *c*, *g*	0.09 §, #	0.48
Arctostaphylos uva-ursi, *Juniperus nana* thermophilous subalpine heath	140 *a*	2.5 ~	0.13 £, #	0.45
Arctostaphylos uva-ursi,*Calluna vulgaris* thermophilous subalpine heath	140 *a*	3.0 ~	0.27 £, #	1.13
Shrubs and forests				
Salix helvetica upper subalpine cryophilous shrubs	130 *a*	2.5 ~	0.14 #	0.46
Alnus viridis mesophilous subalpine shrubs	140 *a*	3.3 *e*	0.11	0.51
Calamagrostis villosa understorey mesophilous subalpine tall-herbs	150 *a*	3.3 ~	5.9	29.2
Larix decidua subalpine forest	150 *a*	1.5 *h*	1.09	2.4
Picea abies subalpine forest	170 *a*	0.5 *h*	0.85	0.7

(a) according to **Theurillat, J.-P., Felber, F., Geissler, P. Gobat, J.-M., Fierz, M., Fischlin, A., Küpfer, P., Schlüssel, A., Velutti, C., and Zhao, G.-F. 1998.** Sensitivity of plant and soils ecosystems of the Alps to climate change. *Views from the Alps: regional perspectives on climate change.* P. Cebon, U. Dahinden, H. C. Davies, D. Imboden, and C. C. Jaeger, *ed.*, Cambridge, Massachusetts, MIT Press, 225-308; *(b)* from **Klug-Pümpel, B. 1989.** Phytomasse und Nettoproduktion naturnaher und anthropogen beeinflusster alpiner Pflanzengesellschaften in den Hohen Tauern. In: Cernusca A, *ed. Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern. Innsbruck: Universitätsverlag Wagner, 331-355*; *(c)* from **Schmidt, L. 1977.** Phytomässevorrat und Nettoprimarproduktivität alpiner Zwergstrauchbestände *Œcol. Plant.* 12: 195-213; (*d*) from **Onipchenko, V. G. 1994.** The structure and dynamics of alpine plant communities in the Teberda Reserve, the Northwestern Caucasus. *Oecologia Montana*, 3: 35-45 and **Onipchenko, V. G., Semenova, G. V., and van der Maarel, E. 1998.** Population strategies in severe environments: alpine plants in the northwestern Caucasus. *Journal of Vegetation Science*, **9:** 27-40; *(e)* from **Klug-Pümpel, B. 1978.** Phytomasse und Primärproduktion von unterschiedlich bewirtschafteten Almflächen im Gasteiner Tal. In: Cernusca A, *ed. Ökologische Analysen von Almflächen im Gasteiner Tal. Innsbruck: Universitätsverlag Wagner, 123-142*; *(f)* **Rehder, H. 1970.** Zur Ökologie insbesondere Stickstoffversorgung subalpiner und alpiner Pflanzengesellschaften im Naturschutzgebiet Schachen (Wettersteingebirge). *Dissertationes Botanicae* 6: 1-90; (*g)* from **Pornon, A., and Doche, B. 1995.** Minéralisation et nitrification de l'azote dans différents stades de colonisation des landes subalpines à *Rhododendron ferrugineum* L. (Alpes du Nord; France*). Comptes Rendus de l'Académie des Sciences, Paris. Série 3. Sciences de la Vie* 318: 887-895; *(h)* litterfall, from **Bray, J. R., and Gorham, E. 1964.** Litter production in forests of the world. *Advances in Ecological Research*, **2:** 101-157, (the annual litterfall is here expressed on a daily basis for easier comparison).

(#) Leaves and wood mean of the ratio herbaceous/woody for aboveground productivity and the mean ratio between the dominant species in the plant community; (~) estimated values.

4.1.5 Discussion

The mean silica content of above ground parts of the alpine plants analysed in this study was 0.6% of their dry biomass, with remarkably different production by different taxa. Although closely related plants tend to have similar opal silica contents, several exceptions can be pointed out. The following discussion considers data from the present study and from the literature (Table 4A.1.4), but it is important to stress that different sampling and extraction methodologies and the very diverse ecological conditions of growth mean that comparisons are not necessary valid.

4.1.5.1 Monocotyledons

Several studies on biogenic silica in grasses, in particular cereals, have been carried out and the literature on phytolith morphology for these plants is extensive (e.g. Mulholland and Rapp, 1992). However, quantitative data on the content of biogenic silica are available for only a few species (Bartoli and Souchier, 1978; Geis, 1978). In the present data set, grasses generally showed the highest content of biogenic silica, but there was considerable variation among grass species with *Poa alpina* yielding the lowest value (0.61%). In the literature *Poa secunda* is reported to contain 2.63% while *P. chaixi* only about 0.8% (Table 4.14). The values for *Calamagrostis villosa* are in the range of those reported in literature for this species (between 3.3 – 7.4%) (Table 4.1.4) and data from other species in the same genus are also in the same range: *Calamagrostis rubescens* 3.29%, *C. inexpansa* 3.8% and *C. epigeios* 4 – 6.3%. The biogenic silica in the samples of *Festuca halleri* and *F. puccinellii* was around 3%. Variability in biogenic silica content has been documented for this genus: *Festuca idahoensis* 3.59%, *F. scabrella* 3.15%, *F. rubra* 2.82% and *F. sylvatica* 0.7 – 1.1% (Table 4.1.4).

Sedges (*Cyperaceae* family) can be an important constituent of alpine pastures and grasslands. There have been few investigations of silica content of the above ground tissues of sedges, though these generally show that these plants are silica accumulators. The amount of biogenic silica deposited in sedge tissues is of the same order as that deposited in the grass tissues (e.g. *Carex atherodes* and *C. filifolia* 2.7%). In the present data set, *Carex sempervirens* contained about double the amount of biogenic silica as *C. curvula* (Table 4.1.4).

4A.1.5.2 Dicotyledons

The biogenic silica extracted from the dicotyledon specimens was substantially lower than that from the monocotyledons (mean of leaves and wood = 0.1%). The highest value was found in *Calluna vulgaris*, which accumulated up to 0.68% of its dry weight, and even higher values (up to 1.7%) have been reported in the literature (Table 4.1.4). The other *Ericaceae* specimens from the studied collection contained much less silica, (*Loiseleuria procumbens* 0.23% and *Vaccinium myrtillus* 0.04%) but higher values (0.1 – 0.3%) have been reported for the latter species (Table 4.1.4). The content in *Alnus viridis* (0.13%) and *Salix herbacea* (0.04%) was low. An extremely wide range of opal silica content has been reported for arborescent dicotyledons belonging to different families (43 species) of temperate regions (between 0.01% and 8.8%, see Table 4.1.4). The herbaceous dicotyledons considered in this study (*Alchemilla pentaphylla*, *Geum montanum*, *Leontodon helveticus*, *Veronica bellidioides*) seem to exclude silicon. The low silica content (0 – 0.11%) and small biomass of these plants mean that they make an extremely limited contribution to the input of particulate biogenic silica to the soil. In general, herbaceous dicotyledons have been reported to contain on average less than 1% of silica (Jones and Handreck, 1967), significantly less than monocotyledons.

4.1.5.3 Conifers

Larix decidua and *Picea abies* accumulated about ten times the weight of silica than the other conifers analysed. The percentage reported elsewhere for samples of *Larix* needles range from 1% to 2.21% (Klein and Geis, 1978; Hodson and Sangster, 1999) and values between 0.3% and 3.7% were reported for bulk-age populations of needles of *Picea abies* (Table 4.1.4). Needles of *Picea abies* “pumila” and *P. abies* “diffusa” contained between 2.78% and 2.35% of opal silica (Hodson *et al.*, 1996). In three other species of the same genus (*P. rubens, P. mariana* and *P. glauca*) the percentages of silica in needles ranged from 0.43% to 1.05% (Klein and Geis, 1978). The degree of needle mineralisation in *Picea* is age related. One year-old needles of *P. abies* contained only 0.14% of silica, but an increasing quantity is recorded even within the same growing season (Wyttenbach *et al.*, 1991). In *P. glauca* the accumulation of silica in needles increased with age from 0.37% (for "zero year-old" needles) up to 1.95% (for 5 years-old needles) (Hodson *et al.*, 1996). This variability should to be taken into consideration when data from needles of different age classes are compared.

The samples of needles from *Pinus cembra* and *P. mugo* contained little biogenic silica (0.13% and 0.10%). For comparison, the silica content of several species of this genus has been shown to range from 0.05% to 1.09% (Klein and Geis, 1978). The content of silica extracted from the needles of different juniper species is similar. In this study, *Juniperus nana* contained 0.08%, while it is reported in the literature that *J. communis* contained 0.04% (Hodson *et al.*, 1996) and *J. virginiana* 0.1% (see reference in Table 4.1.4). The value obtained for *Abies alba* (0.06%) is significantly lower than those reported for other species of the same genus. Needles of *A. balsamea* and *A. fraseri* contained 0.182% and 0.129% (Klein and Geis, 1978) while four other *Abies* species had opal silica percentages ranging from 0.12 to 0.84% (Hodson *et al.*, 1996).

The opal silica content of the needles in this study was always higher than for wood. *Pinus elliotti* and *Juniperus virginiana* are the only conifers for which it has been possible to find data in the literature on the opal silica content of wood (Table 4.1.4). The values are similar to the ones found in the samples of *Pinus* and *Juniper* wood analysed in this study.

Table 4.1.4. Published data on percentages content of biogenic silica in some Angiosperms and Gymnosperms

Taxonomic group	Species	Tissue	Biogenic Silica % of dry weight	Authors
<u>Monocotyledons</u>	*Calamagrostis epigeios* (L.) Roth.	above ground parts	4 - 6.3	1)
	Calamagrostis inexpansa Gray	"	3.80	2)
	Calamagrostis rubescens Buckley	"	3.29	2)
	Calamagrostis villosa (Chaix.) Gmelin	"	3.3 - 7.4	3)
		"	5.90	present paper
	Carex atherodes Spreng.	"	2.71	2)
	Carex curvula All.	"	0.96	present paper
	Carex filifolia Nutt.	"	2.76	2)
	Carex sempervirens Vill.	"	2.29	present paper
	Festuca halleri All.	"	3.27	present paper
	Festuca idahoensis Elmer	"	3.59	2)
	Festuca puccinellii Parl.	"	2.96	present paper
	Festuca rubra L.	"	2.82	2)
	Festuca scabrella Thurb.	"	3.15	2)
	Festuca sylvatica (Pollich) Vill.	"	0.7 - 1.1	4)
	Poa alpina L.	"	0.61	present paper
	Poa chaixi Vill.	"	0.7 - 0.9	3)
	Poa secunda J. S. Presl	"	2.63	2)
<u>Dicotyledons</u>	*Alnus viridis* (Chaix) DC	leaves	0.13	present paper
	Calluna vulgaris L.	"	0.68	present paper
		"	0.3 - 1.7	3)
		"	0.4 - 0.6	4)
	Vaccinium myrtillus L.	"	0.04	present paper
		"	0.1 - 0.3	3)
	Salix herbacea L.	"	0.04	present paper
	Salix spp.	"	0.5	2)
	36 deciduous trees and shrubs	"	0.01 - 3.79	5)

	7 deciduous tree species [a]	"	0.9 - 8.8	6)
Coniferae	*Abies alba* Miller	needles	0.06	present paper
	Abies balsamea (L.) Mill	"	0.182	7)
	Abies fraseri (Pursh.) Poir,	"	0.129	7)
	Abies grandis (Douglas) Lindley	"	0.84	8)
	Abies mariesii Mast.	"	0.12	8)
	Abies nordmanniana (Steven) Spach	"	0.39	8)
	Abies procera Rehder	"	0.93	8)
	Juniperus communis L.	"	0.04	8)
	Juniperus nana Willd.	"	0.08	present paper
	Juniperus virginiana L.	needles and wood	0.10	9)
	Larix decidua Mill.	needles	1.09	present paper
		"	1.372	7)
		"	2.21	8)
		"	0.9 - 1.0	3)
	Picea abies (L.) Karsten	needles	0.85	present paper
		"	0.3 - 3.7	3)
		1 year old needles	0.1423	10)
	P*icea abies* "pumila"	needles	2.35	8)
	Picea abies "diffusa"	"	2.78	
	Picea glauca (Moench.) Voss	"	1.048	7)
		0 year old needles	0.37	8)
		5 years-old needles	1.95	
	Picea mariana (Mill.) B. S. P.	needles	0.168	7)
	Picea rubens Sarg.	"	0.434	7)
	Pinus (12 species) [b]	"	0.01 - 0.73	8)
	Pinus banksiana Lamb.	"	0.184	7)
	Pinus cembra L.	"	0.11	present paper
		wood	0.02	present paper
	Pinus clausa Vasey	needles	0.43	11)
	Pinus elliotti Engelm	wood	0.025	9)
	Pinus mugo Turra	needles	0.01	present paper
		wood	0.07	present paper
	Pinus palustris Mill	needles	1.09	11)
	Pinus resinosa Ait.	"	0.83	7)
	Pinus strobus L.	"	0.085	7)

Pinus sylvestris L.	"	0.05-0.1	3)
	"	0.183	7)

([a]) *Quercus alba* L., *Acer saccharum* Marsh. , *Fagus grandifolia* Ehr., *Ulmus rubra, Tilia americana* L., *Fraxinus americanus* L., *Celtis occidentalis* L.; ([b]) *Pinus armandii* (Cheng & Law) J. Silbe, *P. contorta* Loudon, *P. cooperi* Blanco , *P. flexilis* James, *P. jeffreyi* Grev. & Belf, *P.koraiensis* Sieb. & Zucc., *P. parviflora* Sieb. & Zucc. , *P. peuce* Grieseb. , *P. pinea* ., *P. strobiformis* Engelm., *P. strobus L. "radiata", P. sylvestris L.*.

1) **Twiss, P. C., Suess E., and Smith, R. 1969.** Morphological classification of grass phytoliths. *Soil Science Society of America Proceedings*, **33:** 109-115. 2) **Bezeau, L. M., Johnston, A., and Smoliak, S. 1966.** Silica and protein content of mixed prairie and fescue grassland vegetation and its relationship to the incidence of silica urolithiasis. *Canadian Journal of Plant Science*, **43:** 625-631. 3) **Bartoli, F., and Souchier, B. 1978.** Cycle et rôle du silicium d'origine végétale dans les écosystèmes forestiers tempérés. *Annales des Sciences Forestières.*, **35:** 187-202. 4) **Bartoli, F., and Beaucire, F. 1976.** Accumulation du silicium dans les plantes vivantes en milieux pédogénetiques tempérés aérés. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Série D: Sciences naturelles*, **284:** 1947-1950. 5) **Geis, J. W. 1973.** Biogenic silica in selected species of deciduous Angiosperms. *Soil Science*, **116:** 113-119. 6) **Wilding, L. P., and Drees, L. R. 1971.** Biogenic opal in Ohio soils. *Soil Science Society of America. Proceedings*, **35:** 1004-1010. 7)**Klein, R. L., and Geis, J. 1978.** Biogenic silica in the Pinaceae. *Soil Science*, **126:** 145-156. 8) **Hodson, M. J., Williams, S. E., and Sangster, A. G. 1996**. *Silica deposition in the needles of the Gymnosperms. I. Chemical analysis and light microscopy. First European Meeting on Phytolith Research*, Madrid, 158. 9) **Lanning, F. C., and Eleuterius, L. N. 1983.** Silica and ash in tissues of some coastal plants. *Annals of Botany*, **51:** 835-850. 10) **Wyttenbach, A., Tobler, L., and Bajo, S. 1991.** Silicon concentration in spruce needles. *Zeitschrift für Pflanzenernährung und Bodenkunde*, **154:** 253-258. 11) **Kalisz, P. J., and Stone, E. L. 1984.** The longleaf pine island of the Ocala National Forest, Florida. A soil study. *Ecology*, **65:** 1743-1754.

4.1.5.4 Input and durability of biogenic silica particles in the soil

The estimate of the annual contribution of alpine plant communities stresses the importance of grasslands in the biocycle of silicon in the alpine and subalpine ecosystems. The average production of subalpine grassland communities (9.4 g m^{-2} y^{-1}) is about one order of magnitude higher than those of upper alpine grassland communities (1.3 g m^{-2} y^{-1}), heaths (0.69 g m^{-2} y^{-1}), shrub formations (0.47 g m^{-2} y^{-1}) and litterfall of conifer forests (1.6 g m^{-2} y^{-1}). These estimates were made with the intention of assessing the biogenic silica production in different plant communities and to explore possible implications for palaeoecological studies. To calculate the input of biogenic silica several approximations were applied. The lack of precise data about the ecology of the alpine communities yields significant uncertainty in the absolute measures of silica production. However, valid comparison can be made across plant communities. The difference in production between herbaceous and woody vegetation was about one order of magnitude. Comparable data of biogenic silica input from temperate ecosystems are extremely scarce. The predicted above ground biogenic silica input of mixed tall grasses communities at Trelease Grasslands (Illinois, USA) is 18 g m^{-2} y^{-1}

(Geis, 1978). For *Pinus sylvestris* woodlands has been calculated an input of only 0.2 ± 0.1 g m^2 y^{-1} of silica from needles and 0.1 g m^2 y^{-1} from wood (Bartoli, 1983). The same author estimated that a beech / fir / fescue community had a soil input of biogenic silica five times that of a Scots pine / blueberry / heath community (Bartoli and Beaucire, 1976). A comparison of the biogenic silica contained in grassland soils and adjacent forest soils (both Mollisols) in western Montana (USA) showed that the top horizons of soils dominated by *Festuca idahoensis* Elmer. contained three times the amount of opal of those of forest soils dominated by *Pseudostuga menziensii* (Mirbel) Franco (Bakeman and Nimlos, 1985).

In the present estimates, only the contribution of the above ground phytomass is considered due to the lack of data on below ground productivity. This omission will inevitably lead to an underestimate of the total input. Webb and Longstaffe (2000) estimated that roots and rhizomes contained up to 34% of the silica content of two perennial grass species. However, they argued that the time-integrated contribution of below ground tissues would be modest because of their low turnover rate in comparison with above ground tissues, which are regenerated each year. Nonetheless, it cannot be ruled out that other species may contribute significantly to the input of biogenic silica into the soil through below ground tissues.

Although the theoretical input of biogenic silica by a plant community can be estimated, the phytoliths released into the soil undergo taphonomic processes that must be taken into consideration when the technique is used for the investigation of the fossil record. The biocycle of silicon is complex and its discussion goes beyond the purposes of this work. Nevertheless, some very general considerations relevant for the alpine plant-soil ecosystems can be outlined. The stock of phytoliths present in the soil seems to be mainly determined by dissolution and translocation (Alexandre *et al.*, 1997).

Dissolution: a fraction of the biogenic silica dissolves at the top of the soil profile where intense biological activity leads to the rapid mineralisation and humification of organic matter and to the dissolution of the more soluble phytoliths. The soluble silica is then taken up and recycled by the vegetation, or it is leached from the soil profile in the groundwater. The factors that control the dissolution rate of phytoliths are barely understood and experimental evidence is scarce. One set of factors is related to their intrinsic properties including specific surface area, Si/Al ratio and hydration state (Bartoli and Wilding, 1980; Bartoli, 1985; Hodson and Sangster, 1999). The life span of particulate opal silica in the soil is also determined by soil-plant ecosystem characteristics, including the physical, chemical and biological processes active in the soil (Bartoli and Souchier, 1978). In different ecosystems the estimated turnover rates of biogenic silica are very variable (e.g. Alexandre *et al.*, 1997; Meunier *et al.*, 1999). In a broad-leaved temperate forest ecosystem (beech forest on acid brown soil) 85% of the soluble silica available in the soil was derived from the dissolution of opal silica but only 15% in a coniferous forest on humus-ferruginous podzol (Bartoli, 1983). In alpine soils, the biogenic silica turnover may decrease with increasing altitude as a consequence of reduced biological activity. The range of soil pH in this study (4.5 to 5.5) is considered to be favourable to the preservation of biogenic silica. For example, under experimental conditions, the solubility of synthetic silica gel in water was constant between pH 2 and 8 but it increased at higher pH (Iler, 1979).

Translocation: the fraction of biogenic silica that did not undergo dissolution is stored in the soil profile. It forms a pool of phytoliths with a lower turnover which tend to be translocated downwards to the bottom of the soil (Alexandre *et al.*, 1997).

4.1.6 Conclusions and suggestions for future research

The potential of phytoliths as a palaeoecological tool is principally associated with their ubiquity and durability in Quaternary sediments (e.g. Piperno, 1988; Alexandre *et al*., 1997), soils (e.g. Piperno and Becker, 1996; Madella, 1997; Alexandre *et al*., 1999) and buried soils (e.g. Inoue and Sase, 1996; Fredlund and Tieszen, 1997). The abundant production of biogenic silica by some of the dominant species in the subalpine plant communities (e.g. *Calamagrostis villosa, Carex sempervirens, Festuca* *scabriculmis, Calluna vulgaris, Larix decidua* and *Picea excelsa*) suggests that the application of phytolith analysis in palaeocological studies in subalpine-alpine environments could be a valuable exercise. Alpine soils developed on acidic bedrock present favourable conditions for phytolith preservation, with a slow turnover of biogenic silica creating a stable pool of phytoliths which could act as an archive of the past vegetation history. Production of opal silica in grassland communities is significantly higher than in woodlands, resulting in a higher input of biogenic silica to the soil. Moreover, the production of different phytolith morphologies in monocotyledon and trees/shrubs species could help in identifying diverse plant communities. The altitudinal fluctuations of the treeline during the Holocene at the transition between the alpine and the subalpine vegetation belts are currently under discussion in the context of global climatic change. Since the comparison of woodlands, heaths and grasslands plant-soil ecosytems is especially relevant in this ecocline the total content of biogenic silica in the soil should be regarded as a promising tracer for investigating the evolution of the vegetation in the Alps during the Holocene.

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4.2 Phytolith typologies and frequencies in subalpine-alpine plant species of the European Alps *

A. L. Carnelli, J.-P. Theurillat[2], M. Madella[3]

[1]Institut F.-A. Forel, Université de Genève, 10 route de Suisse, CH-1290 Versoix, Switzerland; [2]Centre Alpien de Phytogéographie, Fondation J.-M. Aubert, CH-1938 Champex, Switzerland and Laboratoire de Biogéographie, Département de Botanique et de Biologie végétale, Université de Genève, 1 ch. de l'Impératrice, CH-1292 Chambésy, Switzerland; [3]The Cambridge Phytolith Project, The McDonald Institute for Archeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, U.K.

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4.2.1 Abstract

Biogenic silica extracted from 21 species commonly occurring in subalpine and alpine plant communities in the central Swiss Alps were examined using light and SEM microscopes; 19 species being screened here for the first time. An inventory of phytolith typologies was supplied and typology frequencies were assessed. Light microscope photographs and SEM micrographs provided iconography of the typologies described. The monocotyledons analysed belonged to the genera *Calamagrostis, Festuca, Nardus, Poa,* and *Carex*. Monocotyledons yielded mainly types of epidermal origin (short cells, rods, cork cells, silicified stomata and trichomas).

Dicotyledons analysed were from five genera of the *Ericaceae* family (*Arctostaphylos, Calluna, Loiseleuria, Rhododendron, Vaccinium*) and from one genus of the *Betulaceae* (*Alnus*). In dicotyledons, silicified epidermal jigsaw cells, stomata complexes and vessels were recovered.

Conifer species of the genera *Abies, Juniperus*, *Picea, Pinus,* and *Larix* were studied. Distinctive conifer cells were mainly silicified endodermids and transfusion tissues. Phytolith taxonomic

diagnostic potential was tested by cluster analysis and principal component analysis. It was shown that grass and sedge species could be easily differentiated on the basis of phytolith typologies. In general, *Ericaceae* and conifers could also be distinguished on the basis of phytoliths, however, some species yielding mainly redundant typologies were not unequivocally identifiable.

4.2.2 Introduction

Opal-A is deposited in the tissues of many vascular plants. These deposits can be cast from the cells, from the infilling of the cell lumen, or by silicification of the cell walls (their shape resembling the outline of the original cell). The silicification can also be found as intercellular deposits in the interstitial vacuums (Carnelli et al., 2001). The term phytoliths is commonly employed to describe silicified cells, either isolated or in tissues. The initial interest in phytolith typology was focused on their diagnostic potential in plant taxonomy and phytoliths were observed in situ (Metcalfe, 1960). More recently, attention has been given to their applications in archeological and palaeoecological studies. Phytoliths released in soils, in sediments or in archeological sites, can be preserved and, eventually, analysed for palaeoecological reconstructions.

The morphology of phytoliths occurring in several crop species has been more extensively described because of its interest for archeological studies (Blackman, 1969; Whang et al., 1998; Rapp and Mulholland., 1992; Ball et al., 1999). In general, grasses were the plants usually chosen for study (Twiss et al., 1969; Blackman, 1971; Palmer, 1976), and only a few non-grass species naturally occurring in a temperate climate have been investigated (Geis, 1973; Klein and Geis, 1978; Bozarth, 1993).

Any attempt to interpret soil-borne phytolith assemblages should be based on a documented inventory relevant for the study area (Bozarth, 1993; Piperno, 1988). Data on species of the European Alps are not available, and we are aware of only one study of a mountain ecosystem, in the Caucasus (Blinnikov, 1994). This paper is the third of a series describing the screening of a set of 21 species occurring in the subalpine-alpine belts of the European Alps. In this paper, the morphology of phytoliths is described. The content of biogenic silica has been already assessed from the same plant material (Carnelli et al., 2001) and the diagnostic potential of aluminium presence in biogenic opal has been tested (Carnelli et al. 2002). The aim of the present work is to supply a screening of phytoliths of dominant alpine species on siliceous bedrock to provide a framework for phytolith-based palaeoecological studies at the treeline in the European Alps. Therefore, light microscopy and scanning electron micrographs are supplied for phytolith identification. In addition, we used cluster analysis and principal components analysis to test the hypothesis that taxonomic groups can be distinguished on the basis of phytolith typologies.

4.2.3 Methods

4.2.3.1 Laboratory procedures and samples

Phytoliths present in the above-ground tissues of 21 species commonly occurring on siliceous bedrocks in the subalpine and alpine vegetation belts in the Central Alps were analysed (Table 4.21). Plant material was collected in Val d'Arpette and at Furka Pass (Central Alps, Valais region, CH). Sampling and extraction procedures have been described elsewhere (Carnelli et al., 2001). The leaves and branches of woody species were analysed separately. Among the plants previously analysed for biogenic silica (Carnelli et al., 2001), species with very low biogenic silica content and rare identifiable phytoliths were not taken into account [i.e.: leaf material from *Alchemilla pentaphylla* L., (*Rosaceae); Geum montanum* L. (*Rosaceae); Leontodon helveticus* Merat (*Asteraceae); Salix herbacea* Vill. (*Salicaceae); Veronica bellidioides* L, (*Scrophulariaceae);* and leaf and wood from *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher, (*Ericaceae*)].

Silica bodies were observed and identified using a petrographic microscope equipped with phase contrast optic and polarised illumination at a magnification of x504 and x800 (oil immersion). Permanent microscope slides were mounted in EUKITT (mounting medium with refractive index of 1.5 at 20°C). A count of 500 identifiable phytoliths per slide was carried out whenever possible. For very poor samples a standardised scanning of three hours was performed. The number of phytoliths counted was on average 300. Non-idioblastic silica particles, such as intercellular deposits or fragments, were not included in the count. Whenever possible the typologies were described quoting the botanical terminology for the plant cells from which they originated (Fahn, 1974), or employing the terminology commonly used in phytoliths studies, and referring to their shape. In this study the phytoliths are identified by an acronym and an outline sketch (Table 4.2.2, Figure 4.2.1). Since several trichoma types are present, they are identified, for simplicity, as "TRI" followed by a number (Figure 4.2.1).

Light microscope photographs were taken using Kodak T MAX 400 asa professional film.

A fraction of the same extract used for light microscopy was spread with the help of a paint-brush on double sided tape, mounted on aluminium stub, coated with gold and examined in a JEOL JSM 6400 scanning electron microscope operating at 15 kV, at a working distance of 15 mm and live time of 50 s. SEM photographs were taken with Agfa Pan APX 100 asa professional film.

4.2.3.2 Cluster analysis and principal components analysis (PCA)

Cluster analysis and PCA analysis were employed to test if taxonomically related species could be identified and grouped on the basis of the presence and frequency of typologies (STATISTICA 4.5 F for Windows). Only loose single typologies were included in the statistical analysis, and fragments of tissues (skeletons) were not considered. In woody species the percentages of typologies were counted separately in leaf and wood tissues: for the analysis wood and leaf typology percentages were added together and the new sum normalised to 100%.

Table 4.2.1 List of species and plant tissues from which biogenic silica was extracted (L= leaves, C= culms, N= needles, W= woody branches). Plant samples were collected in Central Swiss Alps, if not specified in Val d'Arpette, otherwise: [a] Furka Pass.

Species	Plant tissue	Sampling sites altitude (m a.s.l.)
MONOCOTYLEDONS		
Gramineae		
Calamagrostis villosa (Chaix.) Gmelin.	L, C	1900
Festuca halleri All.	L, C	2730
Festuca melanopsis Foggi, Rossi & Signori [= *F. puccinellii* auct.]	L, C	2090
Festuca scabriculmis (Hackel.) Richter	L, C	2300
Nardus stricta L.	L	2300
Poa alpina L. [a]	L	2795
Cyperaceae		
Carex curvula All.	L, C	2470
Carex sempervirens Vill.	L, C	2300
DICOTYLEDONS		
Ericaceae		
Arctostaphylos uva-ursi Spreng.	L,W	2420
Calluna vulgaris L.	L, W	2420
Loiseleuria procumbens Desf.	L, W	2370
Rhododendron ferrugineum Linn.	L, W	2050
Vaccinium myrtillus L.	L, W	2180
Vaccinium vitis-idaea L.	L, W	1980
Betulaceae		
Alnus viridis (Chaix) DC	L, W	2000
CONIFERS		
Pinaceae		
Abies alba Miller	N,W	2050
Juniperus nana Willd.	N	1930
Larix decidua Miller	N, W	2050
Picea abies (L.) Karsten	N, W	2050
Pinus cembra L.	N, W	2050
Pinus mugo Turra	N, W	2050

For cluster analysis (Figure 4.2.2), Ward's method was applied (where the criterion of choice of linkage is the least increase in the sum of squared deviations from cluster means), and the algorithm of the Euclidean distance was used on normalised data (i.e. chord distance). However, in cluster analysis the ordination can be biased by the arbitrary choice of data transformation and linkage algorithms. To test the strength of the ordination obtained, additional tests were also run with square root transformed data and presence/absence data. For comparison PCA was also performed (Figure 4.2.3) on square root transformed data. Finally, to verify the robustness of the ordination, both clustering and PCA were run after adding similar typologies from all categories [respectively all trapezoids (TRA), all rod-like cells (ROD), all *Cyperaceae* conical types (CONE), all trichomas (TRI)].

4.2.4 Typology descriptions and frequencies

Line drawings of the typologies are displayed in Figure 4.2.1 and an explanation of the acronyms in the text is given in Table 4.2.2. Percentage presence of the typologies and SEM micrographs and light microscope are given in Table 4.2.3 and Plates I-III for monocotyledons, in Table 4.2.4 and Plates IV-V for dicotyledons, and in Table 4.2.5 and Plates VI-IX for conifers.

Descriptions of species typologies are divided into three sections: Monocotyledons, Dicotyledons (i.e. mainly *Ericaceae*) and conifers.

4.2.4.1 Monocotyledons (Table 4.2.3; Plates I-III)

The species examined belong to *Gramineae* and *Cyperaceae*.

Bulliform cells (BULL) occurred regularly in monocotyledons but in very low percentages. Rods were common in grasses but not unique to this family, excepting ROD BR that was distinctive of *Nardus stricta* (Plate I, 5-6). Trapezoidal typologies were unique to *Gramineae* (TRA, TRA L, TRA LOB, TRA O,TRA SB,TRA V, TRA CR; e.g.: Plate I, 2-4); other distinctive types were some trichoma types (TRI 2, TRI 5, TRI 7; e.g.: Plate II, 1, 11) and stomata complexes (STO GRA; Plate I, 10).

Distinctive *Cyperaceae* typologies were cones (CONE 1, CONE 2 etc.; Plate III, 13, 16), stomata complexes (STO CYP; Plate III, 13) and, trichoma type TRI 18.

Figure 4.1.1 Outline sketches of phytolith morphotypes

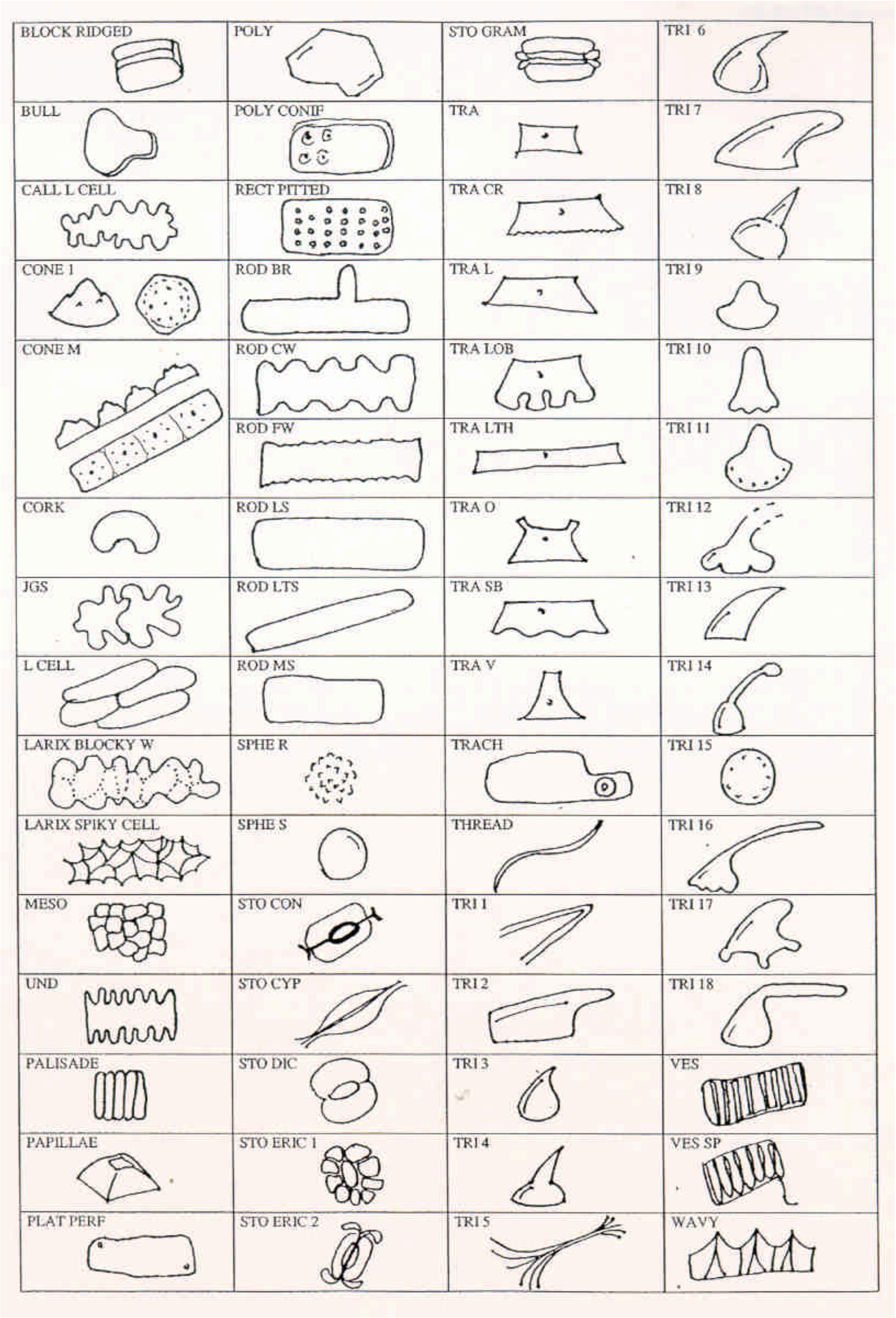


Table 4.2.2 Morphotype acronyms and description, anatomical origin (if known) and, available literature. Occurrence in plants from this data set is summarised as: M (monocotyledons), D (dicotyledons), and C (conifers). For diagnostic morphotypes the species or genus are listed. Outline drawings are in Figure 1.

Acronym	**Description**	**Occurrence in plant taxa**
BLOCK RIDGED	Block with a ridge in the middle, endoderm cells	*P. abies, P. mugo.*
BULL	Bulliform cells (Parry and Smithson, 1958b)	M.
CALL L CELL	Long cells with sinuous edge	*C. vulgaris, V. myrtillus, V. vitis-idaea, R. ferrugineum.*
CONE 1, CONE 2, CONE 3, CONE M	Cones smooth or with sculpturing, distinctive of sedges (Ollendorf et al., 1987, Metcalfe, 1971). Isolated or in skeletons of 2, 3 or more	*C. curvula, C. sempervirens.*
CORK	Cork cells	M.
JGS	Jigsaw epidermal cells	D, C.
L CELL	Epidermal long cells	M, D, C.
L CELL GRAINY	Epidermal long cells with grainy surface	D, C.
LARIX BLOCKY W	Irregular waved blocky, mesophyll cells	*L. decidua.*
LARIX SPIKY CELL	Mesophyll cells	*L. decidua.*
MESO	Mesophyll cells	M, D, C.
UND	Undulated hypodermal cells (Klein and Geis, 1978); (Bozarth, 1993);	*P. abies.*
PALISADE	Mesophyll palysade cells	*A. viridis.*
PAPILLAE	Microhairs	D, C.
PLAT PERF	Irregular rectangular with few pits	M, D, C.
POLY	Polyhedral cells	M, D, C.
POLY CONIF	Blocky polyhedrons transfusion cells often pitted (Klein and Geis, 1978); (Bozarth, 1993);	*A. alba, P. abies, P. cembra, P. mugo.*
RECT PITTED	Rectangular with many pits in rows	D, C.
Rods:		
ROD BR	Branched Rod cells (Parry and Smithson, 1958a)	*N. stricta.*
ROD CW	Rods long coarse wavy	M, *P. abies.*
ROD FW	Rods long smooth fine wavy	M, D.
ROD LS	Rods long smooth ("long cells" in Metcalfe, 1960)	M.
ROD LTS	Rods long thin smooth	M, D, C.
ROD MS	Rods medium smooth	M, D, C.
SPHE R	Spherical rugose	D, C.
SPHE S	Spherical smooth	M, D, C.
STO CYP; STO ERIC 1; STO ERIC 2; STO GRAM; STO CON; STO DIC	Stomata complexes, respectively: *Cyperaceae, Ericaceae, Gramineae*, conifer and, dicotyledon type	
TRACH	Tracheids	D, C.
Trichomas:		
TRI 1 / 18,	Trichomas, see Figure 1 for variants	See Tables 3-5.
THREAD	Monocellular thread-like, non segmented trichomas	M,C, D.
Trapezoids (short cell):		
TRA	Trapezoids ("short cells" in Metcalfe, 1960)	*Gramineae.*
TRA CR	Crenated based trapezoids	*Gramineae.*
TRA L	Long trapezoids	*Gramineae.*
TRA LOB	Lobated based trapezoids	*P. alpina, F. melanopsis.*
TRA LTH	Long thin trapezoids	*Gramineae.*
TRA O	Ornamented trapezoids	*Gramineae.*
TRA SB	Sinuous based trapezoids	*Gramineae.*
TRA V	Narrow, chimney-like trapezoids	*Gramineae.*

VES	Vessels	*A. viridis.*
VES SP	Vessels with spiral thickening	M, D, C.
WAVY	Ridge-like invaginations of the mesophyll	*L. decidua, P. abies.*

4.2.4.2 Gramineae (Plates I-II)

Epidermal cells: elements of silicified epidermis were common in aboveground tissues of grasses (Plate I, 8, 13-14; Plate II, 3-7). The most common typologies were "short cells" (Metcalfe, 1960), in the species examined here their general outline was trapezoidal (TRA), but several variants occurred (Figure 4.2.1). The length of trapezoids ranged from about 15µ for short trapezoids, to about 30 µ for long trapezoids, and width was about 10 µ. Trapezoids (TRA) diagnostic of grasses, were idiomorphic and well silicified (Plate I, 2-4, 7, 11; Plate II 2, 4-6, 13, 18). Short cells were among the first silica bodies to be described (Metcalfe, 1960), they were also defined as "hats" and "wavy-edged coastal rods" (Parry and Smithson, 1964), and as "nodular coastal rods" (Geis, 1978). Among the species examined here, trapezoids with a lobed base (TRA LOB; Plate I, 2-3) were dominant in *Poa alpina* (51%). Sinuous based trapezoids (TRA SB) were common in *Festuca melanopsis* (Plate II, 18)*, Calamagrostis villosa* and *Poa alpina* (Plate I, 11), respectively 50.4%, 27.4% and 23.9%.

Rod-like long cells (ROD) were sub-epidermal columnar or rectangular cells. They were recovered isolated or in skeletons in all grass species, with percentages from 0.2 to 11%. The terminations of rods could be broader or narrower (e.g. Plate I, 11; Plate II, 10). Rods were erratically filled with silica; the silicification may be complete or restricted to the cell walls. Rods varied in length (20-50 µ), in width (5-10 µ) and, in the extent to which the margins were sinuous (e.g. smooth, fine wavy, coarse wavy; see Figure 4.2.1). Projections corresponding to silicified pits may occur (Plate II, 8-9) (Hayward and Parry, 1975). Occasionally, rods presented concave ends in proximity of stomata (Plate I, 11). Branched rods (ROD BR; Plate I, 5-6; about 50 µ length) were unique to *Nardus stricta* (Parry and Smithson, 1958a), a small percentage (4%) was extracted either intact or fragmented. Cork cells were epidermal cells, crescent- or U-shaped (CORK; Plate II, 17; about 10 µ). They were completely silicified and ubiquitous in the different grass species (0.2 - 33.1%); in *Festuca halleri* cork cells had crenate outline due to tiny projections.

Fan shaped bulliform cells (BULL) occurred in the adaxial surface of the leaf blade, they were silicified mainly in old leaves (Parry and Smithson, 1958b); BULL were rare in the species examined (0.2-1.2 %).

Mesophyll cells: sponge-like mesophyll cells (MESO) were only occasionally silicified (0.2-1.4%).

Stomata: silicified stomata complexes (STO GRAM) were present in all grasses as epidermal fragments (silica skeletons) as well as isolated elements (25 μ). They were characterised by the presence of guard-cells having their lumen more constricted in the middle. Stomata in *Calamagrostis villosa* (4.9%; Plate I, 10) and *Festuca melanopsis* (4%; Plate II, 15) had subsidiary cells with spiky edges. In *Festuca scabriculmis* stomata constituted 29.4% of the total phytoliths extracted (Plate II, 14).

Trichomas: trichomas having their lumen partially or totally infilled with silica were commonly recovered in grasses (Plate I, 1, 9; Plate II, 1, 11-12). Tree trichoma types (TRI 2, TRI 5, and TRI 7) were unique to grass species in this data set.

4.2.4.3 Cyperaceae (Plate III)

Epidermal cells: the majority of phytoliths identified in sedges were conical (CONE; Plate III, 2-5, 7-8, 10-13). CONE types mainly occurred in the epidermal cells that overlay the sclerenchima occurring with the vascular bundles of the veins (Metcalfe, 1971; Ollendorf, 1992). From the front, a CONE appeared as a circle within a larger one, positioned on a pentagonal or hexagonal cell. From the side it was triangular. They were recovered as single elements (CONE 1) or arranged in groups of two or three, very common in *Carex sempervirens,* (CONE 2, CONE 3), or as many elements (CONE M), and frequently as skeletons of several elements. *C. sempervirens* and *C. curvula* presented CONEs with psilate (smooth) surfaces (Plate III, 11), and with sculpturing (Plate III, 4, 13). Surface ornamentation was not diagnostic; it consisted of small subsidiary cones (satellites), scattered or clustered on the apex or periphery of the CONE. In *C. curvula* CONE types were about 5 µm in diameter. *C. sempervirens* tissues were more extensively silicified, and CONEs were generally bigger (about 10 µm) with more marked ornamentation. From the side the psilate CONE could be confused with conical trichoma (TRI 9). CONEs were largely dominant in sedges, the different types totalling 47.2 % for *C. curvula* and 80.8 % for *C. sempervirens*.

Other epidermal cells were present in small percentages (ROD FW, ROD CW; Plate III, 12). The sum of ROD types was 10.8 and 3.1 %, for *C. curvula* and *C. sempervirens*, respectively. Rod shaped phytoliths were reported for various species of *Cyperaceae* (Ollendorf et al., 1987).

Stomata: in *Cyperaceae* paracytic silicified stomata complexes (STO CYP; Plate III, 6, 14, 17) had clearly defined elongated dome-shaped subsidiary cells lying parallel to the stomata pore. Silicified stomata (measuring about 45µ in length) were present in both species, although more frequently in *C. curvula* (13.9%), than in *C. sempervirens* (1.6%).

Other cells: rare silicified mesophyll cells (MESO) (about 10 µ) were present only in *C. sempervirens* (0.2%); trichomas were also rare, in all up to 4%). Polyhedrons (POLY; Plate III 2, 5) represented up to 24.7% of the phytolith production observed in *Carex curvula*, and were similar to the polyhedrons found in conifers, although they were generally smaller (about 30 µ) and never yield bordered pits.

4.2.4.4 Dicotyledons (Table 4.2.4; Plates IV-V)

The dicotyledons described here belong to the *Ericaceae* family, with the exception of *Alnus viridis* (*Betulaceae*). Studies of wild dicotyledons are scanty (Bozarth, 1992; Runge, 1997), and in particular the phytolith typology of *Ericaceae* has never been investigated. Phytoliths extracted from leaves and wood were examined separately. Stomata complexes were characteristic in the *Ericaceae* (STO ERIC 1, STO ERIC 2; Plate IV, 5-6, 14, 17; Plate V, 5, 10). TRI 11 was present only in *Loiseleuria procumbens* and *Vaccinium vitis-idaea* (1.3 and 0.3% respectively) and TRI 14 occurred only in *Calluna vulgaris* and *Vaccinium myrtillus* (1.1 and 0.2%, respectively). The typologies most commonly occurring in leaves and wood were jigsaw epidermal cells (JGS; Plate IV, 13; Plate V, 7) these typologies are very common in dicotyledons in general. Silicified vessels and vessels with spiral thickening (VES, VES SP; Plate IV, 12, 15-16; Plate V, 2) were also often recovered from leaf tissues, mainly in *Rhododendron ferrugineum* leaves (VESS SP, 20.6%), these types are not distinctive.

Epidermal cells: epidermal cells presented a wide morphometric variability. Two main groups were recognisable: cells with a sinuous outline (JGS and CALL L CELL) and cells with a polygonal outline (POLY). Silicified jigsaw epidermal cells were frequent (JGS; Plate IV 13; Plate V, 7) and typical of dicotyledon cells. This type is described as anticlinal by Piperno (1988). Cells with a similar shape, however, occurred in a very low percentage in other groups (e.g. conifers; Plate VII, 10). They were usually recovered as silica skeletons. The highest percentages were recorded in *Loiseleuria procumbens* and *Vaccinium vitis-idaea* leaves (56.2% and 45.6%).

Elongated and sinuous cells, probably of epidermal origin, (CALL L CELL; Plate V, 8) were present in *Calluna vulgaris* wood (12.3%; Plate IV, 8), *Vaccinium myrtillus* leaves (2.8%), *V. vitis-idaea* leaves (4.7%) and, *Rhododendron ferrugineum* leaves (12.8%). Polyhedral cells (POLY) do not present distinctive morphological features, they are formed by fragments of silicified tissues of various istological origin. POLY are common in leaves (6.6% - 85.3%) and form most of the phytoliths in wood (from 52.7% -97.9%). These typologies were dominant in *Alnus viridis* leaves and wood (55.9% and 72.3%).

Mesophyll cells: mesophyll cells (MESO) were only occasionally silicified in *Ericaceae* leaves (0.5-0.7%; Plate IV, 2, 9; Plate V, 6, 12). In *Alnus viridis* palisade mesophyll cells (PALISADE; 2.4%) were present.

Stomata: each stomata type (STO ERIC 1, STO ERIC 2; Plate IV, 5-6, 14, 17; Plate V, 4-5, 10) may constitute up to 32.7% of phytoliths in leaves of the *Ericaceae,* and added together up to 65.4% in the leaves of *Vaccinium myrtillus.* They were also present in woody branches of most of the *Ericaceae* examined (0.4% to 23.5%). *Calluna vulgaris* and *Rhododendron ferrugineum* had similar stomata complexes consisting of many neighbouring cells which had no distinctive shape (STO ERIC 1) (this type also occurred in other *Ericaceae* species). The stomata complex may be covered by silicified cuticle. In *R. ferrugineum* stomata were generally bigger (30 μm) than in *C. vulgaris* (20 μm). In the genus *Vaccinium* the stomata apparatus consisted of a pair of guard cells with single subsidiary cells on each side placed parallel to the pore. In *Vaccinium myrtillus* the stomatal edge had a double polar T-piece (STO ERIC 2; Plate IV, 14).

Trichomas: in the species examined, several trichoma types (TRI, Table 4.4.4) were regularly present in leaves although each usually showed low frequency (less than 2%). Only in *C. vulgaris* (total sum 14.5%) and *R. ferrugineum* (total sum 19.3%) were trichomas more abundant while in the remaining heaths trichomas were less common (total from 2.7 to 6.5%). Trichomas typical of *Ericaceae* were TRI 11 and TRI 14. In *Calluna vulgaris* surface hairs were simple uniseriate silicified hairs (THREAD, 26.7%; Plate V,11). Arrow tip-like hairs (TRI 14) were present in this species (1.1%), and in *Vaccinium myrtillus* (0.2%). TRI 11 was present with low frequency in *Loiseleuria procumbens* (1.3%) and *Vaccinium vitis-idaea* (0.3%).

Vascular elements: vascular elements (VES, VES SP) were present in *Ericaceae* leaves (Plate IV, 3, 4, 15, 16) and wood (Plate IV, 7-8, 11-12). VES SP were frequent in *Rhododendron ferrugineum* leaves (20.6%), but seldom in the leaves of the other *Ericaceae* studied (up to 1.8%).

Wood: the most common typologies occurring in wood of *Ericaceae* were not idioblastic. Indeed, POLY were always more than 50%; other common typologies were JGS (in *A. uva-ursi*, 14%; *V. vitis-idaea*, 28.6%; *R. ferrugineum*, 20.6%), and stomata (STO) (*A. uva-ursi*, 15.7%; *V. vitis-idaea*, 17.6%; *R. ferrugineum*, 23.5%).

4.2.4.5 Conifers (Table 4.2.5; Plates VI-IX)

Needle and wood phytoliths were examined separately. The typologies most frequently recovered were not idioblastic, they had a polygonal outline and were of variable size (POLY; e.g.: Plate VI, 10-12). It must be stressed that this typology although not distinctive of conifers was however, the dominant type produced. Indeed, POLY were common in needles (4.4-87.2%), and dominant in wood (91.7-99.7%). In woody tissues, distinctive typologies were rare, nevertheless the abundance of POLY typologies is itself characteristic of wood. Distinctive types in conifers were recovered mainly from needles. Silicified tranfusion cells (POLY CONIF) were common in *Pinus mugo* needles (71.1%; Plate VI, 1-2, 5, 9) and present in needles of *Abies alba*, *Picea abies* and *Pinus cembra* (34.4, 12.3 and, 0.2%, respectively). Silicified endodermal cells (BLOCK RIDGED) occurring in needles were diagnostic of *Picea abies* (18%) and *Pinus mugo* (1%). *Larix decidua* could be distinguished on the basis of mesophyll tissues (LARIX BLOCKY W, 11.6%; Plate IX, 4-6, and, LARIX SPIKY CELL, 31.8%; Plate IX, 11). WAVY type (Plate IX, 1-2) was present only in needles of *Picea abies* and *Larix decidua* (12.6% and 20.9%). Conifer stomata (STO CON; Plate VII, 6) were present with low frequency (0.3% to 11.9%) in all species excepting *Pinus mugo*. UND type (hypodermal cells) were typical of *Picea abies* (33% in needles).

Epidermal cells: in conifers, cells in the inter-stomata files were elongated with smooth edges, similar to grass epidermal cells, albeit generally bigger in size. These cells, once fragmented, were likely to produce fragments with a polygonal outline (POLY) (Plate IX, 7-9). *Juniperus nana* needles contained abundant POLY (Plate VIII, 7-11), probably in part also of epidermal origin. In this species POLY had a grainy aspect when observed under a light microscope, and, when observed at SEM, the surface appeared covered by many small spheres that could be either attached to the external surface or loose (Plate VIII, 6, 11).

Hypodermal cells: *Picea abies* needles yielded characteristic hypodermal cells, with rectangular outline and with mineralised cell walls undulated on the long side and straight on the short side (UND; Plate VII, 3, 7-9), finger-like projections may also occur.

Mesophyll cells: distinctive typologies were present in *Larix decidua* and *Picea abies* (WAVY; Plate IX, 1-2). These types were probably ridge-like invaginations of the mesophyll, which have been described elsewhere as "suspended bridge-like" (Blinnikov, pers. comm.) or "square netting-like fragments" (Rovner, 1971). WAVY type was also recovered in *Pinus sylvestris* (Klein and Geis, 1978), *Pinus banksiana* and *Picea glauca* (Bozarth, 1993). LARIX BLOCKY W types probably also originated from silicified mesophyll cells (Plate IX, 4-6). These cells were completely silicified, they had an undulating outline, grainy aspect and evident three-dimensional relief. LARIX SPIKY cells may be silicified mesophyll cells (31.8% in *L. decidua* needles).

Endodermal cells and Vascular elements. Ridged silicified endodermal cells were present in *P. abies* (BLOCK RIDGED, 18%). Conifers produced cubic to polyhedral blocky elements, consisting of well silicified transfusion elements, scattered or in pairs, often with bordered pits (POLY CONIF). Isolated or in skeletons, they were extremely abundant in *Pinus mugo* (71%; Plate VI, 1-2, 5, 9), less frequent in *Picea abies* (Plate VII, 11), *Abies alba, Pinus cembra,* and absent in *Larix decidua.*

Silicified rectangular platelets with pits (RECT PITTED; Plate IX, 3,10) were rare (up to 1.4% in *Pinus cembra* needles). They originate from transfusion cells and tracheary systems. RECT PITTED were identified in all conifer wood and needle samples except for *Larix decidua* and *Juniperus nana*. These typologies are also present in dicotyledons.

Stomata: silicified stomata (STO CON) were detected occasionally in needles. In *Picea abies* (Plate VII, 6), *Pinus cembra* and *Juniperus nana*, stomata made up about 10% of total typologies. No attempt was made to differentiate between species. Detailed descriptions of conifer stomata morphology are available elsewhere (Trautmann, 1953; Hansen, 1995).

Wood: silicified cells in conifer wood were mainly non-idioblastic polyhedrons (POLY; Plate VI, 10-12; Plate VIII, 2-4; Plate IX, 12). Other types occurring in wood were: POLY CONIF, RECT PITT, and PLAT PERF.

Table 4.2.3 Monocotyledon species: morphotypes counting as percentages and total number counted .

	Calamagrostis villosa	*Festuca melanopsis*	*Festuca halleri*	*Festuca scabriculmis*	*Nardus stricta*	*Poa alpina*	*Carex sempervirens*	*Carex curvula*
Morphotypes unique of monocotyledons								
BULL	1.2	0.4	0.2	0.4	0.4	0.9	0.2	1.5
CORK	11.4	0.2	17.2	16.9	33.1	6.6	0.4	-
STO GRAM	4.9	4	0.2	29.4	0.4	0.9	-	-
TRA	14	7.8	46.9	18.1	31.6	3.8	-	-
TRI 2	1.4	0.2	0.2	0.4	0.6	-	-	-
TRA LTH	0.6	2	0.9	0.2	-	3.4	-	-
ROD LS	4.7	1.4	0.2	-	0.2	0.2	-	-
TRA SB	27.4	50.4	2.1	-	0.6	23.9	-	-
TRA O	-	0.2	1.9	9.1	9.8	-	-	-
TRA L	-	4.2	3.5	0.2	-	0.2	-	-
TRI 7	5.5	2.4	1.2	-	-	-	-	-
TRI 5	0.4	0.2	-	-	-	-	-	-
TRA LOB	-	0.5	-	-	-	51	-	-
TRA V	-	-	2.8	2.2	-	-	-	-
CONE 1	-	-	-	-	-	-	15.5	8.9
CONE 2	-	-	-	-	-	-	36.9	25.9
CONE 3	-	-	-	-	-	-	13.5	2.7
CONE M	-	-	-	-	-	-	14.9	9.7
STO CYP	-	-	-	-	-	-	1.6	13.9
TRA CR	2.4	-	-	-	-	-	-	-
ROD BR	-	-	-	-	4	-	-	-
TRI 18	-	-	-	-	-	-	-	0.4
Morphotypes occurring in monocotyledons and dicotyledons								
ROD FW	-	1.4	2.1	3.6	0.2	0.9	3.6	1.2
TRI 1	0.4	2.2	1.9	0.2	2.5	1.7	-	-
TRI 3	6.7	0.7	-	0.2	0.2	0.6	0.6	-
TRI 4	-	0.2	0.7	4.4	-	-	0.6	0.4
TRI 16	-	4.7	0.2	-	-	0.4	0.4	0.8
TRI 15	0.2	0.9	0.2	-	-	-	-	0.8
TRI 6	-	0.9	0.2	-	-	0.2	-	-
TRI 17	-	-	0.7	0.4	0.4	-	-	-
TRI 12	-	-	0.2	-	0.2	0.2	-	-
TRI 8	-	0.2	-	-	-	-	-	0.8
TRI 13	-	-	0.5	4.6	-	-	-	-
TRI 9	-	-	-	-	-	-	-	0.8
TRI 10	-	-	-	-	-	-	-	0.4
Morphotypes occurring in monocotyledons and conifers								
ROD CW	5.3	7.4	9.0	9.5	11.0	1.3	7.0	1.9
Morphotypes occurring in monocotyledons, dicotyledons and conifers								
ROD MS	0.8	0.2	1.9	0.2	3.2	1.5	0.2	-
L CELL	2.2	6.9	0.2	-	0.4	1.3	2.8	5
POLY	-	-	3.7	-	0.6	0.8	1.4	24.7
ROD LTS	9.1	0.2	0.2	-	-	0.2	-	-
MESO	1.4	0.4	0.7	-	-	-	0.2	-
THREAD	-	-	0.2	-	-	-	-	-
PLAT PERF	-	-	-	-	0.2	-	-	-
SPHE R	-	-	-	-	-	-	0.2	-
VES SP	-	-	-	-	-	-	-	0.4
Tot. %	100	100	100	100	100	100	100	100
N.counted	507	552	431	497	471	469	502	259

Table 4.2.4 Dicotyledon species: morphotypes counting as percentages and total number counted ; L from leaves, W from wood.

	Arctostaphylos uva-ursi		*Calluna vulgaris*		*Loiseleuria procumbens*		*Vaccinium myrtillus*		*Vaccinium vitis-idaea*		*Rhododendron ferrugineum*		*Alnus viridis*
	L	W	L	W	L	W	L	W	L	W	L	W	L
Morphotypes unique of dicotyledons													
STO ERIC 1	8	15.7	27.4	-	0.8	0.4	-	-	-	-	2.9	23.5	-
STO ERIC 2	-	-	-	-	-	-	32.7	1.6	28.8	17.6	-	-	-
CALL L CELL	-	-	-	12.3	-	-	2.8	-	4.7	-	12.8	-	-
TRI 11	-	-	-	-	1.3	-	-	-	0.3	-	-	-	-
TRI 14	-	-	1.1	-	-	-	0.2	-	-	-	-	-	-
STO DIC	-	-	-	-	-	-	-	-	-	-	-	-	3.9
PALISADE	-	-	-	-	-	-	-	-	-	-	-	-	2.4
VES	-	-	-	-	-	-	-	-	-	-	-	-	0.3
Morphotypes occurring in monocotyledons and dicotyledons													
TRI 9	0.5	-	-	-	0.3	-	0.2	-	4.1	-	0.7	-	-
TRI 8	1.3	-	-	-	0.8	-	0.4	-	0.9	-	2.2	-	-
TRI 16	-	-	0.2	-	1.1	-	0.2	-	0.3	-	0.5	-	-
TRI 4	-	-	-	-	0.3	-	1.2	-	0.3	-	3.9	-	-
TRI 3	-	-	-	-	0.3	-	0.4	-	0.3	-	2.9	-	-
TRI 1	-	-	0.9	-	0.3	-	-	-	0.3	-	1.2	-	-
TRI 12	0.3	-	2.6	-	-	-	0.4	-	-	-	2	-	-
TRI 13	-	-	-	-	-	-	-	-	-	-	1.2	-	-
TRI 15	-	-	1.5	-	0.8	-	0.6	-	-	-	3.2	-	-
ROD FW	0.3	-	-	-	0.3	-	-	-	-	-	-	-	-
TRI 6	0.3	-	-	-	-	-	-	-	-	-	1	-	-
TRI 10	0.3	-	-	-	0.5	-	-	-	-	-	-	-	-
TRI 17	-	-	8.2	-	-	-	-	-	-	-	0.5	-	-
Morphotypes occurring in dicotyledons and conifers													
JGS	2.8	14.0	21.2	4.5	56.2	1.3	28.8	-	45.6	28.6	8.6	20.6	3.6
L CELL GRAINY	-	-	-	-	-	-	-	-	-	-	-	-	8.0
PAPILLAE	-	-	-	-	-	-	-	-	-	-	-	-	3.3
SPHE S	0.3	-	-	-	-	-	0.2	-	3.8	-	1.2	-	1.2
RECT PITTED	-	0.8	-	-	-	-	-	-	-	-	-	-	-
TRACH	-	-	-	-	-	0.4	-	-	-	-	-	-	-
Morphotypes occurring in monocotyledons, dicotyledons and conifers													
POLY	85.3	69.4	9.5	82.6	35	97.9	29	96.7	6.6	52.7	33.2	55.9	72.3
VES SP	0.8	-	-	0.3	1.6	-	1.8	-	1.6	-	20.6	-	-
MESO	-	-	0.7	-	0.5	-	-	-	0.3	-	1.2	-	2.4
PLAT PERF	-	-	-	0.3	-	-	-	1.7	0.3	1.1	-	-	-
TREAD	-	-	26.7	-	-	-	-	-	-	-	-	-	-
L CELL	-	-	-	-	-	-	0.8	-	-	-	-	-	1.5
ROD MS	-	-	-	-	-	-	0.2	-	-	-	-	-	0.3
SPHE R	-	-	-	-	-	-	0.2	-	-	-	-	-	0.3
ROD LTS	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Tot. %	100	100	100	100	100	100	100	100	100	100	100	100	100
N.counted	400	121	453	310	377	235	507	120	320	91	407	34	336

Table 4.2.5 Conifer species: morphotypes counting as percentages and total number counted ; N from needles, W from wood.

	Abies alba		*Larix decidua*		*Picea abies*		*Pinus cembra*		*Pinus mugo*		*Juniperus nana*
	N	W	N	W	N	W	N	W	N	W	N
Morphotypes unique of conifers											
POLY CONIF	34.4	0.4	-	-	12.3	-	0.2	-	71.1	0.8	-
STO CON	5.4	-	0.3	-	9.2	-	9.1	-	-	-	11.9
WAVY	-	-	20.9	-	12.6	-	-	-	-	-	-
BLOCK RIDGED	-	-	-	-	18.0	-	-	-	1.0	-	-
UND	-	-	-	-	33	-	-	-	-	-	-
LARIX SPIKY CELL	-	-	31.8	-	-	-	-	-	-	-	-
LARIX BLOCKY W	-	-	11.6	-	-	-	-	-	-	-	-
Morphotypes occurring in monocotyledons and conifers											
ROD CW	-	-	-	-	0.8	-	-	-	-	-	-
Morphotypes occurring in dicotyledons and conifers											
RECT PITTED	1.1	0.4	-	-	-	1.1	1.4	0.3	-	0.4	-
L CELL GRAINY	3.2	-	-	-	0.8	-	33.5	-	18.6	-	-
TRACH	11.8	-	4.8	-	-	-	4.4	-	3.2	-	-
PAPILLAE	6.5	-	-	-	2.7	-	3.0	-	-	-	-
SPHE S	1.1	-	-	-	-	-	-	-	0.2	-	-
JGS	-	-	1.6	-	-	-	-	-	-	-	-
Morphotypes occurring in monocotyledons, dicotyledons and conifers											
POLY	36.6	99.2	10.6	91.7	8.4	94.9	47.6	99.7	4.4	98.8	87.2
PLAT PERF	-	-	-	4.6	-	0.6	0.8	-	-	-	-
THREAD	-	-	6.8	-	2.3	-	-	-	0.2	-	-
L CELL	-	-	7.7	-	-	-	-	-	-	-	-
MESO	-	-	1.3	-	-	-	-	-	-	-	-
ROD MS	-	-	2.6	-	-	-	-	-	0.4	-	-
SPHE R	-	-	-	-	-	-	-	-	0.4	-	-
ROD LTS	-	-	-	-	-	-	-	-	0.2	-	-
VES SP	-	-	-	-	-	-	-	-	0.2	-	-
Tot. %	100	100	100	100	100	100	100	100	100	100	100
N.counted	93	256	311	108	261	178	496	320	495	250	109

4.2.4.6 Clustering analysis and PCA

In the dendrogram shown in Figure 4.2.2 (Wards' method, Euclidean distance, normalized data) species are classified into two main clusters on the basis of phytolith frequency: the first cluster groups monocotyledons (grasses and sedges), and the second cluster groups dicotyledons and conifers. In the monocotyledon cluster, grasses were separated on the basis of short cells (TRA), bulliform cells (BULL), and stomata (STO GRAM). Among grasses, *Poa alpina* and *Festuca scabriculmis* were distinguished from other grasses because of the high frequency of TRA LOB, and STO GRAM, respectively. Within the monocotyledon cluster, *Carex* species were easily differentiated on the basis of CONE and STO CYP presence.

Dicotyledons and conifers were assigned to the same cluster, mainly because of redundant polyhedral typologies (POLY). However, two groups were differentiated: the first consisted of *Ericaceae* and, the second, of conifers and *Alnus viridis*. *Ericaceae* species were distinguished on the basis of the presence of the types STO ERIC 1, STO ERIC 2 and JGS. Conifers were grouped by distinctive types such as POLY CONIF. *Alnus viridis* was grouped with conifers rather than with *Ericaceae* because of the presence of epidermal long cells (L CELL GRAINY) and microhairs (PAPILLAE)**;** typologies absent in the *Ericaceae***.** It should be noted that *Larix decidua* yielded diagnostic typologies (LARIX BLOCKY W, LARIX SPIKY CELL) and that *Pinus mugo* was negatively differentiated from all conifers by the absence of silicified stomata (STO CON), and was characterised by the abundance of POLY CONIF. Thus, they were assigned to distinct branches of the cluster. The robustness of this classification was tested by using different data transformations (not transformed percentage data, root transformed data, and finally, with groups of similar typologies summed in one category, e.g. all trapezoids, not shown). No matter which transformation was applied, the two main clusters were maintained (monocotyledons, dicotyledons-conifers) and the classification of the monocotyledon cluster was unchanged. However, according to the transformation chosen, some species (*Juniperus nana, Alnus viridis* and *Pinus cembra*) were attributed differently within the second cluster.

Discrepancies were as follows. Normalised (Figure 4.2.2) and root transformed data (not shown) gave the same results. If the analysis was run with non transformed percentages, results were unchanged but the cluster grouping *P. cembra, A. viridis* and *J. nana* showed a weak affinity with the Ericaceae. With presence/absence data, *Alnus viridis* and *Juniperus nana* were not well classified within a cluster, and showed only a weak affinity with conifer and *Ericaceae* groups, respectively. Finally, when data of similar typologies were combined in categories (non transformed percentage data; when several variants of a typology were present in a species, they were added together: i.e. all trapezoids, rods, cones, trichomas and polygonal) *P. cembra*, *A. viridis* and *J. nana* were attributed to the *Ericaceae* cluster.

In addition, when a test was run, keeping leaf and wood data separate (percentage data non transformed, Euclidean distance; not shown), the classification was similar but a further cluster, grouping all wood samples, was present. This cluster showed an affinity between wood samples and samples from conifers needles of *J. nana* and, *Ericacea*e leaves of *A. uva-ursi* and *A. viridis*.

PCA classification is a multivariate ordination technique, employed here to examine the degree of correspondence between typologies and taxa (Figure 4.2.3, Table 4.2.6). The first axis of the principal components analysis explains the majority of the variability (45%). Such a high percentage can be explained by the strong diagnostic power of short cells that are unique and largely dominant in grass species.

PCA run on square root transformed data confirmed the classification proposed by the cluster analysis: the species were divided into two main groups (monocotyledons and dicotyledons with conifers). *Carex* species were separate. If the PCA was run with similar typologies added together in categories (as was done for cluster analysis) the classification did not vary, but points were less scattered (not shown).

Figure 4.2.2 Dendrogram resulted from the clustering analysis (Ward's method, Euclidean distance, normalized data). The species are clustered on the basis of phytolith frequency. For the analysis leaf and woody phytoliths were added. Two clusters are individuated: monocotyledons and dicotyledons with conifers. The latter consists of two clusters: *Ericaceae* and conifers with *Alnus viridis*.

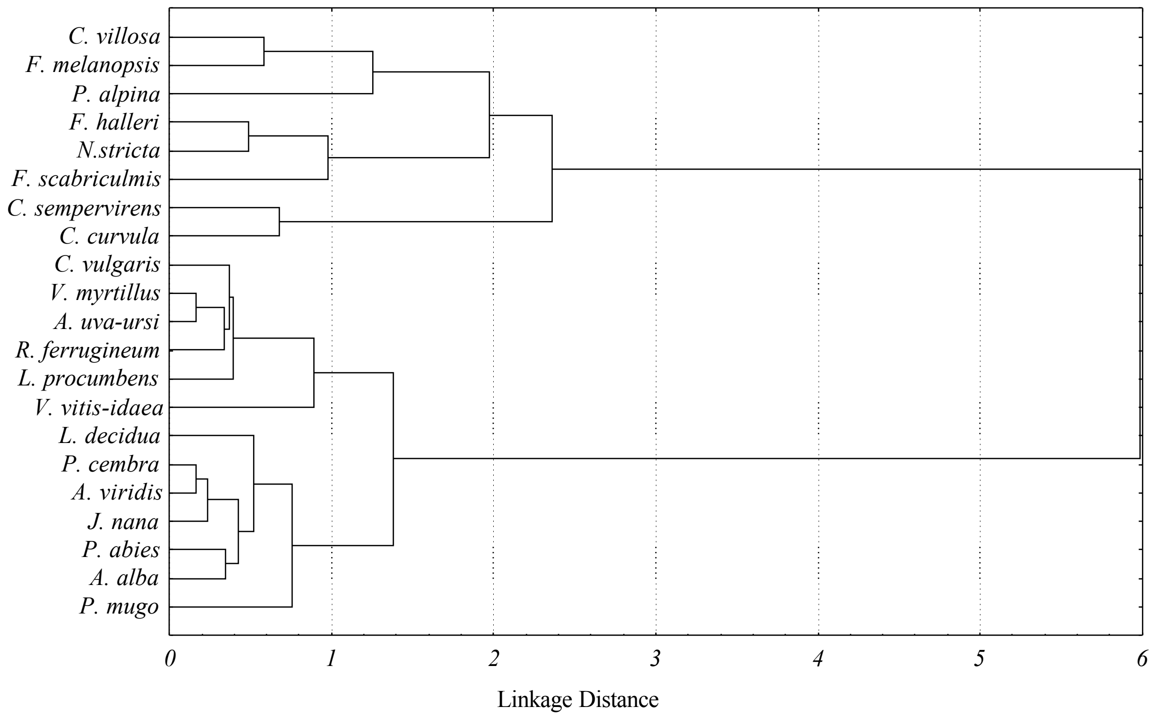
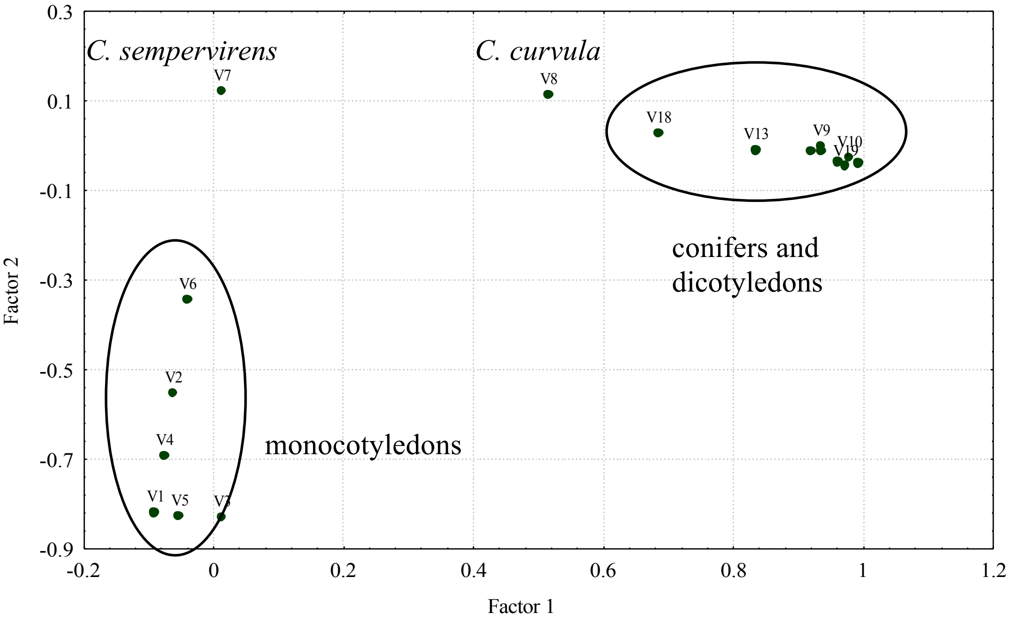


Figure 4.2.3 Scatter plot resulted from the PCA. Species are grouped on the basis of phytolith frequency. For the analysis leaf and woody phytoliths percentage were added. Two groups are individuated: monocotyledons and, conifers with dicotyledons; *Carex* species are isolated. Factor 1 explains 45% of variability of the data; Factor 2 explains 17%. PCA loadings are given in Table 6. Variables V11, V12 and V15 are grouped with V9; variables V14, V16, V17, V20, and V21 are grouped with V10 and V19.

Symbols :V1: *C. villosa,*V2: *F. melanopsis,*V3: *F. halleri,* V4: *F. scabriculmis,* V5: *N. stricta,* V6: *P. alpina,* V7: *C. sempervirens,* V8: *C. curvula,* V9: *C. vulgaris*,V10: *V. myrtillus*, V11: *R. ferrugineum,* V12: *L. decidua,* V13: *P. mugo*, V14: *P. cembra,* V15:*P. excelsa,* V16: *A. alba*, V17: *A. uva-ursi,* V18: *V. vitis-idaea,* V19: *J. nana,* V20: *A. viridis,* V21: *L. procumbens.*



4.2.5 Discussion

In this study, biogenic silica extracted from 21 species either dominant or abundant at the subalpine-alpine ecocline were examined to obtain an inventory of phytolith typologies. Of the 21 species, 19 were studied for the first time.

4.2.5.1 Monocotyledons

It is known that grasses and sedges yield typical phytoliths (e.g. (Twiss et al., 1969; Mulholland and Rapp, 1992; Ollendorf, 1992). A morphological classification for short cells related to grass taxonomy has beeen proposed (Twiss et al., 1969). This classification is based on the fact that short cell morphology is distinctive in three of the five subfamilies occurring in the world: *Festucoideaea, Panicoideae* and *Clorideae* the other two are *Arundinoideae* and *Bambusoideae*). All grasses examined here belonged to the *Festucoideae*, and produced only short cells of trapezoidal shape (TRA sensu lato). Present data confirmed that the genera of this subfamily could not be distinguished on the basis of short cell morphology. In this set of grass species, the only typologies that were characteristic at species level were branched rods (ROD BR) that were unique to *Nardus stricta* (Parry and Smithson, 1958a). However, it should be noted that lobate trapezoids (TRA LOB), although not diagnostic, were largely dominant in *Poa alpina*. CONES were characteristic of the *Cyperaceae* family. However, a study on modern phytolith assemblages of subalpine-alpine grasslands, showed that CONES are poorly preserved in soil (Carnelli, unpublished). *Gramineae* and *Cyperaceae* are known to produce a significant percentage of silicified above-ground tissues of dry plant mass; in a previous study, it was shown that subalpine and alpine grasses and sedges from the Central Alps produced between 0.6% and 5.6% of silicification of dry plant mass.

4.2.5.2 Dicotyledons

Phytolith studies often neglect wild dicotyledon species. The dicotyledons examined here belonged mainly to the *Ericaceae*. Species of this family are often dominant at the treeline, where they can form extensive heaths. We are aware of only one study mentioning the *Ericaceae*; it covers East African plants and discusses the species *Vaccinium stanley* (Runge, 1999). Subalpine-alpine heath species produced silicified cells mainly from the epidermis (JGS). These typologies are, however, commonly recovered in all dicotyledons. Distinctive stomata complexes (STO ERIC 1, STO ERIC 2) were present. The species studied accumulated low percentages of biogenic silica in leaves and wood, with a maximum value for *Calluna vulgaris*, in which silicified tissues were 0.68% of leaves' dry mass (Carnelli et al., 2001).

4.2.5.3 Conifers

Conifers are dominant in the subalpine forest and their contribution to phytolith assemblages cannot be neglected when investigating biogenic silica in plants at the treeline. A few species of conifers, mainly American, have been investigated (Klein and Geis, 1978), but data on European species are lacking: *Picea abies, Abies alba, Juniperus nana*, *Pinus cembra* and *Pinus mugo* were examined here for the first time.

In conifers, silicification was detected both in needles and in wood. Larch epidermal phytoliths, varying greatly in size and shape but very thin and fragile, were earlier described for *Larix laricina* (Du Roi) K. Koch and *Larix decidua* Mill. (Klein and Geis, 1978). Klein and Geis (1978) after examining 15 taxa of *Pinaceae*, stated that the identification of conifers was possible on the basis of tracheary elements, blocky polyhedrons and epidermal cells. However, on the basis of the present result, epidermal cells should not be taken as diagnostic, because they are similar to the long cells occurring in grass species, and fragmentation after deposition in the soil will make distinction impossible (Plate IX, 7-8).

Conifer specific phytoliths (POLY CONIF), produced in tranfusion tracheids and endodermal cells, were very frequent in *Pinus mugo*. This type was also mentioned by Klein and Geis (1978) although frequency was not assessed. The same typologies were extracted from conifer needles (*Abies balsamea, Picea glauca* and *Pinus banksiana*) and topsoils in boreal forest (Bozarth, 1993). Non-idioblastic polyhedral phytoliths (POLY) were dominant in woody tissues. However, being highly redundant, they did not add any relevant taxonomic information.

Among conifers, *Larix decidua* and *Picea abies* contained the highest proportion of biogenic silica (1.09 and 0.85% of dry mass, respectively) (Carnelli et al., 2001) and needles were extensively silicified, including epidermal tissues. In the remaining conifers, silicification was less extensive (about 0.01% of dry mass) and mainly endodermal cells were biomineralised.

4.2.5.4 Cluster analysis and PCA

Cluster analysis and PCA results only partially supported the hypothesis that taxonomically related species can be identified on the basis of typology presence and frequency. Indeed, while monocotyledon plants could be clearly identified, dicotyledons and conifers were less clearly separated. Both classification and ordination methods evidenced that the taxonomical power of phytoliths described here was limited for species yielding mainly redundant typologies such as *Juniperus nana, Alnus viridis* and *Pinus cembra.* These could not be unequivocally identified on the basis of phytoliths. In contrast, idioblastic typologies from key species may be diagnostic at family, genus or even at species level (e.g *Cyperaceae, Pinus mugo, Larix decidua, Calluna vulgaris*). However, it is important to stress that, in general, herbaceous and woody species could be identified, the former yielding diagnostic typologies, the latter being defined by some specific types and by the abundance of polyhedral phytoliths. This finding was relevant when applied to the study of assemblages of fossil phytoliths, e.g. in soils.

4.2.5.5 Potential relevance of phytoliths when studying the subalpine treeline

The subalpine-alpine ecocline is a transition zone of heathland, stunted trees and meadows that occurs above the timberline (i.e. the limit of rather closed forest with trees 6-8 m or taller). The present timberline in the Central Swiss Alps is located between 2000 and 2300 m a.s.l. However, its present elevation is largely anthropogenically determined (e.g. Theurillat et al., 1998, Carnelli et al. submitted, Tinner & Theurillat, submitted). Land use since the Neolithic period has resulted in an artificial extension downward of alpine meadows, both for grazing and timber exploitation. Therefore, the uppermost limit attained by the forest during the Holocene, and even the natural occurrence of alpine meadows and heathlands are debated issues. The history and dynamic of vegetation at the treeline was investigated mainly by means of pollen, plant macrorest and soil charcoal analysis (e.g.: Burga, 1991;1995; Tinner et al., 1996; Wick and Tinner, 1997; Talon et al., 1998; Carcaillet and Brun, 2000, Carnelli et al. submitted, Tinner & Theurillat, submitted). The analysis of soil-borne phytoliths may supply a new perspective in the reconstruction of the history of vegetation at the subalpine-alpine ecocline by enhancing the possibility of detecting taxa, such as monocotyledons, that are usually under-represented in palaeobotanical records. The high frequency of polyhedral cells (POLY) was characteristic of woody species (both heaths and conifers) and could be of interest for quantitative analysis of fossil assemblages. Trichomas (TRI s.l.) were abundant in monocotyledons and dicotyledons but absent in conifers. However, soil-borne phytolith assemblages were of limited use for palaeoecological reconstruction. (1) The diagnostic power of phytoliths was limited by the fact that similar typologies could, in some cases, be produced by plants of unrelated taxa. (2) The occurrence of a given typology in plant tissues did not guarantee that it would be found in soil assemblages, since a differential preservation of phytoliths may occur in soil (Bartoli and Wilding, 1980). (3) Yet the combination of qualitative (i.e. the inventory of typology frequencies) and quantitative (biogenic silica production) analysis may be a promising tool. It was shown in a previous study (Carnelli et al., 2001) that the heavily silicified above-ground tissues of grasses and sedges produce an annual biogenic silica input of 1.9 to 10.3 g m^{-2} in the subalpine and alpine meadows in the Central Alps. In comparison, the estimated annual production of biogenic silica from subalpine heaths would be between 0.19 and 1.13 g m^{-2}, i.e. about one order of magnitude smaller than the predicted input of meadows, as well as the annual input of biogenic silica of a *Larix decidua* subalpine forest (2.4 g m^{-2} y^{-1}) or of a *Picea excelsa* forest (0.7 g $m^{-2}y^{-1}$). Thus, the combination of quantitative analysis of biogenic silica production and the inventory of typology frequencies may provide an estimate of the potential frequency of typologies in soil assemblages (Carnelli et al., 2001) and the comparison with findings in soil should help towards a better understanding of the taphonomical processes phytoliths undergo.

In addition, the chemical composition of opal could be a valuable tool to source phytoliths lacking distinctive morphology: indeed, it was shown that the presence of aluminium in the reticule of biogenic silica was very frequent in woody species phytoliths but negligible in grass and sedge species (Bartoli and Wilding, 1980; Carnelli et al., 2002).

It should be noted that although conifers and dwarf shrubs produced low amounts of silica, phytoliths contained in persistant needles or leaves and in woody tissue persisted in the plant for several years. Therefore, they were less hydrated and often accumulated aluminium (Bartoli, 1985; Carnelli et al., 2002). For these reasons, once released in soil, they were likely to be better preserved than the more soluble phytoliths from yearly abscissed *Larix* needles or grass leaves.

4.2.6 Conclusions

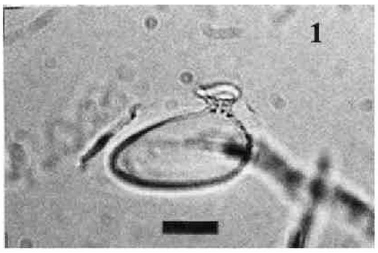
In this paper, descriptions of species and related typologies were grouped under three taxa: conifers, dicotyledons (mainly *Ericaceae*) and monocotyledons. Interestingly, this framework reflected the three main physiognomical units of vegetation at the subalpine-alpine ecocline: coniferous forests, alpine heathlands, (dominated by woody dicotyledons) and alpine meadows (dominated by monocotyledons). Our results showed that it was possible identify these three groups by using phytolith morphology to differentiate them, and that there was a rationale for the utilisation of phytolith soil fossils in order to study past interactions between these plant communities. Indeed, quantitative and qualitative analysis of biogenic silica in subalpine-alpine soils may give a record of past altitudinal fluctuations of woody versus herbaceous vegetation during the Holocene, triggered by variations of climate and/or by the impact of human activities. This is now a subject of general concern in view of the predicted climate modification which is very likely to have an enormous influence on high alpine ecosystems (Theurillat et al., 1998; Theurillat & Guisan, 2001). Information about past ecosystem fluctuations is essential in order to understand patterns of vegetation resistance and resilience and thus be able to forecast future ecosystem responses.

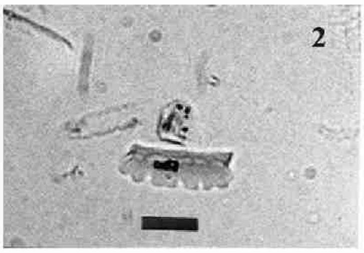
PLATE I

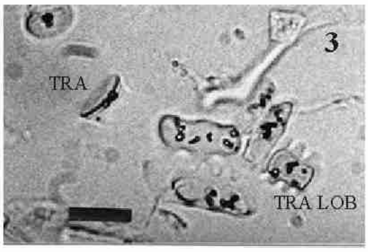
Gramineae. SEM micrographs of silicified tissues from plant leaves; * = light microscope photographs. Scale bar = 10 µm.

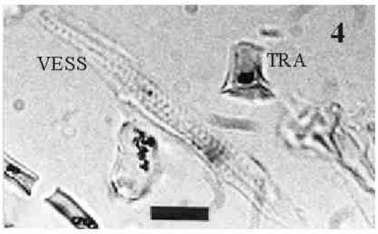
1. *Poa alpina*, trichoma.*
2. *P. alpina*, TRA LOB. *
3. *P. alpina*, TRA, TRA LOB. *
4. *P. alpina,* TRA V, VESS. *
5. *Nardus stricta*, ROD BR.
6. *N. stricta*, ROD BR. *
7. *N. stricta*, TRA. *
8. *N. stricta*, skeleton ROD CW, STO GRAM. *
9. *N. stricta*, TRI 2.*
10. *Calamagrostis villosa*, STO GRAM. *
11. *C. villosa*, TRA CW, ROD MS. *
12. *C. villosa*, EL CELL. *
13. *C. villosa*, ROD FW.
14. *C. villosa*, ROD CW.
15. *C. villosa*, ROD FW.

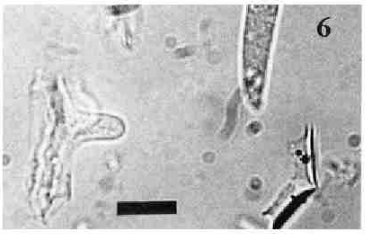
PLATE I

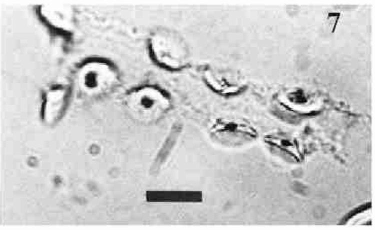


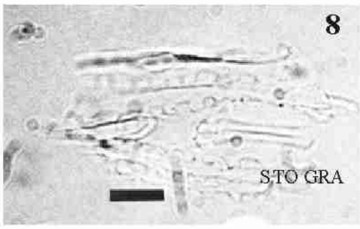


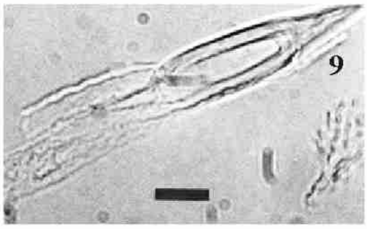


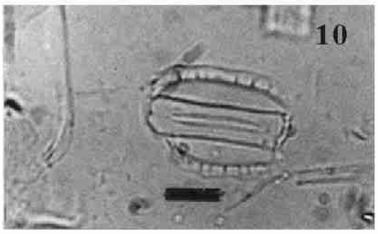


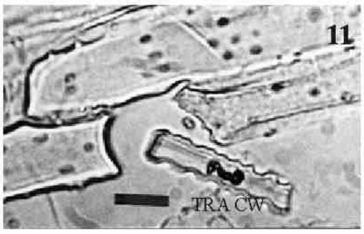


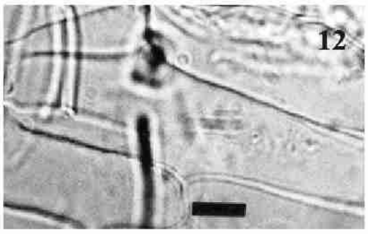












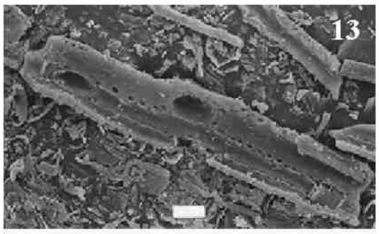
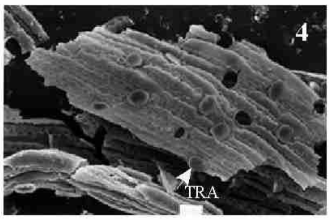


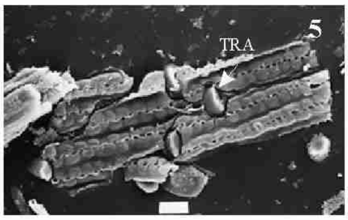
PLATE II

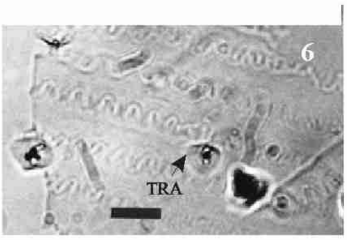
Gramineae. SEM micrographs of silicified tissues from plant leaves; * = light microscope photographs. Scale bar = 10 µm.

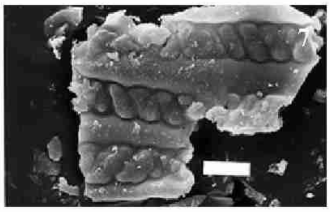
1. *Festuca halleri*, TRI 7.
2. *F. halleri*, ROD LS, TRA SB.
3. *F. halleri*, ROD CW, STO GRAM.
4. *F. halleri*, ROD FW, TRA.
5. *F. halleri*, ROD CW, TRA.
6. *F. halleri*, ROD CW, TRA. *
7. *F. halleri*, skeleton.
8. *F. halleri*, ROD FW with spiny projections. *
9. *F. halleri*, ROD FW.
10. *F. halleri*, ROD CW.
11. *F. halleri*, TRI 4
12. *Festuca scabriculmis*, TRI 2. *
13. *F. scabriculmis*, TRA V. *
14. *F. scabriculmis*, STO GRAM. *
15. *Festuca melanopsis*, STO GRAM.
16. *F. melanopsis*, ROD CW. *
17. *F. melanopsis,* CORK. *
18. *F. melanopsis,* TRA SB. *

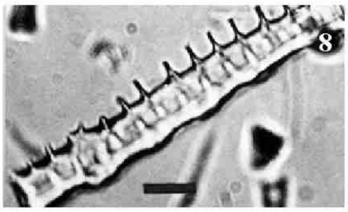
PLATE II

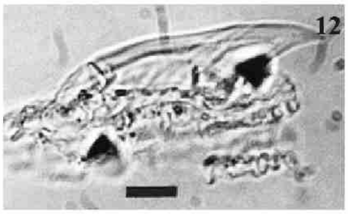


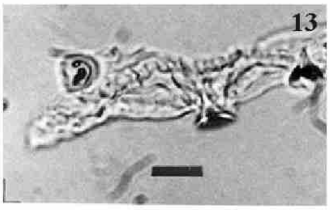


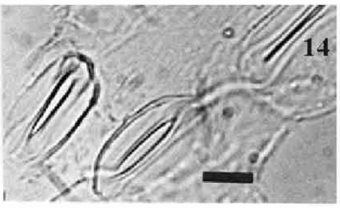


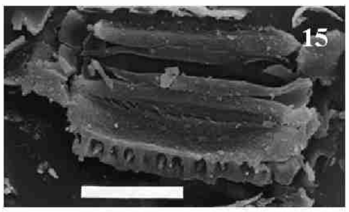


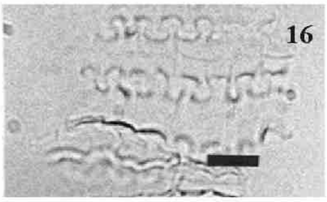


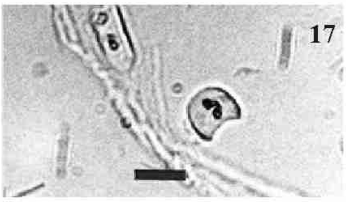












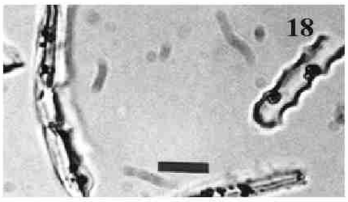
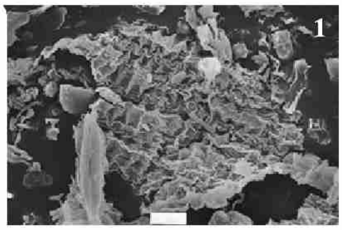


PLATE III
Cyperaceae. SEM micrographs of silicified tissues from plant leaves; * = light microscope photographs. Scale bar = 10 µm.

1. *Carex curvula*, ROD CW.
2. *C. curvula*, CONE M.
3. *C. curvula*, CONE M.
4. *C. curvula*, CONE 2.
5. *C. curvula*, ROD LS.
6. *C. curvula*, STO CYP.
7. *C. curvula*, CONE M, side view. *
8. *C. curvula*, CONE M, top view. *
9. *C. curvula*, STO CYP. *
10. *Carex sempervirens*, ROD CW.
11. *C. sempervirens*, CONE 2, CONE 3.
12. *C. sempervirens*, ROD FW.
13. *C. sempervirens*, CONE 2.
14. *C. sempervirens*, STO CYP.
15. *C. sempervirens*, CONE 3. *
16. *C. sempervirens*, CONE 2. *
17. *C. sempervirens*, STO CYP. *

PLATE III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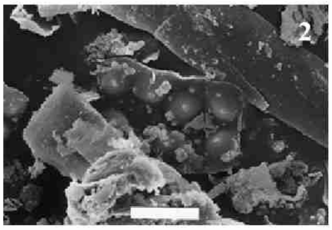
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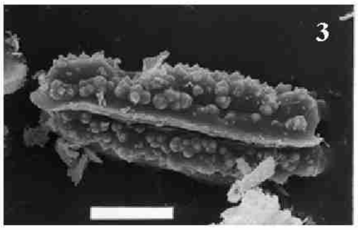
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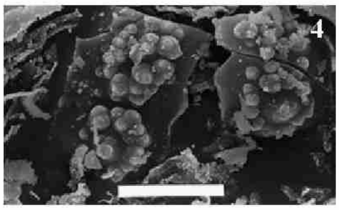
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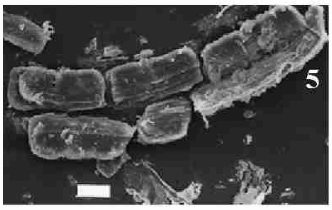
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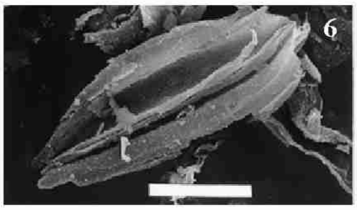
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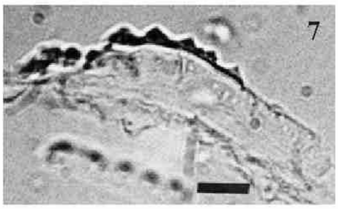
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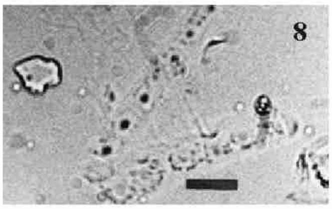
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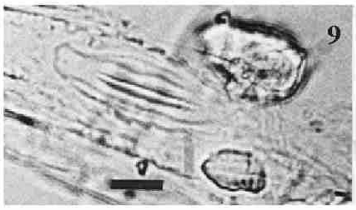
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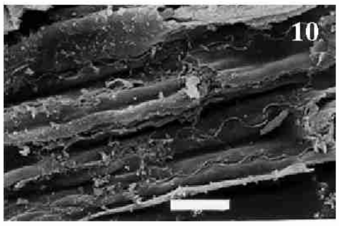
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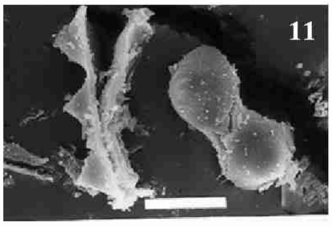
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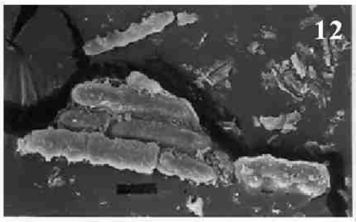
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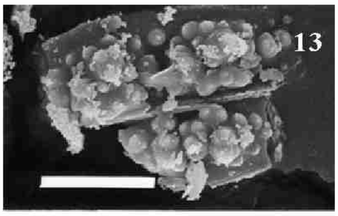
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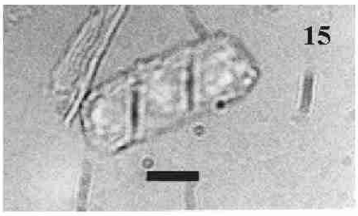
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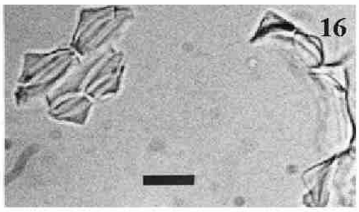
16


17

PLATE IV

Ericaceae. SEM micrographs of silicified tissues from plant tissues (L= leaves, W= wood); * = light microscope photographs. Scale bar = 10 µm.

1. *Rhododendron ferrugineum* (L), unknown.
2. *R. ferrugineum* (L), MESO, VESS SP.
3. *R. ferrugineum* (L), TRACH.
4. *R. ferrugineum* (L), VESS SP.
5. *R. ferrugineum* (L), STO ERIC 1. *
6. *R. ferrugineum* (L), STO ERIC 1.
7. *R. ferrugineum* (W), POLY.
8. *R. ferrugineum* (W), POLY.
9. *R. ferrugineum* (W), MESO.
10. *Vaccinium vitis-idaea* (W), POLY.
11. *V. vitis-idaea* (W), POLY.
12. *V. vitis-idaea* (W), VESS. *
13. *Vaccinium myrtillus* (L), JGS. *
14. *V. myrtillus* (L), STO ERIC 2. *
15. *V. myrtillus* (L), VESS. *
16. *Arctostaphylos uva-ursi* (L), VESS.
17. *A. uva-ursi* (L), unknown.
18. *A. uva-ursi* (L), unknown.

PLATE IV

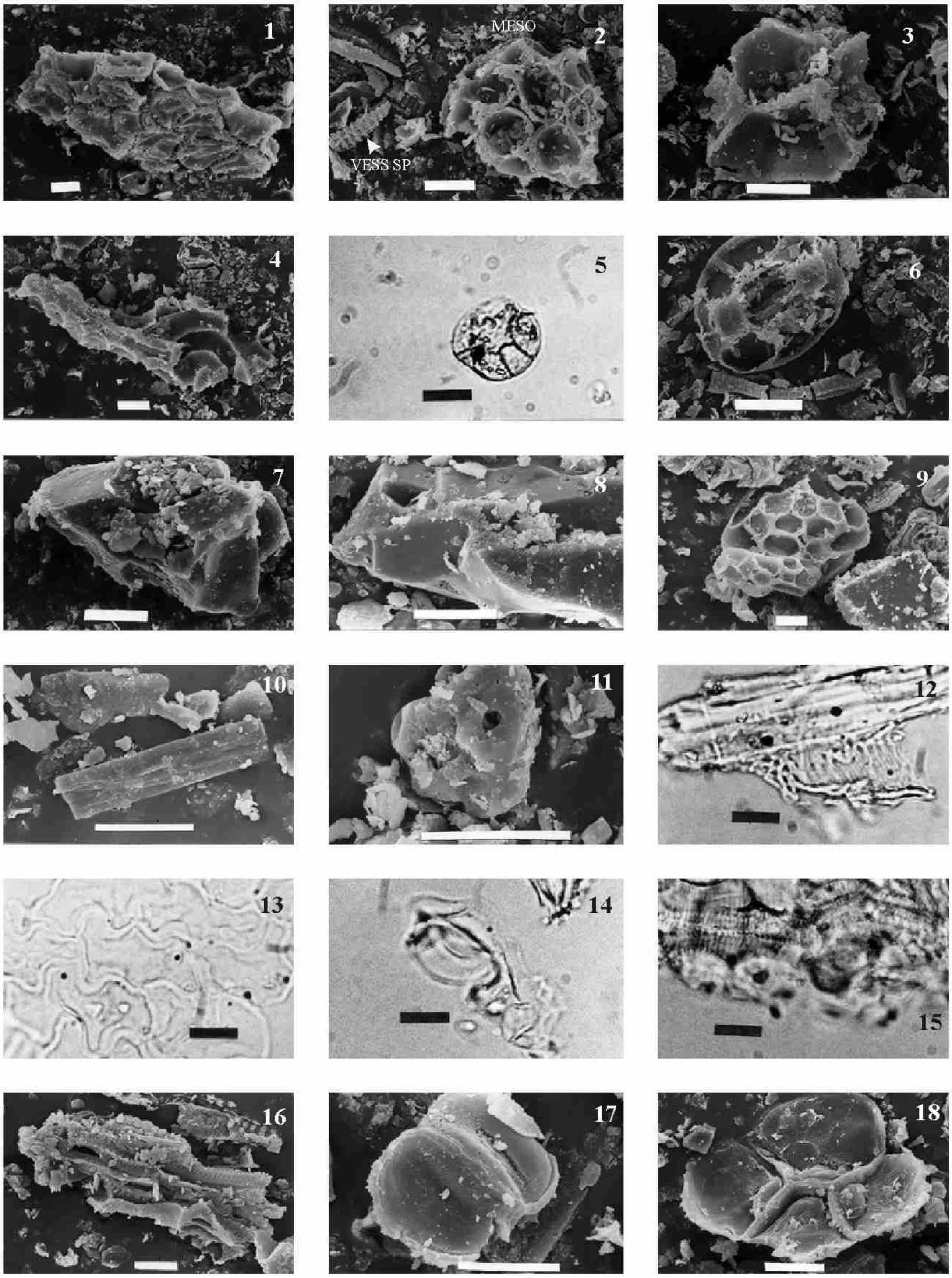

PLATE V

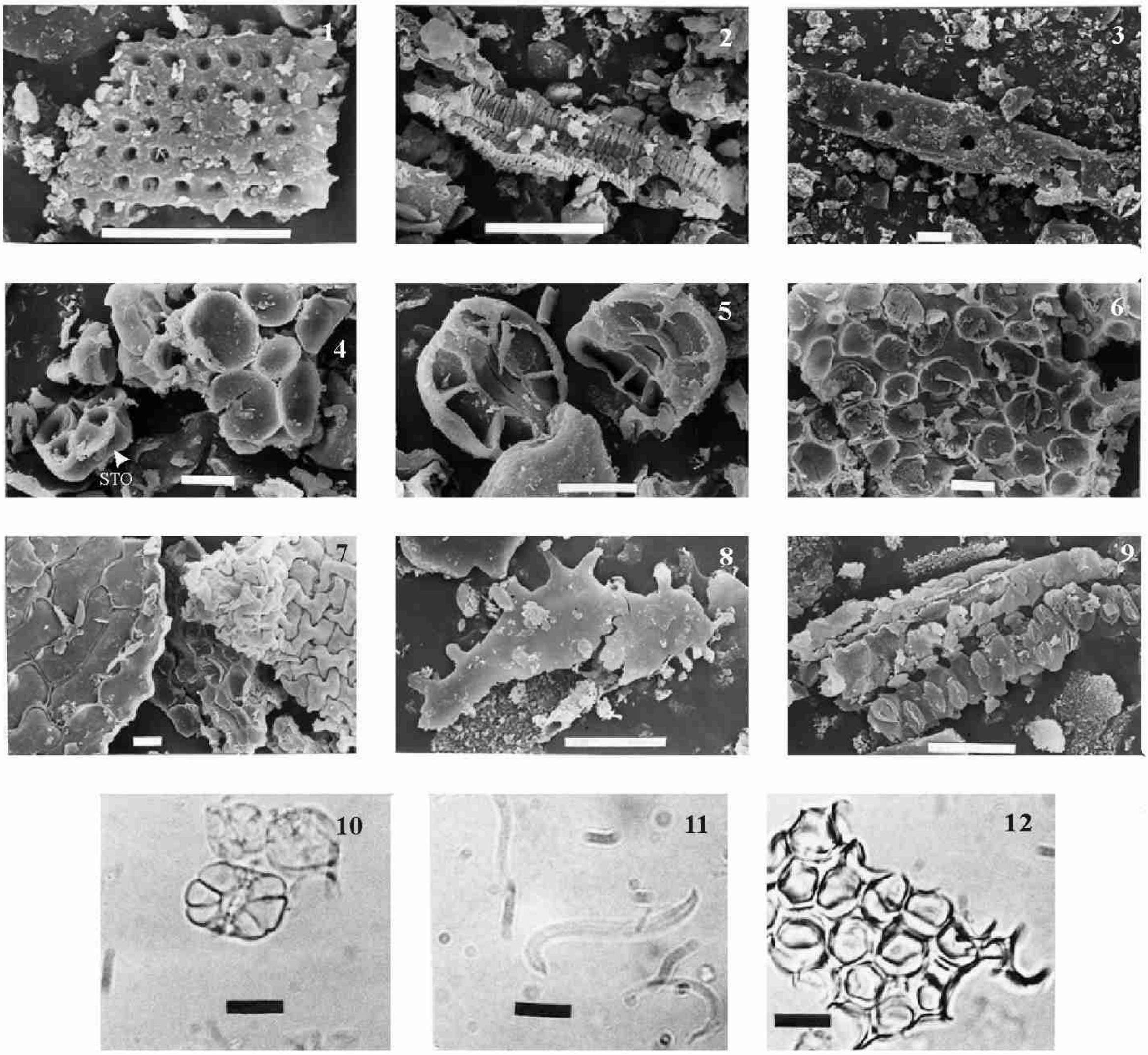

PLATE V

Ericaceae. SEM micrographs of silicified tissues from plant tissues (L= leaves, W= wood); * = light microscope photographs. Scale bar = 10 µm.

1. *Loiseleuria procumbens* (L.), RECT PITTED
2. *L. procumbens* (L), VESS.
3. *L. procumbens* (L), TRACH.
4. *Calluna vulgaris* (L), STO ERIC 1, MESO.
5. *C. vulgaris* (L), STO ERIC 1.
6. *C. vulgaris* (L), MESO.
7. *C. vulgaris* (L), JGS.
8. *C. vulgaris* (W), CALL L CELL.
9. *C. vulgaris* (W), papillated ROD.
10. *C. vulgaris* (L), STO ERIC 1. *
11. *C. vulgaris* (L), TRHEAD. *
12. *C. vulgaris* (L), MESO. *

PLATE VI

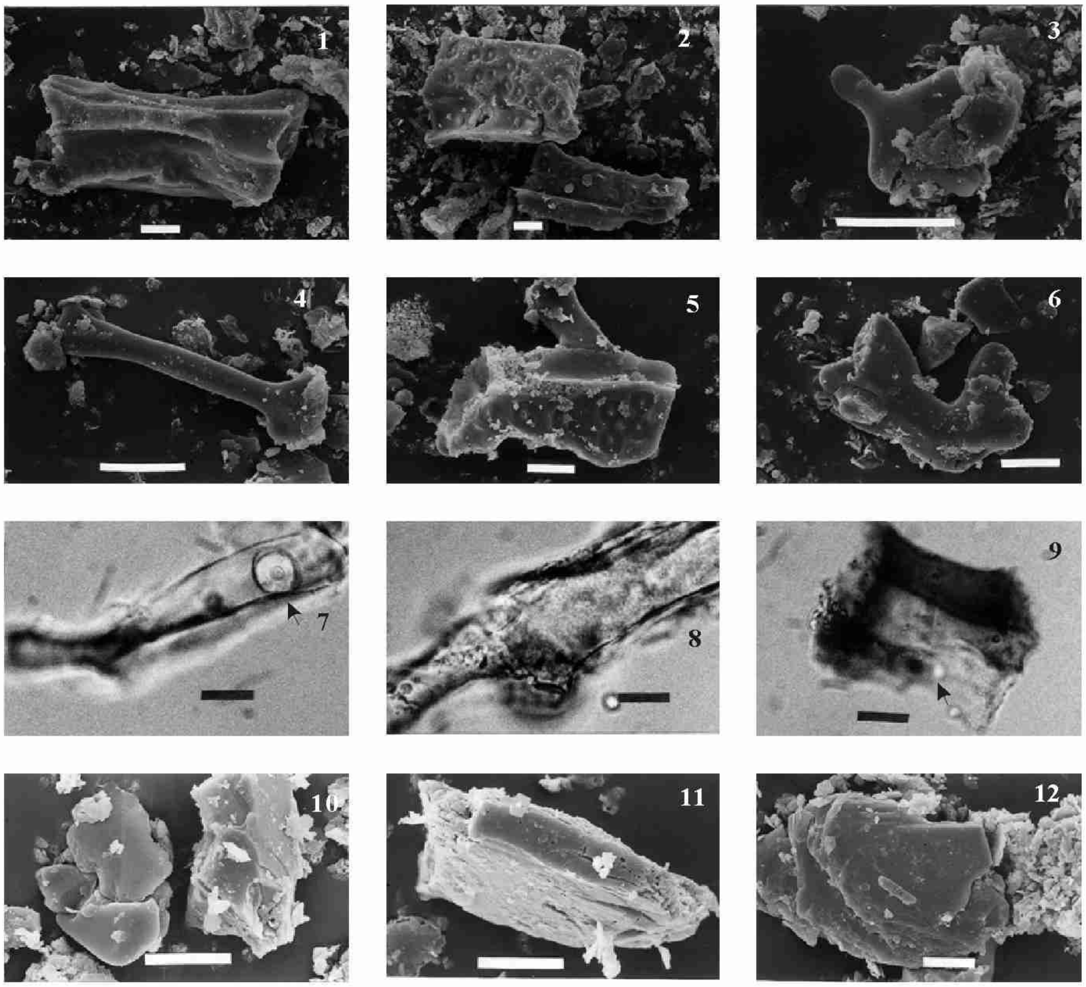

PLATE VI

Conifers. SEM micrographs of silicified tissues from plant tissues (N= needles, W= wood); * = light microscope photographs. Scale bar = 10 μm.

1. *Pinus mugo* (N), POLY CONIF.
2. *P. mugo* (N), POLY CONIF.
3. *P. mugo* (N), unknown.
4. *P. mugo* (N), unknown.
5. *P. mugo* (N), POLY CONIF.
6. *P. mugo* (N), unknown.
7. *P. mugo* (N), TRACH. *
8. *P. mugo* (N), TRACH. *
9. *P. mugo* (N), POLY CONIF. *
10. *P. mugo* (W), POLY.
11. *P. mugo* (W), POLY.
12. *P. mugo* (W), POLY.

PLATE VII

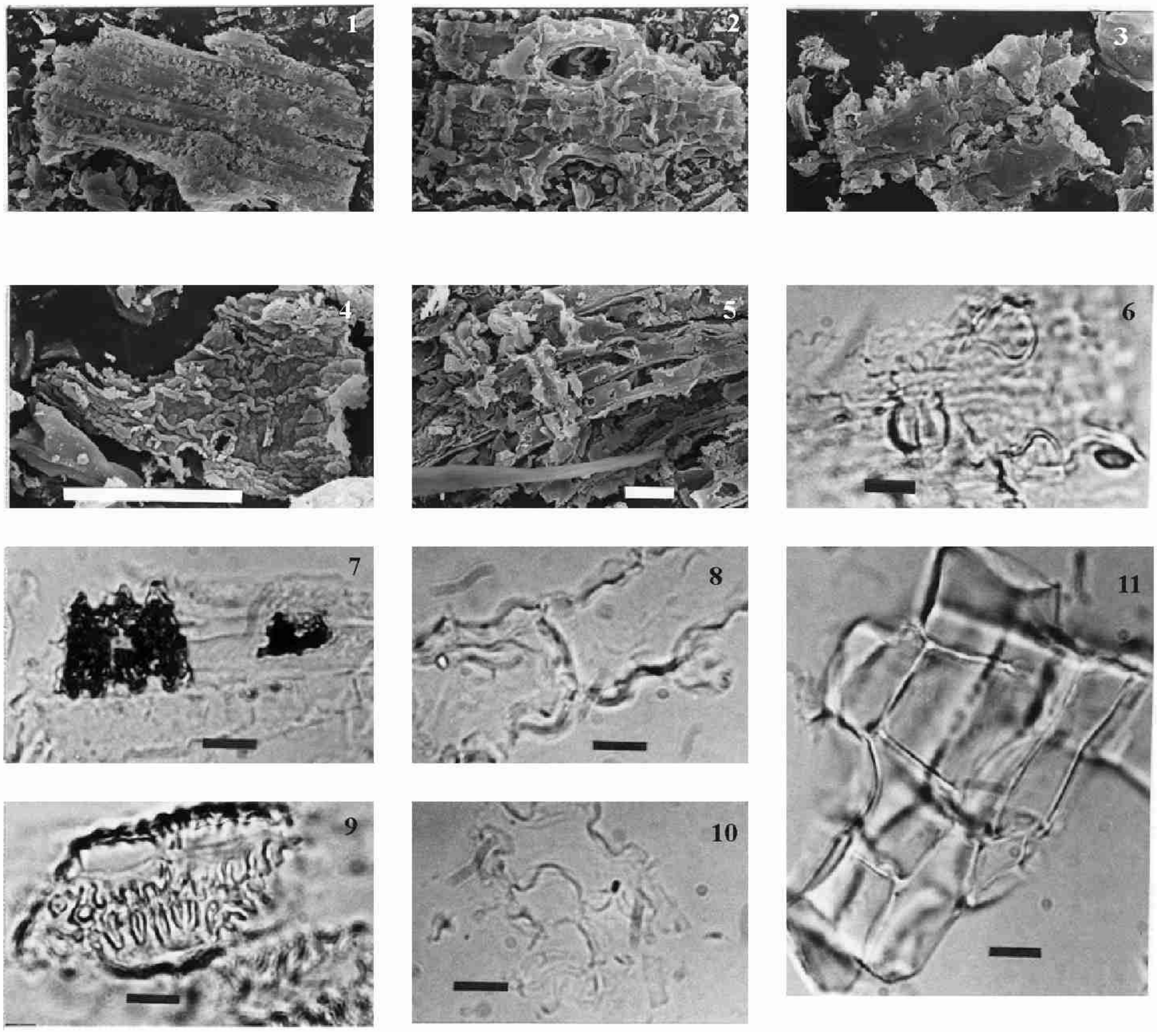

PLATE VII
Conifers. SEM micrographs of silicified tissues from plant tissues (N= needles, W= wood); * = light microscope photographs. Scale bar = 10 µm.

1. *Picea abies* (N), UND.
2. *P. abies* (N), silica skeletons.
3. *P. abies* (N), UND.
4. *P. abies* (N), silica skeletons.
5. *P. abies* (N), TRACH.
6. *P. abies* (N), STO CONIF. *
7. *P. abies* (N), UND. *
8. *P. abies* (N), UND.*
9. *P. abies* (N), UND. *
10. *P. abies* (N), JGS. *
11. *P. abies* (N), POLY CONIF. *

PLATE VIII

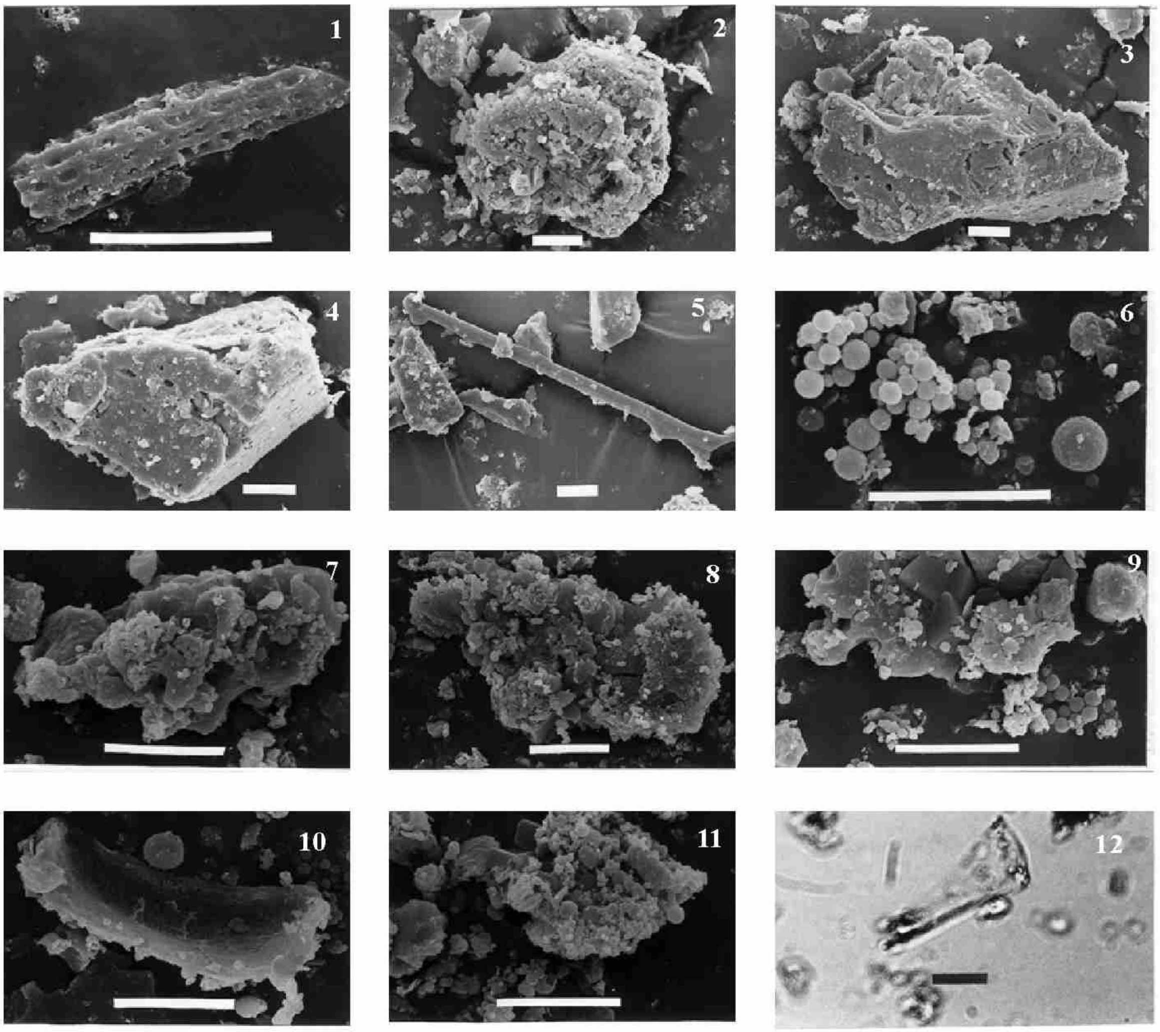

PLATE VIII
Conifers. SEM micrographs of silicified tissues from plant tissues (N= needles, W= wood); * = light microscope photographs. Scale bar = 10 µm.
1. *Pinus cembra* (N), silica skeleton.
2. *P. cembra* (W), POLY.
3. *P. cembra* (W), POLY with perforations scalariform.
4. *P. cembra* (W), POLY.
5. *P. cembra* (W), POLY.
6. *Juniperus nana* (N), SPHE S.
7. *J. nana* (N), POLY.
8. *J. nana* (N), POLY.
9. *J. nana* (N), POLY.
10. *J. nana* (N), POLY.
11. *J. nana* (N), POLY.
12. *J. nana* (N), TRACH. *

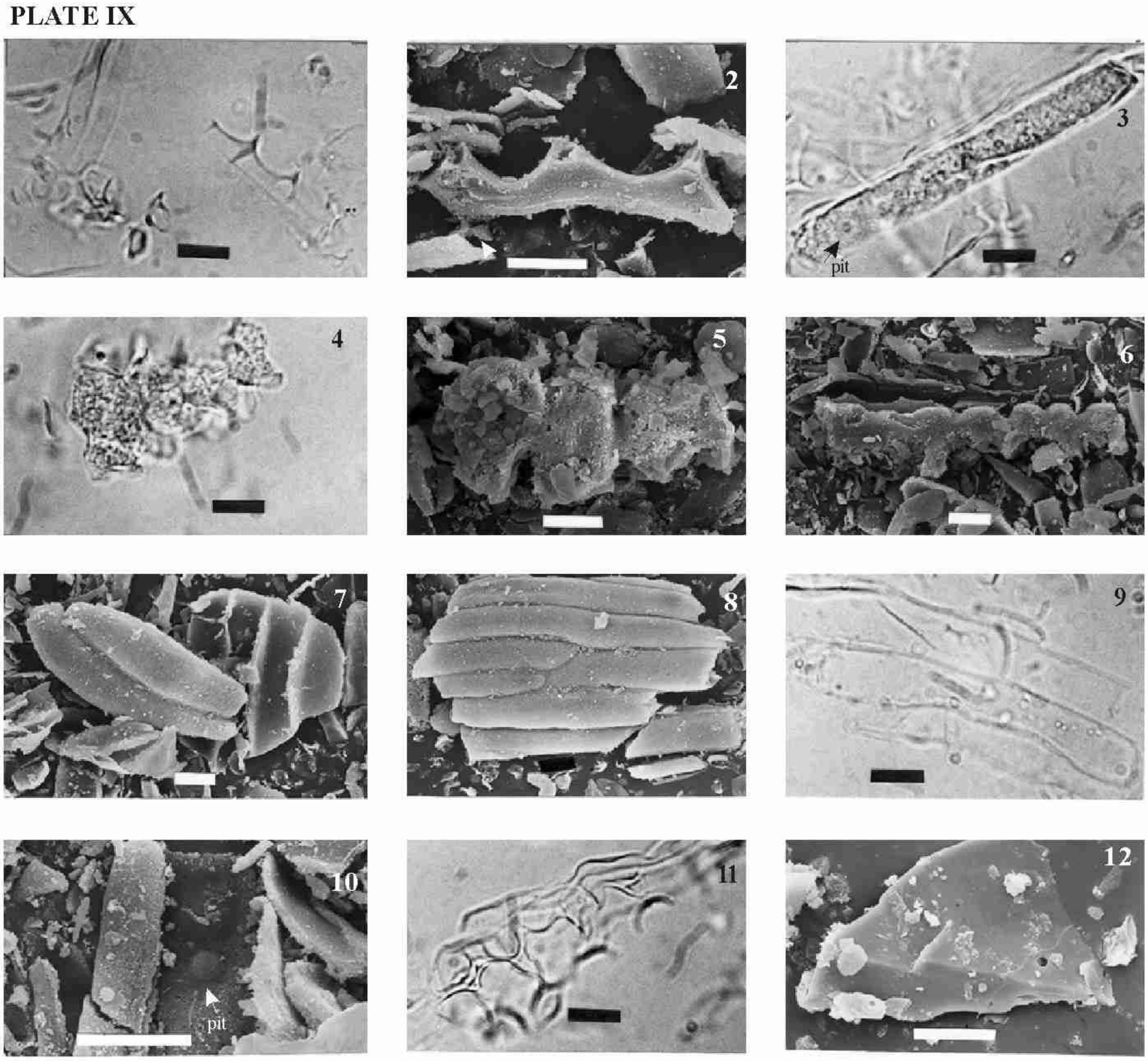

PLATE IX
Conifers. SEM micrographs of silicified tissues from plant tissues (N= needles, W= wood); * = light microscope photographs. Scale bar = 10 µm.
1. *Larix decidua* (N), WAVY. *
2. *L. decidua* (N), WAVY.
3. *L. decidua* (N), TRACH. *
4. *L. decidua* (N), LARIX BLOCKY W. *
5. *L. decidua* (N), LARIX BLOCKY W.
6. *L. decidua* (N), LARIX BLOCKY W.
7. *L. decidua* (N), L CELL.
8. *L. decidua* (N), L CELL.
9. *L. decidua* (N), TRACH. *
10. *L. decidua* (N), LARIX SPIKY CELL.
11. *L. decidua* (W), POLY. *

4.2.7 Acknowledgements

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4.3 Aluminium in the opal silica reticule of phytoliths: a new tool in palaeoecological studies*

[1]A. L. Carnelli, [2] M. Madella,[3] J.-P. Theurillat,[4] and B. Ammann[5]

[1]Institut F. A. Forel, Université de Genève, 10 route de Suisse, CH-1290 Versoix, Switzerland; [3]The Cambridge Phytolith Project, The McDonald Institute for Archeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, UK; [4]Centre Alpien de Phytogéographie, Fondation J.-M. Aubert, CH-1938 Champex and Conservatoire et Jardin botaniques de la Ville de Genève, 1 ch. de l'Impératrice, CH-1292 Chambésy, Switzerland; and [5]Institute of Plant Science, University of Bern, Altenbergrain 21, Ch-3013 Bern, Switzerland

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4.3.1 Abstract

X-ray microanalysis was employed to screen biogenic plant silica extracted from the above ground tissues of 20 species (*Graminae*, *Cyperaceae*, *Ericaceae*, and *Coniferae*) occurring in subalpine and alpine grasslands, heaths, and woodlands on siliceous bedrock in the Valaisan Swiss Alps.

Among the taxa investigated, only woody species produced a high proportion of phytoliths containing aluminium in the form of aluminosilicates. This difference between the chemical composition of wood and that of herbaceous phytoliths has important implications for the sourcing of phytoliths.

As applications for palaeoenvironmental studies can be expected to be far reaching, the potential of this microanalytical technique is discussed.

Key words: Alps, aluminium, *Coniferae*, *Cyperaceae*, X-ray microanalysis, *Ericaceae*, *Graminae*, opal.

4.3.2 Introduction

Silica in the form of opal-A is deposited in many plant tissues and is released in the soil after plant decay in the form of plant microfossils called phytoliths. Fossil phytolith records have been successfully employed in palaeoecological reconstructions and archeological interpretation. In particular, some phytolith morphotypes such as the short cells that are unique to grass species, have been shown to be a valuable source of palaeobotanical information (e.g., Alexandre et al., 1997b; Fredlund and Tieszen, 1997; McClaran and Umlauf, 2000). Several other phytolith morphotypes are known to be diagnostic at different taxonomic levels in many economic plants (e.g., Ollendorf, Mulholland and Rapp, 1987; Piperno, 1988; Mulholland and Rapp, 1992). This is so, for example, of phytoliths produced in the epidermal tissues of palm (diagnostic at family level) and banana leaves (genera *Musa* and *Ensete*) and in leaf and inflorescence tissues of *Oryza sativa* (rice) (for a review see Madella [submitted]). However, the taxonomic resolution of phytoliths is limited because of the intraspecific and interspecific variability of the silicified cells. Unquestionably, phytoliths are often the cast of cells that do not show diagnostic morphologies and their anatomical characteristics are redundant in different taxa (e.g., epidermal or mesophyll cells). Therefore, phytoliths with similar morphology can occur in plants that are not taxonomically related and/or can occur in different organs of the same plant. This intrinsic uncertainty in phytolith analysis has been obviated by the employment of different research approaches. It has been shown, for instance, that the taxonomic diagnostic power of a single phytolith morphotype is enhanced if the morphometric variability was measured and taken into account (Ball, Gardner, and Anderson, 1999). Moreover, the concept of phytolith assemblages (for a review on this subject see Power-Jones et al. [1989]), in which the combination of a statistically meaningful pool of the phytolith morphotypes present in a record is considered (instead of the presence of a single morphotype), was successfully employed as a proxy to describe present plant communities (Powers-Jones, Padmore, and Gilbertson, 1989; Powers-Jones, 1994; Madella, 1997; Fredlund and Tieszen, 1997) and also to interpret the fossil record (Barboni et al., 1999; Fredlund and Tieszen, 1994; Power-Jones et al., 1989; Power-Jones, 1994; Madella, 1997).

In the present work, it is suggested that the elemental characterization of biogenic silica through X-ray microanalysis paired with the phytolith morphology can be employed as a new tool to resolve taxonomic deadlock in the identification of phytoliths. Investigations into the chemical nature of phytoliths evidenced that aluminium is co-deposited in the phytoliths of certain species in the form of aluminosilicate (AS) and/or hydroxyalumino silicate (HAS) (Bartoli and Wilding, 1980; Hodson and Sangster, 1999). They also demonstrated that most of the taxa with Al present in the biogenic silica reticule were woody species (Hodson and Evans, 1995). From these data, we hypothesized that phytoliths formed in the tissues of conifers and arboreal dicotyledons might be characterized by the codeposition of aluminium and silica.

A reference collection of phytoliths from plants occurring in meadows, heaths, and forests of the Valaisan Swiss Alps (Carnelli, Madella, and Theurillat, 2001) was used to test this hypothesis. The analysis focused on 20 species from this collection. We focused in particular on phytoliths with nonidiomorphic shapes, generally irregular polyhedrons, as they could not be identified by a repetitive and clearly defined morphological type (Figs. 4.3.1-8). These morphotypes were tested for the presence of aluminium in the biogenic silica reticule to check if Al presence was diagnostic at any taxonomic level. Polyhedrons most commonly occur in dicotyledons and gymnosperm leaf and wood tissues, but morphotypes with a polyhedral outline are also found in the tissues of monocotyledonous plants (e.g, fragmented epidermal cells; Figs. 4.3.6-8).

4.3.3 Materials and methods

Biogenic silica was extracted from the aboveground tissues of 20 plant species (Table 1). Both leaves and woody tissues were examined (with the exception of *Empetrum nigrum* wood, of which the material available was not sufficient for the analysis). The plant sampling and the extraction procedure are described in Carnelli, Madella, and Theurillat (2001). The observation at SEM does not allow to distinguish between opal and cristalline silica. The degree of purity of the silica extracted from the plant was previously estimated at light microscopy by counting the number of optically isotropic and anisotropic particles in three microscope fields (Carnelli, Madella and Theurillat, 2001). Since oxalates and carbonates had been removed during the extraction procedure, optically anisotropic particles were considered to be crystalline silica, alkali feldspar or micas (the most common minerals in the soil and parent rock in the sampling area) adhering to the plant surface and not removed by the cleaning process. The percentage of particles constituted of opal biogenic silica was very high: on average 96% for monocotyledons, 81% for dicotyledons and, 90% for conifers (Carnelli, Madella and Theurillat, 2001). Although it is not possible to exclude the presence of traces of cristalline silica, only the polyhedrons that could be visually recognized as cast of plant cells, were selected for the X-ray analysis.

A small amount of biogenic silica (approximately 5×10^{-3} g) was extracted from each sample and spread with the help of a paintbrush on double-sided tape that was mounted on aluminium stubs. The stubs were coated with a gold layer (Balzers SCD 004 Sputter coater, Balzers Hochvakuum GMBH, Siemensstrasse 11, 6200 Wiesbaden-Nordenstadt, Germany) and examined in a JEOL JSM 6400 scanning electron microscope operating at 15 kV (JEOL EUROPE S.A., Espace Claude Monet, Ch. de Ronde-Allée de Givenry, 78290 Croissy-sur-Seine, France). An Oxford Link-Isis 300 (Oxford Instr. Sarl Analytical, Bâtiment Ariane, Domaine Technologique de Saclay, 4 rue R. Razel, 91892 Saclay, France) connected to the SEM carried out a semi-quantitative analysis of the pointed phytolith with a beam current of 50 nA, a working distance of 15 mm, and a live time of 50 s. A Si(Li) detector type and a S-ATW window type (organic film) were used. During the analyses, the standard vertical distance and scale were kept constant in order to allow comparison of the data. The presence of Al peaks was visually estimated and considered positive when distinctly higher than the background radiation. Blank trials were run on the coated stubs to check for the presence of contaminants and to verify that the aluminium from the stubs was not interfering with the analysis. No extraneous Al peak was detected. Photographs were taken with Agfa Pan APX 100 ASA professional film.

A total of 100 irregular polyhedral phytoliths were analyzed for each species. As these morphotypes can have a different histologic origin (epidermal cells, tracheary system, mesoderm), phytoliths extracted from the leaves and from the ligneous tissues of woody taxa were analysed separately. The phytoliths were selected on the basis of their morphology only from a randomly selected transect on the stub. This approach reflects the conditions of a soil-born fossil phytolith assemblage of unknown origin.

The standard deviation was calculated employing the binomial distribution. If out of n tests, the presence of aluminium was detected in r cases, the standard deviation of r is: $SD_r = [n * p(1- p)]^{1/2}$, where $p = r/n$. The percent rate was then calculated as $SD_{\%} = [n * p(1- p)]^{1/2}\ 100 / n$.

4.3.4 Results

The proportion of polyhedral phytoliths containing aluminium in each taxa and the relative errors are listed in Table 1. It must be stressed that this microanalytical technique allows only semiquantitative measures, therefore the percentages given here refer only to presence/absence data and not to the amount of Al in the phytolith. The data set shows that monocotyledons did not regularly codeposit Al and Si and that only a small percentage of the phytoliths produced in these plants contains aluminium (mean= 2%). In contrast, woody dicotyledons and gymnosperms systematically co-deposited Al. On average, Al-phytoliths represent 72% of the irregular polyhedron morphotypes found in leaves and woody tissues. It should be noted that phytoliths containing Al were detected in all the samples from ligneous tissues.

4.3.4.1 Monocotyledons

Eight species of monocotyledons belonging to the *Gramineae* and *Cyperaceae* families were investigated. In general, Al-phytoliths were rare or completely absent (Table 4.3.1). In four species

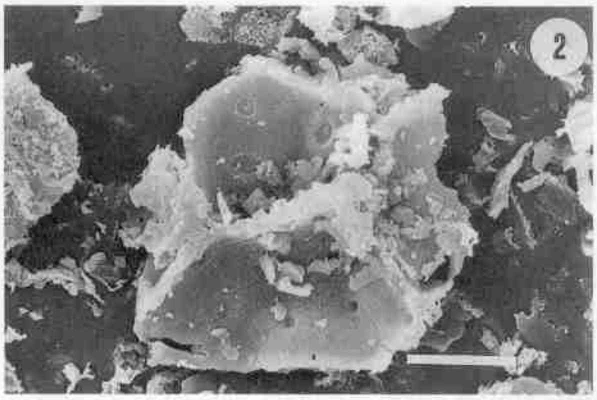
Al-phytoliths were present in up to 10% of the irregular polyhedron morphotypes: *Carex curvula* (10%), *Nardus stricta* (6%), *Calamagrostis villosa* (1%) and *Poa alpina* (2%).

4.3.4.2 Dicotyledons

The seven species analyzed belong to the *Ericaceae* family sensu latu (s. l.). Frequencies of Al-phytoliths in the leaves and in the ligneous tissues were different in all the species (Table 4.3.1). In the phytoliths extracted from the leaves, aluminium was detected in most of the irregular morphotypes from *Calluna vulgaris* (95%), *Loiseleuria procumbens* (86%), *Arctostaphylos uva-ursi* (89%), and *Empetrum nigrum* (72%). In *Rhododendron ferrugineum*, aluminium was present in only 32% of the leaf phytoliths.

Figs. 4.3.1-8**.** Scanning elecron micrographs of polyhedral phytoliths. 1. Phytolith from *Pinus mugo* needles. 2. Phytoliths from *Rhododendron ferrugineum* leaves. 3. Phytolith from *Larix decidua* wood. 4. Phytoliths from *Larix decidua* needles. 5. Phytolith from *Pinus cembra* wood. 5. Phytoliths from *Calamagrostis villosa* leaves. 6. Phytoliths from *Festuca halleri* leaves. Bars = 10 µm.


1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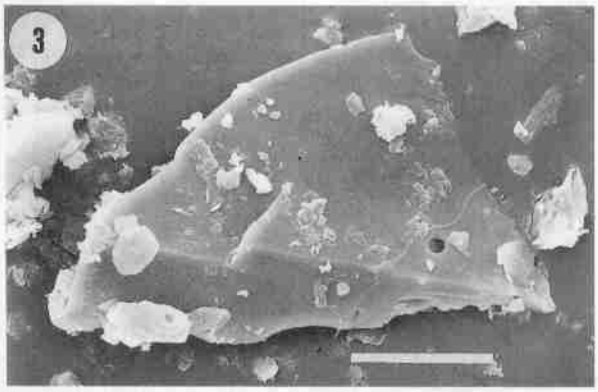
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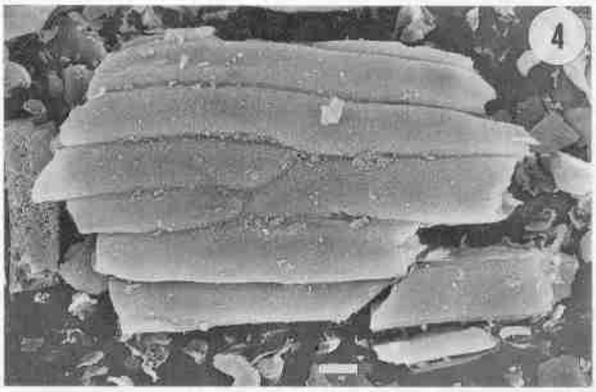
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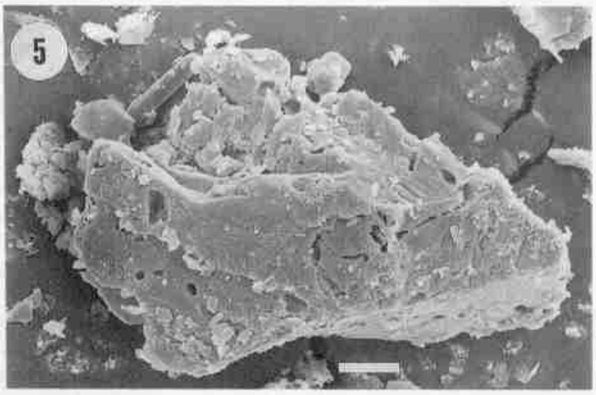
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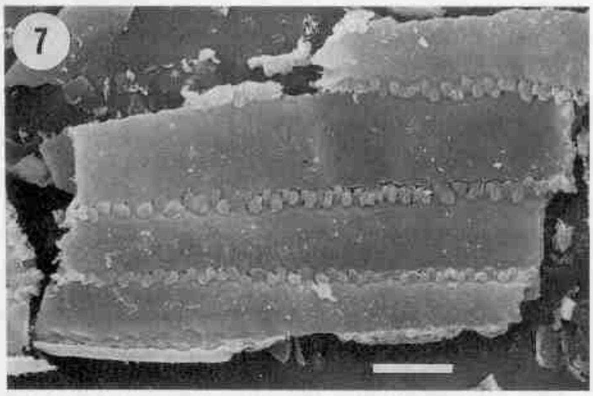
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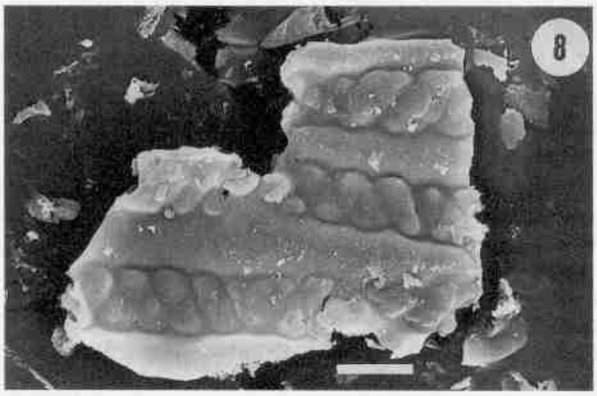
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The percentage of Al-phytoliths extracted from wood was generally very high, ranging from 84% to 95%. The woody tissue from *Vaccinium myrtillus* was the exception, in which the polyhedral phytoliths containing aluminium were only 33% of the total. The *Ericaceae* had the highest combined (leaves and wood) frequency of Al-phytoliths from this data set, with a mean of 76.5%.

4.3.4.3 Conifers

The majority of the phytoliths extracted from the needles of *Juniperus nana* and *Pinus cembra* contained Al (97% and 93%, respectively) (Table 4.3.1). Al-phytoliths were detected in 56% of the needles of *Pinus mugo.* Codeposition of Al was detected in low proportion in *Picea abies* (5%), and was absent in *Larix decidua*. In contrast, phytoliths extracted from the conifers' woody tissues always contained Al in proportions ranging from 67% to 90% (Table 4.3.1). The mean frequency of Al-phytoliths in wood is 81% and the combined (leaves and wood) frequency was 66%.

4.3.5 Discussion

4.3.5.1 Aluminum in plant tissues

Al ions are toxic to plants (for a review see Rengel [1996]). In vascular plants, the endodermis acts as a barrier into the root, but is not completely effective as Al can be detected in the shoots of some species (Hodson and Sangster, 1999). There is evidence that silicon mitigates Al toxicity (Hodson and Evans, 1995), and the mechanism involved may consist in the codeposition of Al and Si, to form insoluble aluminosilicates (Cocker, Evans and Hodson, 1998).

Hodson and Sangster (1999) reported that in shoot tissues of cereals there were undetectable or very small amounts of Al. In the cereal species, Al is probably sequestered in the plant roots' apoplast as microanalytical investigations in maize, sorghum, wheat and oat would seem to suggest (for a review see Hodson and Evans [1995]). These findings are consistent with the results of the present research, which highlighted an absence of aluminium in phytoliths from above ground tissues of grasses.

The data on the uptake of Al and Si in conifer shoots (Hodson and Sangster, 1999; Hodson and Evans, 1995) show that conifer species allow far more Al into the root cortex and transport more to the shoot. These findings seem to be indirectly confirmed by the present results on the composition of conifer phytoliths.

By means of in situ X-ray microanalysis, the codeposition of Al and Si was detected in the needles of four conifers (*Pinus strobus*, *Larix laricina*, *Abies balsamea*, *Picea glauca*). In these species, Al was invariably present in the silicified epidermal walls of the needles, and, in some species, also in the hypodermis, mesophyll, and endodermis (Hodson and Sangster, 1999).

Among the conifers here examined, *Larix decidua* and *Picea abies* have the most heavily silicified needles (biogenic silica is 1.09% and 0.85% of plant dry mass respectively, Carnelli, Madella, and Theurillat [2001]) but the lowest percentages of Al-phytoliths. This indicates that Al and Si in conifer needles are not invariably colocalized as was the case for the species analyzed by Hodson and Sangster (1999).

Aluminium is not generally present in grasses, however a study on Al/Si co-deposition in *Sorghum bicolor* using microanalytical techniques, revealed that HAS/AS are deposited in the outer tangential wall of the root epidermis (Hodson and Sangster, 1993). More evidence on the production of biogenic silica in below ground plant tissues is needed before any estimate of Al-phytolith production in grass roots can be attempted.

4.3.5.2 Aluminium in phytoliths

The frequency of Al-phytoliths was remarkably higher in *Ericaceae* and conifers (up to 97%) than in *Cyperaceae* and *Gramineae* (maximum of 10%). Phytoliths from wood always contained Al in a proportion as high as 80% (even in the case of *Vaccinium myrtillus*, which has less lignified tissue, a fact which explains its low 33% value).

Monocotyledonous species produce the highest quantity of biogenic silica (Table 4.3.1); however, most of the taxa analysed did not contain Al-phytoliths at all, or only contained a small percentage. Comparative data concerning the codeposition of Al in biogenic silica from monocotyledons are scanty. The few data available revised by Hodson and Evans (1995) concern three grass species and are not directly comparable as they were obtained by quantitative chemical analysis. The content of Al was measured in the phytoliths obtained from the leaves of the grasses *Festuca sylvatica* (1.9 % on dry mass basis), *Sasa* sp. (0.03%) and *Miscanthus* sp. (0.01%). The present study revealed that Al was primarily deposited in the phytoliths of *Ericaceae* and conifers. Quantitative chemical analyses performed by other authors confirm these results to some extent: in the phytoliths extracted from the leaves of the grass *Festuca sylvatica*, aluminium accounted for 1.9% of the dry mass, in *Calluna vulgaris* for 2.1%, and in *Pinus sylvestris* for 4.4% (Bartoli and Wilding, 1980). For these species, it is reported that between 60 and 95% of leaf Al was incorporated into phytoliths.

In the present data set, Al-phytoliths were detected in all woody tissues, even in species that were taxonomically unrelated. A functional interpretation of this evidence goes beyond the purpose of the present work; however, it may be argued that it is the result of a time integrated codeposition. It is known that the concentration of several elements (among them Al) increases in plant tissues with time (e.g., in Norway spruce needles, (Wyttenbach and Tobler, 1988) and should therefore be higher in tissues with a longer lifespan such as wood. Further investigations are needed to test if this trait is common to wood phytoliths from other taxa.

The physical-chemical properties of opal were investigated in detail on the phytoliths of *Pinus sylvestris*, *Fagus sylvatica*, *Calluna vulgaris*, *Abies alba*, and *Festuca sylvatica* (Bartoli, 1985). The Si/Al ratios for whole phytoliths and for the phytolith surface were compared, showing that the latter always had a higher Al content. In particular, pine and fir phytoliths revealed the greatest content of surface aluminium. It was speculated that their surfaces might be coated with an octahedrally coordinated form of Al (Bartoli, 1985 p. 339). Isomorphous substitution of Al for Si in the internal tetrahedral network of opal is less common and Al is normally deposited after Si deposition.

Moreover, the lower solubility of conifer phytoliths in comparison with those of other species analyzed was attributed to the higher surface content of chemiadsorbed Al (Bartoli, 1985).

4.3.5.3 Implications for palaeoecological studies

The hypothesis that the presence of Al-phytoliths can be regarded as a potential tracer for woody taxa was verified for those species most commonly occurring in subalpine and alpine vegetation on siliceous bedrock in the Alps, i.e., the conifers that form the timberline, the ericaceous dwarf shrubs and some grasses and sedges of the alpine grassland. This focus on the dominant and most common plants was undertaken with a view to applying this technique to the investigation of treeline and more specifically to subalpine-alpine fluctuations in the Alps during the Holocene. Although a few important subalpine species are not taken into account in the present study, such as *Abies alba* Mill. (conifer), *Alnus viridis* (Chaix) DC., *Salix helvetica* Vill. (dicotyledon shrubs), and *Vaccinium uliginosum* L. *(Ericaceae),* this is unlikely to make a difference to the results obtained according to the first analyses of their production of biogenic silica (Carnelli, Madella and Theurillat, 2001).

Indeed, although the European alpine treeline is possibly the most intensively studied of all distributional tree boundaries, conclusive functional explanations are akward (Körner, 1998, 1999). It is acknowledged that treelines generally correspond to stress gradients (e.g. thermal, hydric, nutritional, disturbance) but the factors that determine the present alpine treeline need to be investigated on the timescale by means of comparison of palaeoecological data.

In the case of the European Alps, the locations of past treelines have been reconstructed mainly by means of pollen, plant macrofossil, and charcoal analysis (e.g. Burga, 1991; Carcaillet and Thinon, 1996; Tinner, Amman and German, 1996; Tinner and Wick, 1997; Carcaillet, 1998; Carcaillet and Brun, 2000; Carcaillet, Talon and Thinon, 1998). The possibility of definitely assigning nonidiomorphic phytoliths to herbaceous or ligneous plants creates a new method of investigating the dynamics of the timberline during the last postglacial in the Alps.

Table 4.3.1**.** List of the species investigated, percentage of the phytoliths in which aluminium was detected in leaves and wood respectively (**%Al**) and standard deviation rate (**s.d.**$_{\%}$). Total content in biogenic silica (percentage on a dry-weight basis) in the tissues (**Si** $_{\textbf{tot}}$ **%**) (after Carnelli et al. 2001).

Species	Phytoliths from Leaves		Phytoliths from Wood		Biogenic Silica in Leaves	Biogenic Silica in Wood
	%Al	s.d.$_{\%}$	%Al	s.d.$_{\%}$	Si $_{tot}$ %	Si $_{tot}$ %
Monocotyledons						
Calamagrostis villosa (Chaix.) Gmelin	**1**	0.99			5.90	
Carex curvula All.	**10**	3.00			0.95	
Carex sempervirens Vill.	**0**	0.00			2.27	
Festuca halleri All.	**0**	0.00			3.27	
Festuca puccinellii Parl	**0**	0.00			2.96	
Festuca scabriculmis (Hackel.) Richter	**0**	0.00			2.41	
Nardus stricta L.	**6**	2.37			2.55	
Poa alpina L.	**2**	1.40			0.61	
Dicotyledons						
Arctostaphylos uva-ursi Spreng.	**89**	3.13	**80**	4	0.02	0.21
Calluna vulgaris L.	**95**	2.18	**95**	2.18	0.68	-
Empetrum nigrum subsp. *hermaphroditum* (Hagerup)[a]	**72**	4.49	**-**		0.16	0.11
Loiseleuria procumbens Desf.	**86**	3.47	**95**	2.18	0.23	0.08
Rhododendron ferrugineum Linn.	**32**	4.66	**84**	3.67	0.03	0.01
Vaccinium myrtillus L.	**71**	4.54	**33**	4.70	0.04	0.03
Vaccinium vitis-idaea L.	**78**	4.14	**85**	3.57	0.03	0.03
Coniferae						
Juniperus nana Willd.	**97**	1.71	**88**	3.25	0.07	0.15
Larix decidua Miller	**0**		**90**	3.00	1.09	0.53
Picea abies (L.) Karsten	**5**	2.18	**78**	4.14	0.85	0.17
Pinus cembra L.	**93**	2.55	**83**	3.76	0.12	0.02
Pinus mugo Turra	**56**	4.96	**67**	4.70	0.9	0.06

[a]: data for wood are not available

Recently, we suggested that when investigating the history of the main plant communities of the subalpine-alpine ecocline, the production of biogenic silica should be considered in parallel with the morphological approach (Carnelli, Madella, and Theurillat, 2001). Indeed, we estimated that upper subalpine to low alpine swards have a mean silica production of one order of magnitude greater than heaths, both for a mesophilous (mean= 9.4 vs. 0.37 g m^{-2} yr^{-1}) and a thermophilous ecosystem (mean= 10.3 vs. 0.79 g m^{-2} yr^{-1}). However, the production of biogenic silica of true alpine swards with *Carex curvula* All. (mean= 1.2 g m^{-2} yr^{-1}) is close to that of upper subalpine to low alpine heaths and thus would not be distinguished definitely on a solely quantitative basis. In the same way, although the biogenic silica produced by the litterfall of an upper subalpine forest may be estimated to be of the order 1.5 g m^{-2} yr^{-1} on average, the production of its grassy understorey can be as high as 29.2 g m^{-2} yr^{-1} and thus may not differ so much from the production of a subalpine grassland. As the production of Al-phytoliths appears to distinguish woody taxa, different plant communities, characterized by herbaceous vs. arboreal taxa, should vary consequentially in the production of Al-phytoliths. The phytolith fossil record present in a soil should thus be a valuable marker of vegetation and vegetation shifts. The potential production of Al-phytoliths of a plant community can be estimated by calculating its annual biogenic input and the fraction of Al-phytolith input into the soil. Subalpine and alpine grasslands are the most active accumulators of biogenic silica but Al-rich phytoliths in grasses are very rare, representing only 2% on average. In contrast, subalpine woody/arboreal vegetation accumulates less opal silica but, on average, 72% of the phytoliths from leaves and wood of conifers and woody *Ericaceae* contain Al.

In case further investigations of different taxa confirm that the codeposition of Al and Si in phytoliths is more frequent in or characteristic of woody tissues, this technique could still find wider applications. Ecotonal shifts involving a change in life-form dominance occurred in many biomes worldwide during the history of vegetation (e.g., dense forest/savanna, forest/steppe). As the presence of Al-phytoliths in conifers was confirmed for several species (Bartoli 1980; Hodson and Sangster 1999), it can be argued that this method should be useful in those cases where there is investigation of conifer species (e.g., *Pinus* and *Ericaceae* matorral in the Mediterranean region, boreal forest, and steppe-tundra ecotone in North Eurasia).

Finally, a further implication of the presence of Al in phytoliths is related to the interpretation of phytolith assemblages. The taphonomic processes undergone by phytoliths in the soil are little understood, though this aspect of the phytolith "life cycle" is crucial for the interpretation of opal silica in palaeoecological archives. The durability of phytoliths in the soil appears to be related to several physical and chemical factors of the medium as well as to their own intrinsic characteristics: the presence of Al seems to increase their resistance to dissolution (Bartoli, 1985). The differential preservation of phytoliths should lead to a relative time-integrated enrichment of the morphotypes more resistant to dissolution in the deeper horizons of undisturbed soils (Alexandre et al., 1997a). Therefore, data on the Al-content of phytoliths in different taxa are of general interest in the correct interpretation of fossil assemblages.

4.3.6 Summary of conclusions

In the samples of biogenic silica from subalpine-alpine species, Al was always present in woody species phytoliths, on average in 72% of the cases (wood and leaf samples); it can be hypothesized that the presence of Al in phytoliths of unknown shape and origin in fossil assemblages would lead one to deduce that they were produced by woody species. The application of microanalytical techniques to phytolith analysis in palaeoecological investigations should enhance the diagnostic taxonomical power of such analysis. In the present work we focused on polyhedral morphotypes because of the difficulty to distinguish them on a solely morphological basis, nevertheless this technique may be applied to other morphotypes. The prospect of identifying phytoliths originating in woody taxa, not only by using the established morphological approach (e.g., Piperno, 1985; Bozarth, 1993; Alexandre et al., 1999; Barboni et al., 1999; Runge, 1999) but also by microanalytical techniques, can clarify a part of the uncertainty arising from redundant production of phytolith morphotypes in distinct taxa. In this way, X-ray microanalysis on phytoliths, can supply another proxy with a theoretically unlimited availability of sampling sites, as they can be extracted from any soil, and a relatively high spatial resolution power. Biogenic silica produced by species from vastly different kinds of vegetation should be tested for the presence of Al. If the presence of Al in woody species is confirmed, the chemical composition of biogenic silica may be a powerful tool to investigate past shifts in herbaceous and woody vegetation produced as a result of climatic variation and of human activities.

In the context of global change, palaeoecological data are needed to validate climate models to predict the response of the ecosystems to future climate changes. When the reconstruction of the history of vegetation is based on multi-proxy evidence, it provides more precise and quantitatively reliable estimates. This method could open a new avenue of phytolith investigation that could be of interest not only for the Alps but anytime we are confronted with the need to understand past environments and the shift of two major types of vegetation: grasslands vs. woodlands.

4.3.7 Acknowledgements

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CHAPTER 5: BIOGENIC SILICA IN SOILS AT THE SUBALPINE-ALPINE ECOCLINE

Chapter 5 is concerned with the study of biogenic silica in soil. Firstly, the formation of phytolith assemblages occurring in topsoil under subalpine and alpine grasslands were investigated (study of modern analogs) (5.1). Secondly, the content of biogenic silica, aluminium phytoliths and monocotyledon phytoliths in the mineral horizons of the soil profiles is discussed (5.2).

5.1 MODERN PHYTOLITH ASSEMBLAGES IN ALPINE GRASSLANDS IN THE SWISS CENTRAL ALPS

5.1.1 Abstract

Twelve top soils of alpine grasslands were sampled along four altitudinal transects between 2400 and 2800 m a.s.l. (Valais region, Swiss Central Alps). Biogenic silica content, aluminium phytolith frequency, and phytolith morphotypes are discussed in relations with present plant cover. The theoretical deposition of phytoliths from the present-day plant stand is estimated and compared with the measured data. On the basis of these data, hypotheses on formation of soil assemblages of phytoliths are discussed. Short cell frequency in alpine meadows is shown to be predictable on the basis of solely local phytolith input. Subalpine and alpine grasslands are dominated by grass and sedge species. However, all alpine grasses belong to the same subfamily (Festucoideae), and therefore, they only produce short cells of trapezoidal type. Thus, they cannot be differentiated on the basis of grass short cell morphology as it is possible for subtropical grass species. Here, it is shown that as a consequence of the poor preservation of sedge morphotypes, it is not possible to differentiate among alpine meadows on the basis of top soil phytolith assemblages.

Key words: grasslands, Alps, phytolith, biogenic silica, modern assemblages.

5.1.2 Introduction

Phytoliths (silicified plant cells) recovered from soil have been employed in palaeocological studies as a proxy to reconstruct plant communities history. Since their first applications in palaeoecological studies, it was clear that a floristic interpretation of soil phytolith assemblages based on the direct link species-morphotype was not advisable. Indeed, because of the presence of similar morphotypes in taxonomically unrelated species (redundancy), the vegetational approach was shown to be more adequate to interpret fossil assemblages in palaeocological studies. The latter is based on the hypothesis that a given phytolith assemblage reflects the species composition of the plant community that produced it, and no attempt is made to identify the single plant source (Power-Jones and Padmore, 1993).

To understand the processes leading to the formation of phytolith assemblages, it is necessary to investigate the relationships between the production of phytolith in the plant communities and the actual phytolith records in the soil. This will give a stronger rationale for the interpretation of phytolith fossil assemblages on the principle known as actualism or uniformitarianism (Birks and Birks, 1980). In this context, data on plant community and topsoil phytolith assemblage must be investigated to develop models for phytolith deposition and dispersal. Data on modern phytolith assemblages are rare. Modern analogs were investigated in in tropical and subtropical Africa were also carried out (Alexandre et al., 1997; Barboni et al., 1999), in the temperate regions of the northen emisphere in the aspen parklands (Bozarth, 1993), and in the North American Great Planes grasslands (Fredlund and Tieszen, 1994). In the American Great Planes it was shown that modern phytolith assemblages are a reliable proxy for July mean air temperature (Fredlund and Tieszen, 1997). From the taxonomical point of view it was also evidenced that the deposition of allochtonous phytoliths in this area, is an important phenomenon (estimated between 30% and 70% of the input) and that the stock of phytolith in soil is the result of inheritance and dispersal, on both regional and local scale (Fredlund and Tieszen, 1994). The presence of regional input was also detected in modern assemblages from the African tropical grasslands (Alexandre et al., 1997). In the same area it was shown grasslands can be differentiated on the basis of distinctive C_3/C_4 grass phytoliths (following Twiss et al., 1969). However, this methodology cannot be applied to alpine environments where only C_3 grass species occur. In the alpine ecosystems, the hypothesis that alpine and subalpine grasslands can be separated on the basis of phytolith typologies need to be tested.

In the present study, the content of biogenic silica (B.S.), the proportion of phytoliths containing aluminium and the frequencies of phytolith morphotypes are investigated in twelve top soils from alpine meadows. In order to verify if phytolith assemblages in soil can be predicted solely on the basis of stand biomass and composition, the expected theoretical phytolith input was calculated on the basis of plant cover, species biogenic silica production (Carnelli et al., 2001) and morphotypes frequencies (Chapter 4.2; Carnelli et al., in press). Modern analogs are here discussed in the framework of a larger project in which phytoliths are employed to reconstruct the past uppermost limit of the treeline at the subalpine-alpine ecocline in the Central Alps. Indeed, a better knowledge of phytolith signature given by present vegetation should allow for an improved fossil record interpretations. Future investigations on modern analogs of conifer forests and alpine heathlands would further contribute to a better understanding of biogenic silica deposition in subalpine vegetation.

5.1.3 Methods

Four altitudinal transects situated in lateral valleys of the upper Rhone Valley (47°N, Central Swiss Alps), above the treeline in subalpine-alpine meadows, were investigated. For each transect, three soils at increasing altitude were sampled (Table 5.1.1). The first transect is located in Val d'Arpette (AR), a valley in the Mt. Blanc massif (AR1, 2375 m; AR2, 2565 m; AR3, 2720 m). Two transects are located in the Aletsch Glacier Region: Belalp transect (BA-HO) situated along the Mt. Hofathorn southern slope (BA-HO1, 2358 m; BA-HO2, 2570 m; BA-HO4, 2830 m) and Belalp-Lengi Egga (BA-LE) situated on the S-E slope of Mt. Sparrhorn (BA-LE7, 2035 m; BA-LE6, 2451 m; BA-LE5, 2550 m); and one transect located in proximity of the Furka Pass (FK), on the S slope of Tällisegg, Tällisgrat, Tällisker peaks (FK1, 2403 m; FK2, 2618 m; FK3, 2785 m). The parent rock material is acidic (granite in Val d'Arpette and gneiss elsewhere).

5.1.3.1 Climate and vegetation

In the upper Rhone valley (Figure 2.1) the degree of continentality increases eastward from Martigny to Visp, then it slightly decreases from Visp to Furka Pass. Average daily summer air temperature and annual precipitation are in Val d'Arpette: 9.8° to 12.3°C, and 1524 mm m^{-2}; 8.6° to 11.7°C, and 908 mm m^{-2} at Belalp, respectively (Schlüssel, 1999). At Furka, mid summer air temperatures varies between 7° and 10°C, and precipitation peak is in summer, with an annual sum of about 1500 mm m^{-2} (Körner et al., 1997).

Vegetation relevés were performed on a surface of 4 m^2, (following Barkman, 1964). The relevés are listed in Table 5.1.2. Plant species cover were then transformed in the percentage cover (Table 5.1.3) using the central values of each class: r = 0; + = 0,02%; 1m = 0,02%; 1= 2,5%; 2m = 2,5%; 2a = 10%; 2b = 20%; 3a = 31%; 3b = 44%; 4a = 56%; 4b = 69%; 5a = 81%; 5b = 94% (Barkman, 1964).

Fitosociological classification follows (Theurillat et al., 1995).

5.1.3.2 Soil types

Soil horizons were described according to Baize and Jabiol (1995); while the soil classification follows AFES, (1998).

The soils investigated belong to three major types: PODZOSOL, ALOCRISOL, and BRUNISOL (Table 5.1.1). For a detailed soil descriptions refer to Chapter 3 and Annexe A.

The soils in Val d'Arpette show a marked decrease of the podzolic activity with increasing altitude: in AR1 (2375 m a.s.l.) the soil is a PODZOSOL OCRIQUE, in AR2 (2565 m a.s.l.) is ALOCRISOL TYPIQUE, and BRUNISOL OLIGOSATURÉ in AR3 (2720 m a.s.l.). Humus are of moder type in AR1 and AR2 and mull in AR3. In Belalp soils the podzolic activity is present up to 2550 m a.s.l.: BA-HO1 (2358 m a.s.l.) is a PODZOSOL MEUBLE, and BA-HO2 (2570 m a.s.l.) is a PODZOSOL OCRIQUE. The higher altitude soil BA-HO4 (2830 m a.s.l.) is an ALOCRISOL TYPIQUE. In the transect FK: podzolisation is active in the low altitude soil FK1 at 2403 m a.s.l. (PODZOSOL MEUBLE). FK2 (2618 m a.s.l.) and FK3 (2785 m a.s.l) soils are ALOCRISOLS TYPIQUES.

Samples for the analyisis of modern phytolith assemblages were taken from the horizons O and A. The humus were of moder type along the whole transect BA-HO. In the transect BA-LE: BA-LE7 has humus of dysmull type, signal of good biological activity, although alpine conditions slow down decomposition leading to the formation of a thin holorganic OFOH layer. BA-LE6 humus type is dysmoder and BA-LE5 humus type is dysmoder with discontinuous hemimoder. In sites at Furka, humus types were: mor in FK1 and, mull in FK2 and FK3.

5.1.3.3 Biogenic silica sampling and extraction procedure

The present work considers only the uppermost part of soil, however, the whole profile was sampled and described elsewhere (Chapter 5.2). Soils were sampled at the same location of the vegetation relevé. Both the holorganic horizons (OH, OF), and mineral-organic horizons (A, AE) were sampled. In an exploratory framework several samples at increasing depth were taken to verify the more representative sampling depth for modern analogs. Each soil sample weighted about 20 g: samples were taken for each soil horizon and for the thicker horizons at regular intervals, every 2 cm. Dried soil samples were sieved on a mesh (1 mm) to separate roots and gravel. B.S. was extracted from about 5 g sieved soil (Madella et al., 1998). The total fraction of opal silica was recovered Chapter 5.2).

5.1.3.4 Phytolith classification and counts

Silica bodies were observed with an optical microscope equipped with phase contrast optic and polarised illumination at a magnification of 504x. Permanent microscope slides were mounted in EUKITT (refractive index 1.5 at 20°C) and a standardised scanning was performed for each slide. The number of phytoliths counted was on average 1000. The morphotypes were described quoting the botanical terminology for the plant cells from which they originated or the terminology commonly used in phytoliths studies (Chapter 4.2).

5.1.3.5 Aluminium phytoliths

The percentage of phytoliths containing aluminium (Al phytoliths) was determined by means of X-rays microanalysis. A subsample of the biogenic silica residue was examined with a JEOL JSM 6400 scanning electron microscope. A sample of about 60 irregular phytoliths (polyhedrons) was checked for the presence of aluminium in the biogenic silica reticule. The procedure is described in Carnelli et al. (2002). Standard deviation rate was calculated with the binomial distribution.

To allow the comparison between the mass of biogenic silica and the frequency of Al–phytoliths in the samples, the punctual values of B.S. and Al-B.S. were estimated in the soil horizons as follows (Table 5.1.2; Figure 5.1.3).

The mass of the soil horizon is given by its thickness (m), multiplied for the bulk density of the horizon (Kg m^{-3}). The average bulk density of the soil horizons considered is approximately as follows (Kg m^{-3}) : O= 100, OA= 250, A=800. To calculate the total weight of B.S. per horizon: the mass of the soil horizon was multiplied for the percentage weight of B.S.. For a more accurate comparison of the mass of B.S. and Al-B.S, the values were then reported to punctual values: punctual mass of B.S= B.S% * soil horizon bulk density; and Al-phytoliths punctual mass= Al-phytolith%* punctual mass of B.S.. The ratio of punctual mass of Al-B.S and total B.S. in all the sites is plotted in Fig. 5.2.6.

51.3.6 Predicted phytolith morphotypes production of alpine grasslands

For each sampling site it was calculated the theoretical input of morphotypes that is produced by the plant stand.

To calculate the theoretical input of phytoliths it is needed:

1) The biogenic silica production (Carnelli et al., 2001);
2) the frequencies of phytolith morphotypes (Chapter 4.2) that were previously assessed on a plant reference collection;
3) the plant cover given by the vegetation relevés (Table 5.1.2);

4) the plant species cover transformed in percentage cover that gives an estimate of relative species biomass (Table 5.1.3). (Total cover may exceed 100% because of canopy stratification effect).

The relative production of phytoliths for each species was derived in two main steps according to the following procedure. Firstly, was calculated the theoretical input of biogenic silica for each species in the community.

In a vegetation relevé (Table 5.1.3), the percentage cover of one species (C_S) gives the estimate of its relative contribution to the community biomass. As consequence of canopy stratification, the sum of cover of all the species of the relevé may exceed 100%. Therefore, the percentage cover of the species was normalised to 1: i.e. the sum of all normalised species covers C_{SN} in each relevé equals 1 (Table 5.1.4).

The theoretical input of biogenic silica (I_S) for a species S is:

$I_S = C_{SN} \cdot P_a$;

where P_a = the annual production of biogenic silica for the species S;

and $P_a = \text{B.S.} \cdot \text{Plant Productivity} \cdot G$.

Where:

B.S. = the percentage content of biogenic silica for the species S (on dry-mass), taken from the reference collection. For woody species, the B.S. value is the average of leaf and wood values (Carnelli et al., 2001).

Plant Productivity = the daily mean above-ground productivity of dry matter for the species S; expressed as dry mass for one square meter ($g\ m^{-2}\ d^{-1}$) (see Carnelli, 2001).

G = the length of the growing season (days) in the sampling sites (Table 5.1.1).

Secondly, the theoretical input of phytolith typologies for each species was calculated as follows.

The species S yields a set of phytolith typologies (α, β, γ, …), each of them occur with frequencies ($\alpha_{\%}$, $\beta_{\%}$, $\gamma_{\%}$,…) assessed on the reference collection (Carnelli et al., in press; Chapter 4.2). The input of biogenic silica of a species (I_S) is then multiplied for the frequency of each phytolith type ($\alpha_{\%}$, $\beta_{\%}$, $\gamma_{\%}$,…). The result gives the proportional theoretical input of phytolith typologies of the species S (= T_S):

$T_S = (I_S \cdot \alpha_{\%}) + (I_S \cdot \beta_{\%}) + (I_S \cdot \gamma_{\%}) + \ldots$

The same calculation was applied to all the species occurring in the community (T_{S1}, T_{S2},…)

The sum of T_S for all the species in a site gives the total theoretical production of phytolith types in a site (= P_{THEO}). This value is a proportion and it is expressed as percentage to allow the comparison between the theoretical input of phytoliths and the countings from the soil assemblages (Tables 5.1.5-5.1.8).

The following approximations were applied during the above calculations:

(1) Plant productivities were assumed to be the ones of the dominant species in a given plant community. Indeed, the majority of the productivity in a dwarf shrub heath or in sward in the upper subalpine in the alpine belts relies on one dominant species, or a few co-dominant ones. These species are also responsible for the majority of the B.S. (*Gramineae, Cyperaceae, Ericaceae*). Hence, overestimated productivity, if ever, relates mainly to species with a low cover and, generally, a low B.S.. Values of plant productivity were taken from literature (for full references see: Carnelli et al., 2001).

(2) Values of plant productivity are not available for all the species occurring in the sites. In these cases productivity was approximated taking the values of taxonomically related species with similar ecology. For *Festuca halleri* and *Poa alpina* data from of *Nardus stricta* were taken; for *Vaccinium vitis-idaea* productivity was considered the same of *Vaccinium uliginosum*; finally for *Pinus cembra* and *Juniperus nana*, the productivity of *Picea abies* was taken.

(3) To calculate as accurately as possible the length of the growing season, sites' altitude and local variations in the degree of continentality were taken into account. Given the regular temperature decrease with elevation it is considered that an increase of 100 meters shortens the growing season by 9.8 days on average (Theurillat et al., 1998). For the European Alps, the altitude of the lower alpine

belt is taken as reference for a growing season of about 115 days (Theurillat et al., 1998). However, the altitude of this belt may vairy locally with the degree of continentality. At Belalp and Arpette the altitude of the lower alpine belt corresponds to the one of the Internal Alps (in Arpette the continentality is increased by the very steep rocky slope). At Furka continentality corresponds to the situation of the Intermediate Alps. Following these considerations, the lower alpine belt is placed at about 2300 m for Belalp and Arpette, and 2200 m at Furka.

(4) Some *Gramineae* and *Cyperaceae* species that were present in the relevés were, however, not available in the reference collection. Therefore values for B.S. content, morphotypes occurrence and plant productivity were taken from taxonomically related species in the reference collection (Carnelli et al., 2001). Data from *Festuca scabriculmis* were used for the congeneric *Festuca nigrescens.* Among alpine grasses *Nardus stricta* has average values of B.S. and productivity, and its values were used for the following grasses: *Agrostis rupestris, A. schraderiana, Anthoxantum alpinum, Briza media, Festuca halleri, Deschampsia flexuosa* and *Helictotrichon versicolor*. For *Carex pallescens* data from the congeneric *C. sempervirens* were taken.

(5) For *Juniperus communis* subsp. *nana,* data on phytolith frequency for wood are missing (because of the very low B.S. recover from plant sample): it was therefore used the phytolith frequency from the wood of *Picea abies*. For the *Ericaceae* species *Vaccinium uliginosum,* the content in B.S. values was measured, but morphotype frequencies are missing (because of the very low B.S. recover from plant sample) and were taken from *V. myrtillus.*

(6) Some species, mainly herbaceous dicotyledons, were not taken into consideration when calculating the theoretical input of phytoliths, because no data on B.S. and phytolith production are available. However, the relative percentage cover of all these species was considered in the calculation, to keep the real proportion of biomass in the plant community. This exclusion should not account for any significative underestimate, because in general their contribution to the stand biomass is limited. In addition, herbaceous dicotyledons yield negligible B.S. content (Carnelli et al., 2001): e.g. 0.04% for *Alchemilla pentaphylla,* 0.11% for *Geum montanum,* negligible for *Leontodon helveticus. Trifolium alpinum* has high covers (40 - 80%) in BA-LE6 and BA-LE7, however, its exclusion should not be relevant as *Fabaceae* are generally silica excluders (Jones and Handrek, 1967). The woody

dycotyledons *Salix herbacea* and *Empetrum nigrum*, were considered negligible for their low cover and production of B.S. (*S. herbacea* has 0.43% cover and 0.035% B.S; *E. nigrum* has and 0.16% cover, and 0.13% B.S).

Although *Juncaceae* (*Juncus jacquinii, J. trifidus, Luzula lutea, L. multiflora, L. spicata*) have a potentially high B.S., they were discarded because data is not available for any related species. However, their contribution to the total biomass is negligible, with one exception: *J. jacquinii* (FK3).

5.1.3.7 Statistical analysis

Descriptive statistic (principle components analysis, PCA; STATISTICA 4.5 F for Windows) was used to extract the major trends of phytolith distribution in the study sites. Data were square-root transformed before performing the PCA. Other data transformations were also tested without any significative difference in the output.

PCA was applied:

1) to sort out the relationship between the different grassland in the sampling sites using species covers (only dominat species were included in the analysis, the same species used to calculate the theoretical input of phytoliths P_{THEO});

2) to illustrate the variability of phytolith distribution among the sites; at this scope, a PCA ordination was run excluding not idioblastic phytoliths (i.e. polyhedrons) that are mainly background noise;

3) to test, using the theoretical percentages of phytoliths calculated for each site (P_{THEO}), if the theoretical inputs of phytoliths have the potential to individuate grassland types that would match the real vegetation.

In addition, clustering was also performed on the vegetation relevés using all the species occurring in the sites, to analyse the similarity between the different grasslands. The chord distance was used to calculate the similarity between the relevés.

The ordinations of the cluster analysis (run with all the species) and PCA (run only with dominant species) were compared to verify if a loss of information occurrs.

5.1.4 Results

5.1.4.1 Subalpine and alpine swards compositions (Figure 5.1.1; Table 5.1.2)

The cluster analysis for the vegetation (Figure 5.1.1) higlighted seven groups at an intermediate linkage distance, namely

1) AR1,
2) BA-OH4,
3) BA-OH1, BA-LE6, BA-LE7,
4) BA-LE5, FK1,
5) AR2, AR3,
6) BA-HO1,
7) BA-OH2, FK2, FK3.

Table 5.1.3 lists the complete relevés according to the groups distinguished by the clustering, yet with the fifth cluster (AR2, AR3) placed in third position for a more clear presentation. The species are listed according to visual diffential groups and decreasing frequency. The species used for the reduced set of the phytoliths analysis are evidenced in Table 5.1.3.

1) The first cluster connsists of AR1: this grassland type corresponds to a transition between dwarf shrubs and a sward of the *Festuca varia* group. The latter is a typical low alpine belt grassland type on steep slopes, and facing south. *Festuca scabriculmis* subsp. *luedii* generally co-dominate with *Calluna vulgaris, Juniperus communis* subsp. *alpina, Vaccinium vitis-idaea* and *Vaccinium uliginosum* subsp. *microphyllum*.

2) The second cluster (BA-OH4) corresponds to a cool alpine sward in moist conditions, dominated by the clonal grass *Agrostis schraderiana* (other species often present: *Alchemilla fissa, Juncus jacquinii, Cerastium cerastioides, Cirsium spinosissimum*).

3) The third cluster (BA-LE6, BA-LE7) corresponds to an upper subalpine-low alpine, mesophilous-thermophilous sward probably formed by centuries of grazing on a transitional sward with dwarf shrubs. Typically, this type of swards are not very rich in species. It is co-dominated by *Carex sempervirens, Trifolium alpinum* and, to some extent, *Nardus stricta.* BA-LE7, dominated by *Trifolium alpinum,* is especially poor in species (10).

4) The fourth cluster (BA-LE5, FK1) is an intermediate sward between cluster 3 and cluster 6 differentiated by the dominance of matgrass *(Nardus stricta)* and the presence of the alpine *Carex curvula*. Such a transitional stage is very likely the results of long pasturing activities on gentle slopes.

5) The fith cluster (AR2, AR3) is an alpine sward on steep slopes, co-dominated by *Festuca nigrescens, Geum montanum,* plus *Agrostis schraderiana, Carex sempervirens, Nardus stricta* and *Deschampsia flexuosa.* This type of sward replaces the *Festuca varia* swards in cooler conditions with a longer snow cover. It can be quite rich in species and it is characterized by the regular presence of subalpine dwarf shrubs and even small *Pinus cembra.*

6) The sixth cluster (BA-OH1) represents a species rich sward with 35 species in the 4 m^2 of the relevé (plus 4 additional species in the immediate vicinity of the relevé). The vegetation corresponds to a moister variant of cluster 3 (abundance of *Carex sempervirens, Trifolium alpinum* and, to some extent, of *Nardus stricta,* presence of *Solidago virgaurea* subsp. *minuta*). The main differential species are *Ranunculus villarsii, Plantago alpina, Soldanella alpina, Alchemilla glabra, Crocus albiflorus, Trollius europaeus.*

7) The seventh cluster (BA-OH2, FK2, FK3) corresponds to the typical alpine sward on not too steep conditions (dominance of *Carex curvula*) in tendentially dry conditions (presence of *Veronica bellidioides*) but nevertheless with a good snow cover, especially in the case of FK3 with *Salix herbacea* and *Alchemilla pentaphyllea.*

Phytosociologically, all the relevés belong to the class *Juncetea trifidi* Hadac 1946, following Theurillat *et al.* (Theurillat et al., 1995) for the classification in higher units and Schlüssel (1999) for the plant communities otherwise indicated. The first cluster (AR1) belongs to the alliance *Festucion variae* Guinochet 1938 (order *Festucetalia spadiceae* Barbero 1970) and corresponds to a *"Festucetum scabriculmis callunetosum"* community. The second cluster pertains to an *"Agrostietum schraderianae"* community of the alliance *Agrostion schraderianae* Grabherr in Grabherr et Mucina 1993 (order *Caricetalia curvulae* Braun-Blanquet in Braun-Blanquet et Jenny 1926). All the other clusters corresponds to plant communities belonging to the alliance *Caricion curvulae* Braun-Blanquet in Braun-Blanquet et Jenny 1926 (order *Caricetalia curvulae*). The third (BA-LE6, BA-LE7) and the sixth clusters (BA-OH1) correspond to a *"Trifolio-Caricetum sempervirentis",* the fourth cluster (BA-

LE5, FK1) to a transition between the *Nardion* and the *Caricion curvulae* alliances. It could be attributed to the *Carici-Nardetum* Oberdorfer 1959. The fifth cluster (AR2, AR3) forms an undescribed community, and the seventh cluster (BA-OH2, FK2, FK3) corresponds to the *Caricetum curvulae* Rübel 1911 s.l..

.Figure 5.1.1 Tree diagram of the vegetation releveés, Chord distance

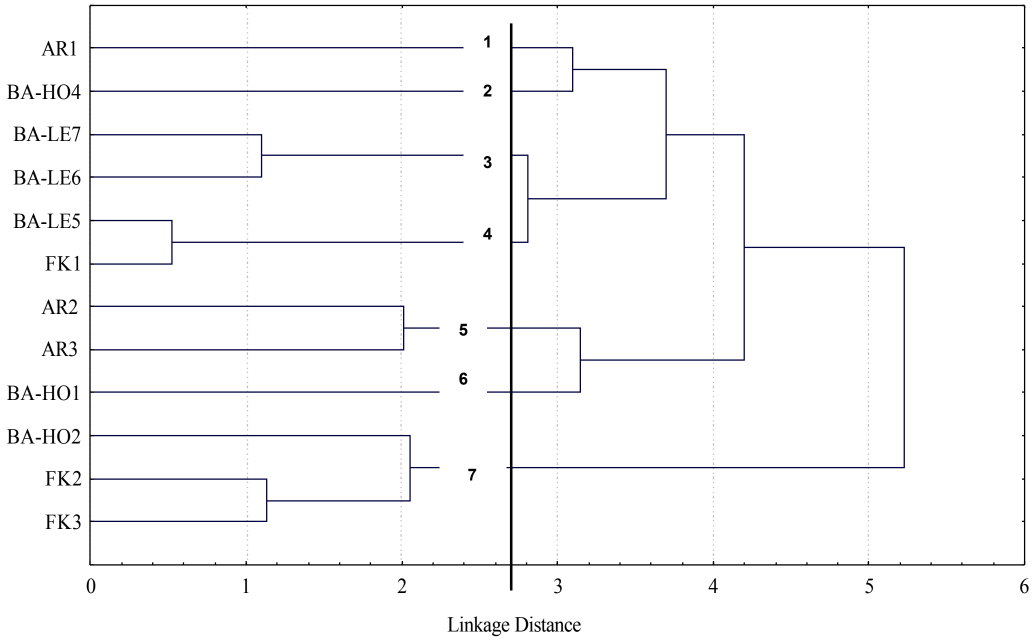


Figure 5.1.2 Principal components analysis, species used for calculating the theoretical input. square transformed data

P. components	Eigenval	Variance	Eigenval	%
1	4.683799	39.03166	4.683799	39.03166
2	2.988573	24.90477	7.672372	63.93643

	Factor 1	Factor 2
AR1	-.068344	.162599
AR2	.747820	.329822
AR3	.452897	.434763
BA-Ho1	.813060	.360781
BA-HO2	.439261	-.839665
BA-HO4	-.074759	.102205
BA-LE7	.917599	.074981
BA-LE6	.851782	.226224
BA-LE5	.870804	-.299890
FK1	.840088	-.185090
FK2	.089360	-.898617
FK3	.124963	-.911144
Expl.Var	4.683799	2.988573
Prp.Totl	.390317	.249048

(Marked loadings are > .700000)

To some extend, the seven groups formeded by the cluster analysis are also recognisable in the ordination (PCA) of the reduced relevés (Figure 5.1.2). The two relevés of the first and second cluster (AR1, BA-OH4) are very close. The relevés of the third and sixth (BA-OH1, BA-LE6, BA-LE7) and the fourth cluster (BA-LE5, FK1) are grouped together. For the fifth cluster (AR2, AR3), one relevé (AR2) is closer to the group of the third cluster, leaving AR3 isolated. For the seventh cluster (BA-OH2, FK2, FK3), BA-OH2 is isolated from FK2 and FK3, but the three relevés are nevertheless more separated from all the other relevés than they are between them. The most striking feature of the ordination on the reduced relevés is the fact that AR1 and BA-OH4 come very close because the two reduced relevés do not contain any common species. The explanation would be a very strong " horse shoe effect" starting form AR1 and coming back to BA-OH4. The underlying gradient going through AR3, AR2, BA-LE7, BA-LE5, BA-OH2, FK3 and FK2 would represent a moisture-coolness gradient, starting from the dryer, warmer site AR1 to the moist and cool site BA-OH4. A detrended canonical analysis (DCA) performed with CANOCO (not shown) confirms the "shoe horse effect" with AR1 and BA-OH4 being opposite, both along the first and second axes.

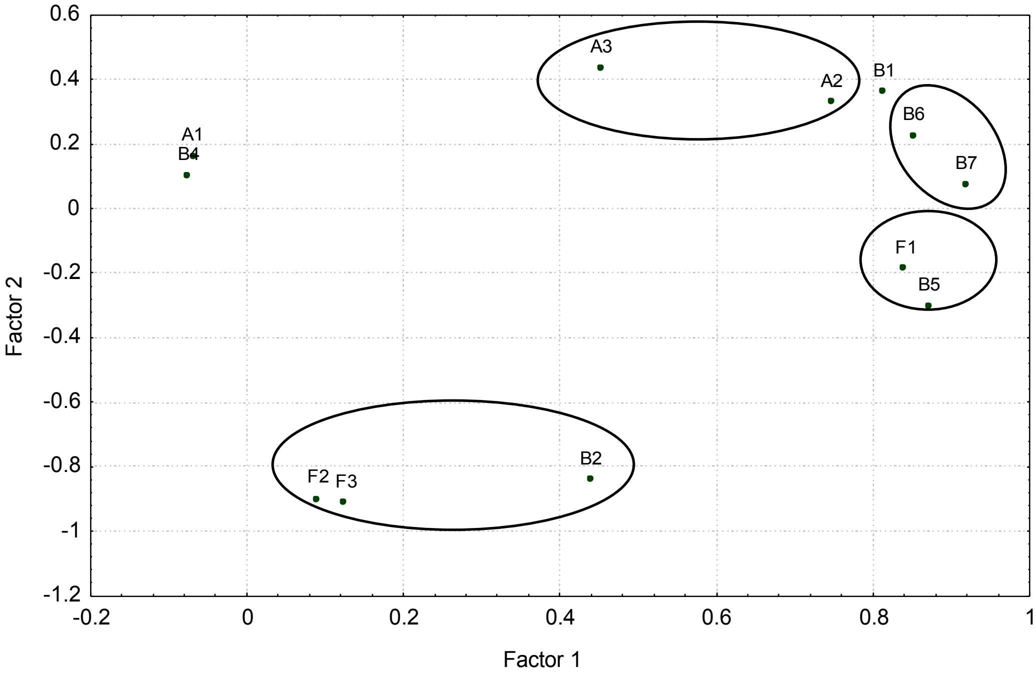
5.1.4.2 Biogenic silica content (Fig. 5.1.3; Table 5.1.1)

The content of B.S. of the top horizons was higher in the sites at lower elevation. If only the topmost sample for each soil is plotted (Figure 5.1.3), it is possible to note that a difference in B.S. production occurs between 2550 and 2660 m a.s.l.. Above 2600 m the content in biogenic silica is generally around 5% or lower, while below this elevation is generally around 10% or higher (up to 25.5% in FK1). Exception is the horizon OF/OH from the site BA-HO1 (in which B.S. is 1.3%).

5.1.4.3 Ratio of Al and B.S. content in soil horizons (Fig. 5.1.3; Table 5.1.2)

The ratio of Al-biogenic silica and B.S. punctual contents in the topmost horizon of each site is plotted in Figure 5.1.3; the sites below about 2600 m a.s.l. (podzosols) have higher ratio of aluminious silica (up to 8.96), while above 2600 m a.s.l. (alocrisols and brunisols) this ratio is lower (in general less than 3).

PCA analysis was performed also including all the species in the ordination procedure. The result of the ordination did not change. Therefore, it can be argued that the simplification applied to calculate the theoretical input of phytoliths (P_{THEO}) should not reduce significatively the differences between grassland types



5.1.4.4 Morphotype percentages in top soil (Fig 3; Tables 5.1.5- 5.1.8)

Grass short cells were the dominant idioblastic typology in all the sites. Frequency of short cells increases with depth, ranging from about 15% in the holorganic horizons (OF and OH) to about 40% in the organic-mineral horizons (A). Short cells are up to 70% of the total phytoliths at the base of A, in the transition horizon AE. Other grass diagnostic phytoliths (bulliform cells, rods, cork cells) are present in low frequencies. Cones, the distinctive sedges' morphotypes are less then 2% in all the sites, while trichomas are ubiquituos, with frequencies ranging from 3% to 28%. Stomata with circular outline, originated from dicotyledon tissues (Chapter 4.2) have low frequency, and they are present mainly in the uppermost horizons. Dicotyledon phytoliths (mesophill cells, vessels with spiral thickening and, spherical types) are also very rare. Jigsaw cells, generally occurring in dicotyledons, show frequencies of up to 9.6%. Polyhedrons (non-idioblastic phytoliths) are abundant in all sites, with frequencies ranging from 30% to 70% of the assemblage.

Table 5.1.1 Altitude, site, horizon and samplig depth of the top soils. Biogenic silica content (B.S.) percentages on dry soil weight basis (% s.d.w.); percentage of aluminium phytoliths (Al phytolith) and standard deviation (s.d.). The lenght of the growing season is calculated following Theurillat (1998) modified.

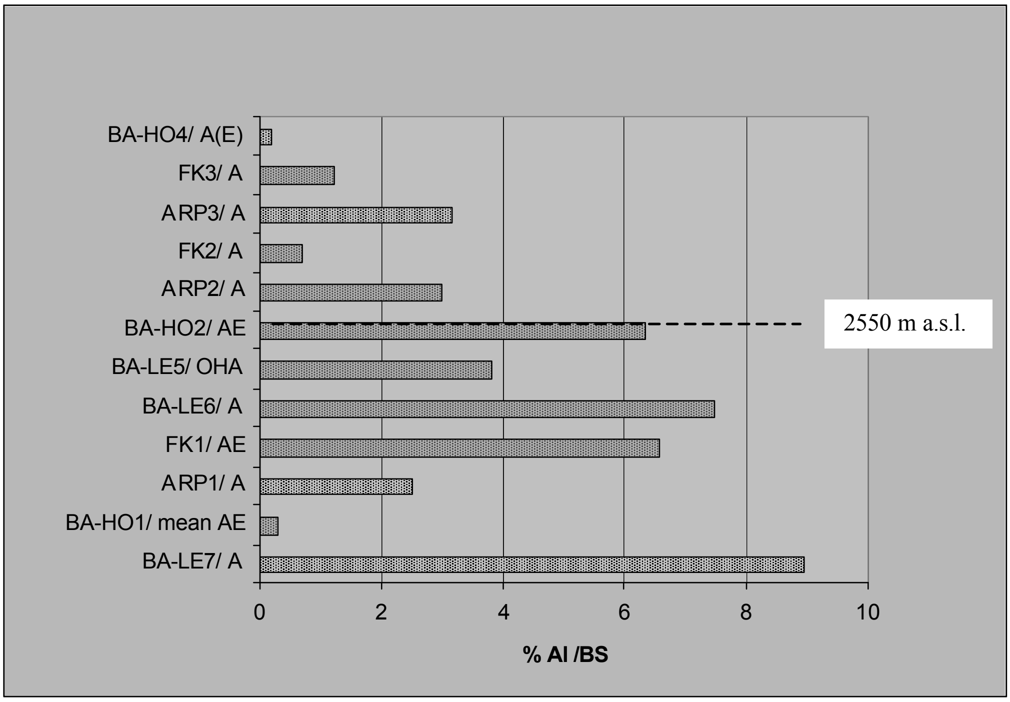
Altitude (m a.s.l.)	Site	Horizon	Sampling Depth (cm)	B. S. (% s.d.w.)	Al phytoliths (% ± s.d.)	Lenght of the growing season (days)
2375	AR1[a, d]	OH	5-10	10.8	63.5 ± 6.1	108
	AR1	A	7-12	3.5	71.7 ± 5.8	
2565	AR2[b, -]	A	5-2	7.2	41.7 ± 6.4	90
2720	AR3[c, -]	OA	0-2	3	54.9 ± 7	76
	AR3	A	2-7	4.9	64.5 ± 6.1	
2358	BA-HO1[a, e]	OF/OH	0-1	1.3	73.3 ± 5.7	110
	BA-HO1	OF	2-3	0.4	61.3 ± 6.2	
	BA-HO1	AE	3-4	0.8	63.3 ± 6.2	
	BA-HO1	AE	5-6	0.7	30.6 ± 5.8	
	BA-HO1	AE	8-9	0.7	31.7 ± 6	
2570	BA-HO2[b, f]	OF1	1-2	2.2	37.9 ± 6.4	90
	BA-HO2	OF2	2-3	9.7	75 ± 5.6	
	BA-HO2	AE	3-6	8.2	77.6 ± 5.5	
2830	BA-HO4[b, e]	OF	0-3	5.4	6.2 ± 3	66
	BA-HO4	A(E)	3-4	2.1	10 ± 3.9	
	BA-HO4	A	4-7	2.3	6.8 ± 3.3	
2305	BA-LE7[a, h]	A	1-3	11.2	80 ± 5.2	115
	BA-LE7	A/EH	3-4	14.5	100± 0	
2451	BA-LE6[a, f]	A	3-4	11.5	65 ± 6.2	101
2550	BA-LE5[a, d]	OHA	1.5-3.5	4.6	83.3 ± 3.8	92
	BA-LE5	AE	2-6	0.9	27.5 ± 4.7	
2403	FK1[a, g]	OH	1.5-3	25.5	78.3 ± 5.3	96
	FK1	AE	3-6	6.8	96.8 ± 2.2	
2618	FK2[b, i]	A	0-3	1.2	56.7 ± 6.4	76
2785	FK3[b, j]	A	0-3	5.4	22.4 ± 5.5	61

Soil types are: [a] PODZSOL; [b] ALOCRISOL; [c] BRUNISOL.
Humus types are: [d] dysmoder; [e] eumoder; [f] hemimoder; [g] mor; [h] dysmull; [i] mesomull, [j] eumull, [-] not identified.

Table 5.1.2 Altitude, profile and horizons and punctual ratio of aluminious biogenic silica and biogenic silica. (*= PODZOSOLS)

Altitude	Profile, horizon	Punctual Al/ BS
2305*	BA-LE7 (A)	8,96
2358*	BA-HO1 (mean AE)	0,3
2375*	ARP1 (A)	2,51
2403*	FK1 (AE)	6,58
2450*	BA-LE6 (A)	7,47
2550*	BA-LE5 (OHA)	3,83
2570*	BA-HO2 (AE)	6,36
2565	ARP2 (A)	3
2618	FK2 (A)	0,68
2720	ARP3 (A)	3,16
2785	FK3 (A)	1,21
2830	BA-HO4 [A(E])	0,21

Figure 5.1.3 Punctual Al-B.S./B.S. content in the top horizons (see Table 5.1.2). Sites are displayed with increasing elevation.



PCA ordinations of the phytolith assemblage compositions were run to investigate variability in the phytolith assemblages (Figure 5.1.5). Polyhedrons (non-idioblastic phytoliths) were excluded, since they may be the result of taphonomic processes. When all sampled horizons are analysed togheter (holorganic and organo-mineral), the first axis account for over 82% of variance (Figure 5.1.5). Ten groups were indentified on the basis of morphotype frequency:

1) BA-HO4 all the horizons :OF, A, AE;
2) BA-HO2: OF1, FK3: A;
3) BA-HO1: OF/OH, AE 8-9 cm, AE 5-6 cm;
4) AR3: OA, BA-LE6: AE;
5) AR2: A, FK1: OH;
6) FK2: A, BA-LE5: OHA;
7) AR1: OH; BA-HO4, A(E);
8) FK1:AE; BA-LE6: A;
9) BA-HO1: AE; BA-HO2:OF2; AR3: A;
10) BA-HO1: AE; BA-LE5: AE.

The identified groups either associate several horizons of the same soil (ex. group 1 and 3), or similar horizons of different soils (ex. group 4 and 8). In some cases the groups do not seem to show any clear trend.

In addition, if PCA is run for the holorganic horizons "O" and the organo-mineral horizons "A" separately, all the variance is explained by only one factor, i.e. no significative variability exists among sites if only similar horizon types are taken.

5.1.4.5 Theoretical input of phytoliths (Tables 5.1.5-5.1.8)

In Tables 5.1.5- 5.1.8 the results of the frequency of phytoliths and the theoretical phytolith percentage (P_{THEO}) are compared. The agreement between predictions and findings was different for different morphotypes. In general, in the uppermost horizons (O), the agreement between counted phytoliths and theoretical production was high. In particular the frequency of short cells in the horizons O showed to be predictable on the basis of grassland theoretical production. In the horizons A, instead, short cells are accumulated with values that are about twice the predicted ones, (e.g. the surface ones in AR2, AR3, BA-LE6, BA-LE5, FK2 and BA-HO1). For other grass morphotypes findings were less consistent with predictions. Cork cells predictions were much higher than real findings in all the sites, and also epidermal silicified cells (rods) are present in much lower percentages than expected. Bulliform cells, were rare in soil as expected. For the conical morphotypes, distinctive of *Cyperaceae* (sedges), the divergence between expected and measured values is very high. Interestingly, predictions of trichoma production were constantly underestimated.

PCA ordination of sites on the basis of the theoretical input of phytolith (P_{THEO}) higlighted 5 groups (Fig. 5.1.6):

1) BA-LE5, BA-LE7, AR2, AR1: this group is characterised by high frequency of short cells (>37%), and a low concentration of cones (between 3.46 and 11.58%); AR1 is partly separated because of the high concentration of polyhedrons (10.02%).

2) BA-HO1, BA-HO2, BA-HO4, FK1 sites are dominated by grasses, they result grouped by a very high concentration of short cells (always > 41%), cones are nearly absent.

Groups 1 and 2 are very close, having in common an high concentration of rods and corks.

3) FK2 and BA-LE6: these sites are dominated by *Carex* species and are grouped because of the high expected frequency of cones (29.58% and 54.75%).

4) AR3 stands alone and it is distinguished by the high values both of cones (34.42%) and short cells (25.49%).

5) FK3 is distinguished by high frequency of cones (46.83%), polyhedrons (24.5%), and stomata (13.7%).

Figure 5.1.4 Biogenic silica percentage content (dry soil weight); frequency of Al phytoliths; frequency of some selected morphotypes (Tables 5.1.5-5.1.18).

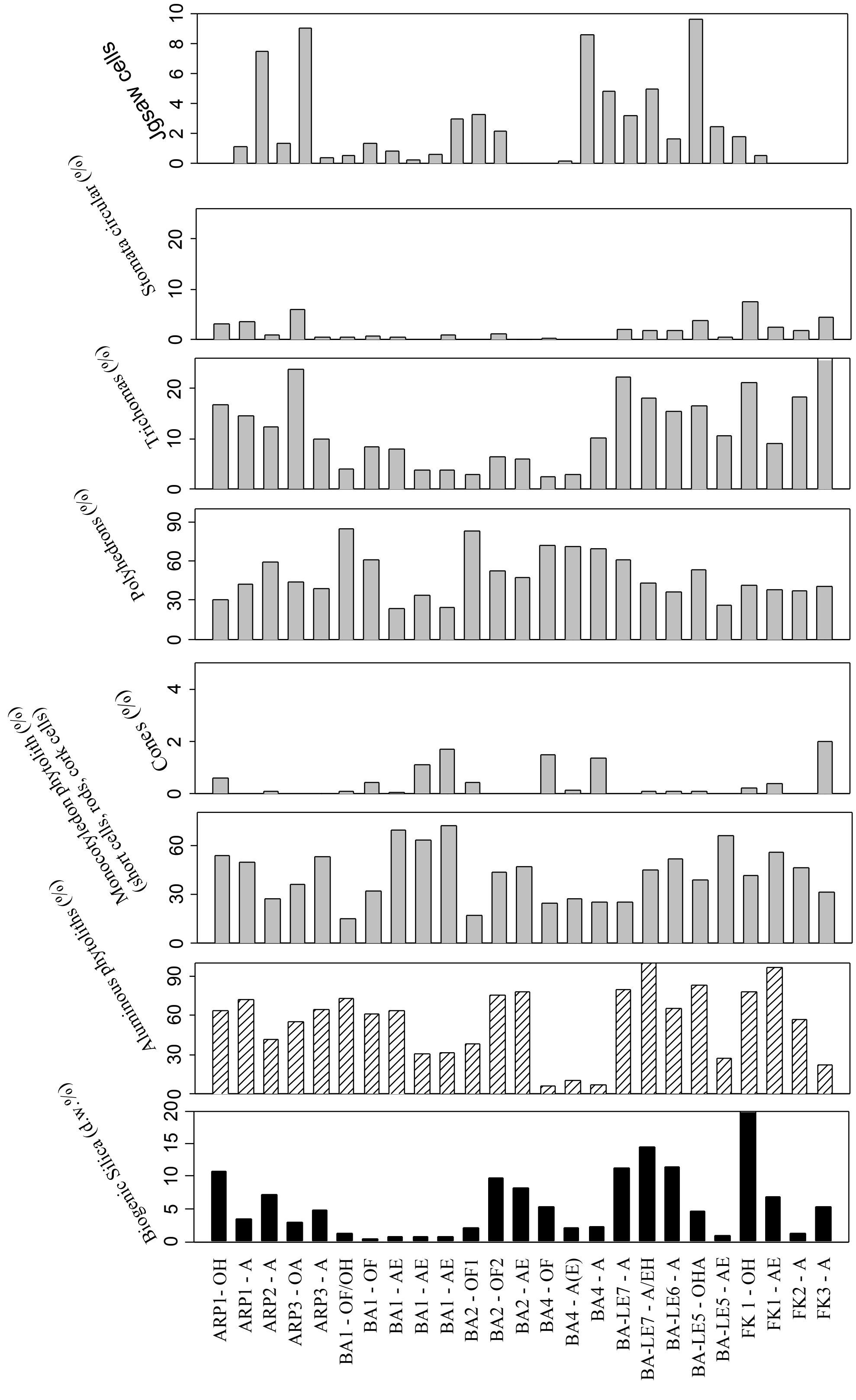
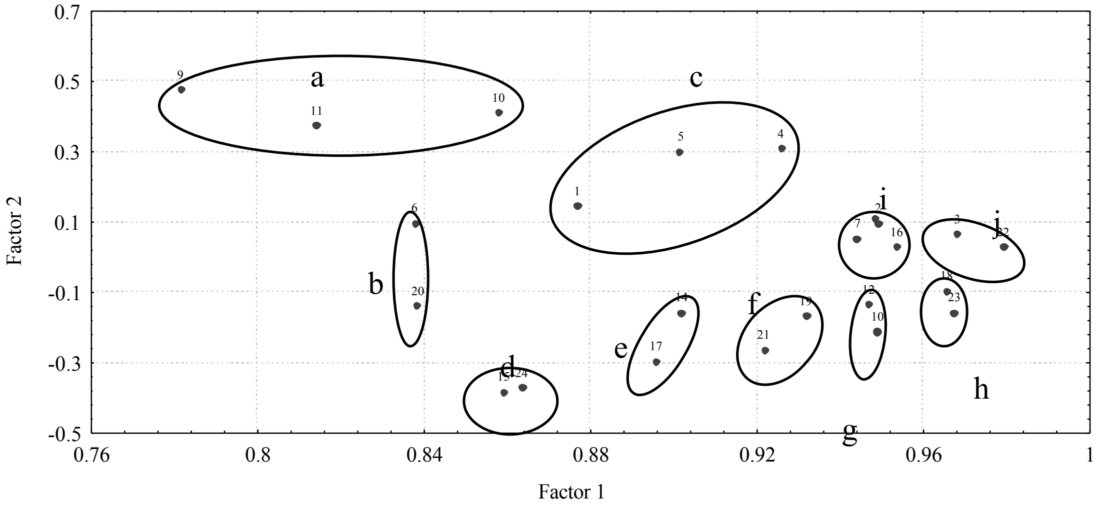


Figure 5.1.5 PCA analysis of phytoliths counts in all the samples. Data were square root transformed; polyhedrons were excluded.



Legend:

N°	Site	Horizon	Depth (cm)	Factor 1	Factor 2
1	BA-HO1	OF/OH	0-1	.87685	.146067
2	BA-HO1	AE	2-3	.94921	.097611
3	BA-HO1	AE	3-4	.96826	.065503
4	BA-HO1	AE	5-6	.92588	.306784
5	BA-HO1	AE	8-9	.90170	.298990
6	BA-HO2	OF1	1-2	.83793	.097195
7	BA-HO2	OF2	2-3	.94423	.051988
8	BA-HO2	AE	3-6	.94851	.108681
9	BA-HO4	OF	0-3	.78166	.473945
10	BA-HO4	A(E)	3-4	.85807	.408664
11	BA-HO4	A	4-7	.81430	.374622
12	ARP1	OH	5-10	.94697	-.134952
13	ARP1	A	7-12	.94914	-.211477
14	ARP2	A	5-2	.90196	-.159056
15	ARP3	OA	0-2	.85911	-.384182
16	ARP3	A	2-7	.95377	.028396
17	FK 1	OH	1.5-3	.89587	-.296890
18	FK1	AE	3-4/6	.96567	-.096364
19	FK2	A	0-3	.93202	-.169277
20	FK3	A	0-3	.83852	-.138523
21	BA-LE5	OHA	1.5-3.5	.92189	-.263985
22	BA-LE5	AE	2-6	.97934	.029310
23	BA-LE6	A	3-4	.96756	-.158337
24	BA-LE7	A	1-2/3	.86368	-.372625
Expl. Var				19.83828	1.390974
Prp.Totl				.82660	.057957

Factor	Eigenval.	Variance	Eigenval
1	19.83828	82.65952	19.83828
2	1.39097	5.79572	21.22926

Figure 5.1.6 PCA ordination of the sites on the basis of the theoretical phytolith input of phytoliths (P_{THEO}). Extraction of principal components.
1) BA-LE5, BA-LE7, AR2, AR1; 2) BA-HO1, BA-HO2, BA-HO4, FK1

	Factor 1	Factor 2
AR1	-.912426	-.096812
AR2	-.957205	.032618
AR3	-.883769	.386920
BA-HO1	-.948748	-.196080
BA-HO2	-.950174	-.212180
BA-HO4	-.946805	-.212877
BA-LE7	-.967496	-.041982
BA-LE6	-.353837	.862315
BA-LE5	-.962305	-.121365
FK1	-.948448	-.205342
FK2	-.504068	.817651
FK3	.063158	.961928
Expl.Var	8.374108	2.685032

Factor	Eigenval	% total variance	Cumul. Eigenval	Cumul. %
1	8.374108	69.78424	8.37411	69.78424
2	2.685032	22.37526	11.05914	92.15950

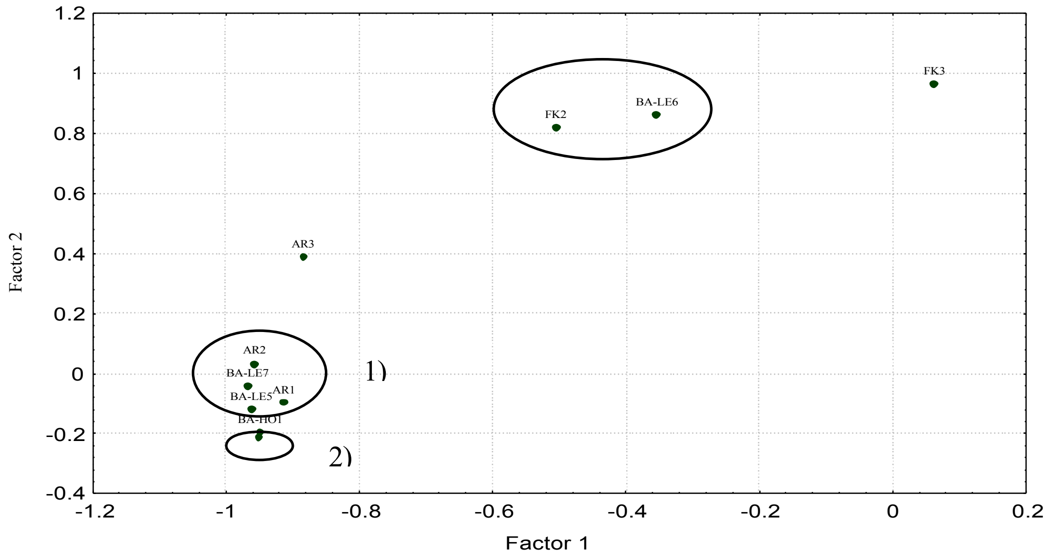


Table 5.1.3 Vegetation relevées.

Species	ARP1	BA4	ARP2	ARP3	BA1	BA-LE6	BA-LE7	BA-LE5	FK1	BA2	FK2	FK3	Frequency
Elevation (m a.s.l.)	2375	2830	2565	2720	2358	2450	2305	2550	2403	2570	2618	2785	
Aspect	S	E	S	S	ESE	S	S	ESE	SE	-	-	WNW	
Slope (°)	33	20	33	32	18	12	20	12	12	3	2	16	
Soil	podzol	alocrisol	alocrisol	brunisol	podzol	podzol	podzol	podzol	podzol	podzol	alocrisol	alocrisol	
Humus type	dysmoder	hemimoder	dysmoder	-	eumoder	hemimoder	dysmull	eumoder	mor	hemimoder	mesomull	mesomull	
Surface (m^2)	4	4	4	4	4	4	4	4	4	4	4	4	
Number of species ()= slightly >4m2	29	15 (16)	20 (26)	30 (35)	33 (39)	11	10	12 (13)	20	19 (22)	11	14	
Juniperus communis subsp. *nana* Syme	2.3b		(+.2)	(+)									3
Festuca scabriculmis subsp. *luedii* (Hackel.) Richter	3.2b												1
Calluna vulgaris (L.) Hull	3.2a												1
Veronica fruticans Jacq.	+.2												1
Agrostis schraderiana Bech.		3.5b	+.2	2.3a						+.2			4
Alchemilla fissa aggr.		2.3b			+								2
Juncus jacquinii L.		2.2b											1
Cerastium cerastioides (L.) Britton		1.1											1
Cirsium spinosissimum (L.) Scop.		1.3											1
Festuca nigrescens Lam.			3.2b	2.2b	2.2b		+.2		+.2				5
Vaccinium vitis-idaea L.	2.2a		(+.2)	(+)									3
Vaccinium myrtillus L.	+		(+.2)	+					+.2				4
Rhododendron ferrugineum Linn.	+.2		(+.2)	(+)									3
Pinus cembra L.			(+.2)	(+)									2
Sibbaldia procumbens L.			+.2	1.2									2
Senecio incanus L.			r	+									2
Solidago virgaurea subsp. minuta (L.) Archangeli					(+)	+.2	+.2						3
Trifolium alpinum L.					2.2b	3.3b	5.4a	+.2	1.2				5
Nardus stricta L.	1.2		2.2b	1.2	2.2b	3.2a	3.2a	4.4b	4.5b	2.2a			9
Carex curvula All.								2.2a	1.2	3.4b	4.5b	3.3a	5
Veronica bellidioides L.				+.2						(+.2)	1.2	1.3	4
Leontodon helveticus Merat	+.2	1.2	+.2	1.2	2.2a	+	+.2	2.2a	2.2b	3.2a	2.2a	+.2	12
Anthoxantum alpinum Löve et Löve	+.2	1.2a	+.2		1.1	+.2	+.2	2.2a	1.2	+.2			9
Geum montanum L.	+.2	2.3b	2.2b	2.3b	1.1			+	+	1.2			8
Carex sempervirens Vill.	1.2		2.2a	2.2	3.2b	3.2b	1.2	1.2	+.2				8
Potentilla aurea L.		+.2	2.2a	1.3	1.2	+.2		1.2	1.2	3.2a			8
Poa alpina L.		2.2	+.2	1.1	1.1a				+	2.2m	r	+.2	8
Leucanthemopsis alpina (L.) Heywood		(+)		1.2		+.2		(+.2)	+.2	+.2	1.2	+	8
Helictotrichon versicolor (Vill.) Pilger	+.2					+.2		1.2	1.2m	2.2a	+.2	+.2	7
Euphrasia minima Schl.			1.2m	1.2	+.2				+.1	+	r	+.2	7
Homogyne alpina (L.) Cassini			+	+.2	2.2a			+.2	+.2	+			6

Agrostis rupestris All.				1.2m	+.2				+.2	+.2	2.2.a	+.2	6
Campanula scheuchzeri Vill.	+	1.2a	+	1.2m	+					+.2			5
Luzula lutea (All.) DC.	+.2	+	2.1m	+.2						(+.2)			5
Deschampsia flexuosa (L.) Trinius	+.2		(+.2)	2.3b					1.2m				4
Phyteuma hemisphaericum L.			+	1.2							+.2	+.2	4
Ligusticum mutellina (L.) Crantz					2.2b			2.2a	+	2.3b			4
Ranunculus villarsii DC.	+.2		+		2.2b								3
Vaccinium uliginosum subsp. *microphyllum* L.	2.2a			+					+.2				3
Veronica alpina L.		1.2a	+	1.2									3
Sempervivum montanum L.		(+.2)	+			+.2							3
Plantago alpina L.				+.2	2.2					+.2			3
Gnaphalium supinum L.				+.2						+.2	+.2		3
Campanula barbata L.	+				1.2								2
Soldanella alpina L.	+				2.2								2
Phyteuma betonicifolium Vill.	+				+								2
Leucorchis albida (L.)	+						+						2
Luzula spicata (L.) DC.				+.2					+				2
Festuca halleri All.				+.2						+.2			2
Ligusticum mutellinoides (Crantz) Vill.				+								1.1m	2
Luzula multiflora (Retzius) Lejeune					+	+							2
Potentilla erecta (L.) Räuschel					(+.2)		1.1						2
Phleum rhaeticum (Humpries) Rauschert					+					1.2			2
Arnica montana L.					+					(+.2)			2
Polygonum viviparum L.					1.2							1.1m	2
Bupleurum stellatum L.	+.2												1
Gentiana campestris L.	+												1
Lotus corniculatus L.	+.2												1
Pedicularis tuberosa L.	+												1
Pulsatilla *alpina* subsp. *sulphurea* (L.) DC.	+												1
Pulsatilla vernalis (L.) Miller	+												1
Silene rupestris L.	+.2												1
Taraxacum gr. *alpinum*		1.2											1
Juncus trifidus L.			+.2										1
Alchemilla conjunta aggr.				1.2									1
Sedum alpestre Vill.				+.2									1
Empetrum nigrum subsp. *hermaphroditum* (Hagerup) Böcher				(+)									1
Pedicularis kerneri Dalla Torre				r									1
Alchemilla glabra aggr.					+								1
Briza media L.					(+.2)								1
Carex pallescens L.					+								1
Coeloglossum viride (L.) Hart.					(+)								1
Crocus albiflorus Kitaibel					+.2								1
Gentiana acaulis L.					1.2								1
Helianthemum nummularium subsp. *grandiflorum* L.					(+)								1
Hieracium lactucella Wallroth					+								1
Lotus alpinus >*corniculatus* (DC.) Ramond					+								1

Nigritella rhellicani Teppner et Klein					+.2								1
Trifolium pratense subsp. *nivale* (Koch) Archangeli					+								1
Trollius europaeus L.					(+.2)								1
*Viola cal*carata L.					+								1
Hieracium pilosella L.							+.2						1
Loiseleuria procumbens (L.) Desvaux								+.2					1
Soldanella pusilla Baumgarten											+.2		1
Salix herbacea L.												2.3b	1
Minuartia sedoides (L.) Hiern												+.2	1
Alchemilla pentaphyllea L.												+	1

Table 5.1.3 Species cover percentage in the sampling sites. (* = species employed in the calculation of the theoretical input of phytoliths P_{THEO})

Species	AR1	AR2	AR3	BA-HO1	BA-HO2	BA-HO4	BA-LE7	BA-LE6	BA-LE5	FK1	FK2	FK3
* *Agrostis rupestris* All.			0.02	0.02	0.02					0.02	1	0.02
* *Agrostis schraderiana* Bech.		0.02	1		0.02	44						
* *Anthoxantum alpinum* Löve et Löve	0.02	0.02		2.50	0.02	2.50	0.02	0.02	1	2.50		
* *Briza media* L.				0.02								
* *Calluna vulgaris* (L.) Hull	31											
* *Carex curvula* All.					44				1	2.50	69	31
* *Carex pallescens* L.				0.02								
* *Carex sempervirens* Vill.	2.50	1	2	44			2.50	44	2.50	0.02		
* *Deschampsia flexuosa* (L.) Trinius	0.02	0.02	2							0.02		
* *Festuca halleri* All.			0.02		0.02							
* *Festuca nigrescens* Lam.		44	2	2			0.02			0.02		
* *Festuca scabriculmis subsp. luedii* (Hackel.) Richter	44											
* *Helictotrichon versicolor* (Vill.) Pilger	0.02				1			0.02	2.50	0.02	0.02	0.02
* *Juniperus communis subsp. Nana* Syme	2	0.02	0.02									
* *Nardus stricta* L.	2.50	2	2.50	2	1		31	31	69	69		
* *Pinus cembra* L.		0.02	0.02									
* *Poa alpina* L.		0.02	2.50	2.50	2.50	15				0.02	0.01	0.02
* *Rhododendron ferrugineum* Linn.	0.02	0.02	0.02									
* *Vaccinium myrtillus* L.	0.02	0.02	0.02							0.02		
* *Vaccinium uliginosum subsp. microphyllum* L.	1		0.02							0.02		
* *Vaccinium vitis-idaea* L.	1	0.02	0.02									
Alchemilla conjunta aggr.			2.50									
Alchemilla fissa aggr.				0.02		2						
Alchemilla glabra aggr.				0.02								
Alchemilla pentaphyllea L.												0.02
Arnica montana L.				0.02	0.02							
Bupleurum stellatum L.	0.02											
Campanula barbata L.	0.02			2.50								
Campanula scheuchzeri Vill.	0.02	0.02	0.02	0.02	0.02	2.50						
Cerastium cerastioides (L.) Britton						2.50						
Cirsium spinosissimum (L.) Scop.						2.50						
Coeloglossum viride (L.) Hart.				0.02								
Crocus albiflorus Kitaibel				0.02								
Empetrum nigrum subsp. hermaphroditum (Hagerup) Böcher			0.02									
Euphrasia minima Schl.		0.02	2.50	0.02	0.02					0.02	0.01	0.02
Gentiana acaulis L.				2.50								
Gentiana campestris L.	0.02											
Geum montanum L.	0.02	2	2	2.50	2.50	2			0.02	0.02		
Gnaphalium supinum L.			0.02		0.02						0.02	
Helianthemum nummularium subsp. grandiflorum L.				0.02								
Hieracium lactucella Wallroth				0.02								

Hieracium pilosella L.							0.02					
Homogyne alpina (L.) Cassini		0.02	0.02	1	0.02				0.02	0.02		
Juncus jacquinii L.						2						
Juncus trifidus L.		0.02										
Leontodon helveticus Merat	0.02	0.02	2.50	1	31	2.50	0.02	0.02	1	2	1	0.02
Leucanthemopsis alpina (L.) Heywood			2.50		0.02	0.02		0.02	0.02	0.02	2.50	0.02
Leucorchis albida (L.)	0.02						0.02					
Ligusticum mutellina (L.) Crantz				2	2				1	0.02		
Ligusticum mutellinoides (Crantz) Vill.			0.02									0.02
Loiseleuria procumbens (L.) Desvaux									0.02			
Lotus alpinus (DC.) Ramond				0.02								
Lotus corniculatus L.	0.02											
Luzula lutea (All.) DC.	0.02	2.50	0.02		0.02	0.02						
Luzula multiflora (Retzius) Lejeune				0.02				0.02				
Luzula spicata (L.) DC.			0.02							0.02		
Minuartia sedoides (L.) Hiern												0.02
Nigritella rhellicani Teppner et Klein				0.02								
Pedicularis kerneri			0.01									
Pedicularis tuberosa L.	0.02											
Phleum rhaeticum (Humpries) Rauschert				0.02	2.50							
Phyteuma betonicifolium Vill.	0.02			0.02								
Phyteuma hemisphaericum L.		0.02	2.50								0.02	0.02
Plantago alpina L.			0.02	15	0.02							
Polygonum viviparum L.				2.50								0.02
Potentilla aurea L.		1	2.50	2.50	31	0.02		0.02	2.50	2.50		
Potentilla erecta (L.) Räuschel				0.02			2.50					
Pulsatilla alpina subsp. sulphurea (L.) DC.	0.02											
Pulsatilla vernalis (L.) Miller	0.02											
Ranunuculus villarsii DC.	0.02	0.02		2								
Salix herbacea L.												2
Sedum alpestre Vill.			0.02									
Sempervivum montanum L.		0.02				0.02		0.02				
Senecio incanus L.		0.01	0.02									
Sibbaldia procumbens L.		0.02	2.50									
Silene rupestris L.	0.02											
Soldanella alpina L.	0.02			15								
Soldanella pusilla Baumgarten											0.02	
Solidago virgaurea subsp. minuta (L.) Archangeli				0.02			0.02	0.02				
Taraxacum gr. alpinum						2.50						
Trifolium alpinum L.				2			81	44	0.02	2.50		
Trifolium pratense subsp. nivale (Koch) Archangeli				0.02								
Trollius europaeus L.				0.02								
Veronica alpina L.		0.02	2.50			2.50						
Veronica bellidioides L.			0.02		0.02						2.50	2.50
Veronica fruticans Jacq.	0.02											
Viola calcarata L.				0.02								

Table 5.1.4 Vegetation relevees in the sampling sites used for calculating the theoretical input of phytoliths. Percentage cover is here normalized to one. (* = species employed in the calculation of the theoretical input of phytoliths P_{THEO})

Species		AR1	AR2	AR3	BA-HO1	BA-HO2	BA-HO41	BA-LE7	BA-LE6	BA-LE5	FK1	FK2	FK3
Agrostis rupestris All.	*			0.00017	0.00009	0.00013					0.00020	0.10627	0.00037
Agrostis schraderiana Bech.	*		0.00019	0.08666		0.00013	0.32216						
Anthoxantum alpinum Löve et Löve	*	0.00017	0.00019		0.01180	0.00013	0.01830	0.00017	0.00017	0.08576	0.02518		
Briza media L.	*				0.00009								
Carex curvula All.	*					0.28616				0.08576	0.02518	0.73326	0.57707
Carex pallescens L.	*				0.00009								
Carex sempervirens Vill.	*	0.02076	0.09356	0.17333	0.20761			0.02135	0.36925	0.02144	0.00020		
Deschampsia flexuosa (L.) Trinius	*	0.00017	0.00019	0.17333							0.00020		
Festuca halleri All.	*			0.00017		0.00013							
Festuca nigrescens Lam.	*		0.41168	0.17333	0.09437			0.00017			0.00020		
Festuca scabriculmis subsp. luedii (Hackel.) Richter	*	0.36533											
Nardus stricta L.	*	0.02076	0.18713	0.02167	0.09437	0.06504		0.26469	0.26015	0.59177	0.69500		
Poa alpina L.	*		0.00019	0.02167	0.01180	0.01626	0.10983				0.00020	0.00011	0.00037
Calluna vulgaris (L.) Hull	*	0.25739											
Rhododendron ferrugineum Linn.	*	0.00017	0.00019	0.00017									
Vaccinium myrtillus L.	*	0.00017	0.00019	0.00017							0.00020		
Vaccinium uliginosum subsp. microphyllum L.	*	0.08303		0.00017							0.00020		
Vaccinium vitis-idaea L.	*	0.08303	0.00019	0.00017									
Juniperus communis subsp. nana Syme	*	0.16606	0.00019	0.00017									
Pinus cembra L.	*		0.00019	0.00017									
Helictotrichon versicolor (Vill.) Pilger		0.00017				0.06504			0.00017	0.02144	0.00020	0.00021	0.00037
Pedicularis kerneri				0.00009									
Loiseleuria procumbens (L.) Desvaux										0.00017			
Alchemilla conjunta aggr.				0.02167									
Alchemilla fissa aggr.					0.00009		0.14643						
Alchemilla glabra aggr.					0.00009								
Alchemilla pentaphyllea L.													0.00037
Arnica montana L.					0.00009	0.00013							
Bupleurum stellatum L.		0.00017											
Campanula barbata L.		0.00017			0.01180								
Campanula scheuchzeri Vill.		0.00017	0.00019	0.00017	0.00009	0.00013	0.01830						
Cerastium cerastioides (L.) Britton							0.01830						
Cirsium spinosissimum (L.) Scop.							0.01830						
Coeloglossum viride (L.) Hart.					0.00009								
Crocus albiflorus Kitaibel					0.00009								
Euphrasia minima Schl.			0.00019	0.02167	0.00009	0.00013					0.00020	0.00011	0.00037
Gentiana acaulis L.					0.01180								
Gentiana campestris L.		0.00017											
Geum montanum L.		0.00017	0.18713	0.17333	0.01180	0.01626	0.14643			0.00017	0.00020		
Gnaphalium supinum L.				0.00017		0.00013						0.00021	
Helianthemum nummularium subsp. grandiflorum L.					0.00009								
Hieracium lactucella Wallroth					0.00009								
Hieracium pilosella L.								0.00017					
Homogyne alpina (L.) Cassini			0.00019	0.00017	0.04718	0.00013				0.00017	0.00020		
Juncus jacquinii L.							0.14643						
Juncus trifidus L.			0.00019										
Leucanthemopsis alpina (L.) Heywood				0.02167		0.00013	0.00015		0.00017	0.00017	0.00020	0.02657	0.00037
Leucorchis albida (L.)		0.00017						0.00017					
Ligusticum mutellina (L.) Crantz					0.09437	0.13007				0.08576	0.00020		
Ligusticum mutellinoides (Crantz) Vill.				0.00017									0.00037
Lotus alpinus (DC.) Ramond					0.00009								
Lotus corniculatus L.		0.00017											
Minuartia sedoides (L.) Hiern													0.00037
Nigritella rhellicani Teppner et Klein					0.00009								
Pedicularis tuberosa L.		0.00017											
Phleum rhaeticum (Humpries) Rauschert					0.00009	0.01626							
Phyteuma betonicifolium Vill.		0.00017			0.00009								
Phyteuma hemisphaericum L.			0.00019	0.02167								0.00021	0.00037
Plantago alpina L.				0.00017	0.07077	0.00013							
Polygonum viviparum L.					0.01180								0.00037
Potentilla aurea L.			0.09356	0.02167	0.01180	0.20161	0.00015		0.00017	0.02144	0.02518		
Potentilla erecta (L.) Räuschel					0.00009			0.02135					
Pulsatilla alpina subsp. sulphurea (L.) DC.		0.00017											
Pulsatilla vernalis (L.) Miller		0.00017											

Ranunuculus villarsii DC.	0.00017	0.00019		0.09437								
Sedum alpestre Vill.			0.00017									
Sempervivum montanum L.		0.00019				0.00015		0.00017				
Senecio incanus L.		0.00009	0.00017									
Sibbaldia procumbens L.		0.00019	0.02167									
Silene rupestris L.	0.00017											
Soldanella alpina L.	0.00017			0.07077								
Soldanella pusilla Baumgarten											0.00021	
Solidago virgaurea subsp. minuta (L.) Archangeli				0.00009			0.00017	0.00017				
Taraxacum gr. alpinum						0.01830						
Trifolium alpinum L.				0.09437			0.69160	0.36925	0.00017	0.02518		
Trifolium pratense subsp. nivale (Koch) Archangeli				0.00009								
Trollius europaeus L.				0.00009								
Veronica alpina L.		0.00019	0.02167			0.01830						
Veronica bellidioides L.			0.00017		0.00013						0.02657	0.04654
Veronica fruticans Jacq.	0.00017											
Viola calcarata L.				0.00009								
Leontodon helveticus Merat	0.00017	0.00019	0.02167	0.04718	0.20161	0.01830	0.00017	0.00017	0.08576	0.20145	0.10627	0.00037
Luzula lutea (All.) DC.	0.00017	0.02339	0.00017		0.00013	0.00015						
Luzula multiflora (Retzius) Lejeune				0.00009				0.00017				
Luzula spicata (L.) DC.			0.00017							0.00020		
Salix herbacea L.												0.37230
Empetrum nigrum subsp. hermaphroditum (Hagerup) Böcher			0.00017									

Table 5.1.5 Val d'Arpette. Phytoliths morphotypes (%) in the soil horizons, sampling depth (cm), and total number of phytoliths counted (Total). The theoretical percentage input of morphotypes (P_{THEO}) calculated on the basis of present vegetation phytolith production.

	ARP1			ARP2		ARP3		
Horizon	OH	A	P_{THEO}	A	P_{THEO}	OA	A	P_{THEO}
Depth (cm)	5-10	7-12		5-2		0-2	2-7	
Morphotypes	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Short cells	52.5	49.0	47.44	27.0	46.73	35.7	53.1	34.42
Bulliforms	0.0	0.0	0.18	0.0	0.24	0.0	0.0	0.27
Rods	0.3	0.6	11.69	0.4	14.06	0.0	0.1	14.35
Cork cells	0.0	0.0	14.72	0.0	17.91	0.0	0.0	17.39
Cones	0.6	0.0	3.46	0.1	11.58	0.0	0.0	25.49
Trichomas	16.8	14.6	6.17	12.4	5.10	23.8	10.1	3.94
Jigsaw cells	1.1	7.4	2.07	1.3	0	9.0	0.4	0
Stomata	3.3	3.8	2.38	1.0	0.44	6.4	0.4	0.72
Mesophyll cells	0.1	0.0	0.62	0.0	0.49	0.0	0.1	0.30
Spherical	0.0	0.0	0.01	0.1	0.03	0.0	0.6	0.06
Vessel spiral thickenings	0.0	0.0	0.03	0.3	0	0.0	0.0	0
Polyhedrons	25.2	24.5	10.02	57.1	2.77	25.1	35.2	1.88
Others	0.1	0.0	1.22	0.3	0.65	0.0	0.0	1.17
Total counted	1487	994		1344		454	786	

Table 5.1.6 Belalp Hofathorn. Phytoliths morphotypes (%) in the soil horizons, sampling depth (cm), and total number of phytoliths counted (Total). The theoretical percentage input of morphotypes (P_{THEO}) calculated on the basis of present vegetation phytolith production.

	BA-HO1						BA-HO2				BA-HO4			
Horizon	OF/OH	AE	AE	AE	AE	P_{THEO}	OF1	OF2	AE	P_{THEO}	OF	A(E)	A	P_{THEO}
Depth (cm)	0-1	2-3	3-4	5-6	8-9		1-2	2-3	3-6		0-3	3-4	4-7	
Morphotypes	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Short cells	13.1	29.8	68.3	58.1	64.0	51.76	13.9	41.7	44.8	43.33	16.2	21.0	17.6	42.17
Bulliforms	0.3	0.6	0.1	0.4	0.6	0.29	0.4	0.0	0.5	0.42	1.5	0.2	1.8	0.40
Rods	0.9	1.1	0.7	2.6	5.0	15.49	2.1	1.2	0.7	18.25	4.1	5.0	4.0	18.67
Cork cells	0.4	0.1	0.1	0.7	0.8	23.74	0.4	0.5	0.6	32.46	0.7	0.6	0.4	33.23
Cones	0.1	0.4	0.0	1.1	1.7	0.04	0.4	0.0	0.0	0	1.5	0.1	1.3	0
Trichomas	4.1	8.4	8.0	3.7	3.9	5.22	3.0	6.4	6.1	3.89	2.5	2.9	10.1	3.92
Jigsaw cells	0.5	1.3	0.8	0.2	0.6	0	3.0	3.3	2.1	0	0.0	0.0	0.1	0
Stomata	0.5	0.9	0.6	0.0	0.8	0.29	0.0	1.2	0.1	0.42	0.3	0.0	0.0	0.40
Mesophyll cells	0.0	0.0	0.1	0.0	0.0	0.40	0.0	0.0	0.0	0	0.0	0.0	0.0	0
Spherical	0.5	0.0	0.4	0.2	0.0	0	0.0	0.0	0.0	0	2.9	0.0	0.0	0
Vessel spiral thickenings	0.0	0.0	0.0	0.0	0.3	0	0.4	0.2	0.1	0	0.0	0.0	0.0	0
Polyhedrons	79.8	57.9	21.0	33.4	22.9	2.38	76.8	45.5	45.5	0.61	71.7	70.4	66.4	0.60
Others	0.0	0.0	0.0	0.0	0.0	0.38	0.0	0.0	0.0	0.62	0.0	0.0	0.0	0.60
Total	1158	996	2792	458	358		237	580	1279		870	941	672	

Table 5.1.7 Belalp Lengi-Egga. Phytoliths morphotypes (%) in the soil horizons, sampling depth (cm), and total number of phytoliths counted (Total). The theoretical percentage input of morphotypes (P_{THEO}) calculated on the basis of present vegetation phytolith production.

	BA-LE7			BA-LE6		BA-LE5		
Horizon	A	A/EH	P_{THEO}	A	P_{THEO}	OHA	AE	P_{THEO}
Depth (cm)	1-3	3-4		3-4		1.5-3.5	2-6	
Morphotypes	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Short cells	24.8	45	37.69	50.4	13.59	38.1	63.4	39.21
Bulliforms	0.1	0.0	0.38	0.1	0.26	0.0	0.3	0.42
Rods	0.4	0.1	17.83	0.4	13.34	0.2	2.0	17.91
Cork cells	0.0	0.0	29.72	0.1	10.98	0.0	0.0	30.92
Cones	0.0	0.1	8.61	0.1	54.75	0.0	0.2	4.73
Trichomas	22.4	18	3.67	15.4	2.35	16.7	10.6	3.83
Jigsaw cells	8.6	5.0	0	9.6	0	4.9	1.6	0
Stomata	2.0	2.0	0.53	2.5	1.21	4.1	0.8	0.83
Mesophyll cells	0.0	0.1	0.02	0.0	0.14	0.0	0.1	0.01
Spherical	0.6	0.3	0.02	0.0	0.14	0.2	0.6	0.01
Vessel spiral thickenings	0.4	0.1	0	0.2	0	0.5	0.5	0.01
Polyhedrons	40.8	30	0.69	21.3	1.14	35.1	20.1	1.31
Others	0.1	0.0	0.84	0.0	2.09	0.1	0.0	0.82
Total	1583	2105		1828		1013	1892	

Table 5.1.8 Furka. Phytoliths morphotypes (%) in the soil horizons, sampling depth (cm), and total number of phytoliths counted (Total). The theoretical percentage input of morphotypes (P_{THEO}) calculated on the basis of present vegetation phytolith production.

	FK 1			FK2		FK3	
Horizon	OH	AE	P_{THEO}	A	P_{THEO}	A	P_{THEO}
Depth (cm)	1.5-3	3-6		0-3		0-3	
Morphotypes	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Short cells	40.6	54.6	41.83	45.5	15.68	28.4	0.27
Bulliforms	0.0	0.0	0.41	0.0	1.09	0.0	1.49
Rods	0.5	0.1	18.54	0.2	8.89	0.2	3.18
Cork cells	0.0	0.0	32.95	0.0	12.36	0.2	0.18
Cones	0.2	0.4	0.40	0.0	29.58	2.0	46.83
Trichomas	21.2	9.2	3.92	18.4	4.21	27.9	4.39
Jigsaw cells	9.6	2.5	0	1.8	0	0.5	0
Stomata	7.4	2.8	0.51	2.0	8.86	4.5	13.79
Mesophyll cells	0.0	0.0	0	0.0	0	0.0	0
Spherical	0.2	0.2	0	0.2	0	0.0	0
Vessel spiral thickenings	0.1	0.0	03	0.0	0.25	0.7	0.40
Polyhedrons	20.0	30.2	0.79	32.1	15.71	34.9	24.51
Others	0.0	0.0	0.638	0.0	3.36	0.5	4.96
Total	914	1259		664		401	

5.1.5 Discussion

5.1.5.1 Biogenic silica content (Fig.5.1.3; Table 5.1.1)

The content of biogenic silica in top soils is higher (about 10%) in the sites at lower altitude, between about 2300 and 2600 m a.s.l.. At this elevation subalpine meadows are dominated by silica accumulator species (i.e.: *Carex sempervirens*, *Nardus stricta* and *Festuca varia*). In the sites at higher altitude (from above 2600 to about 2800 m a.s.l.) the concentration of biogenic silica in top soil is generally lower than 5%. The change in B.S. values coincides with the transition podzosols/alocrisols (2550-2660 m a.s.l.). Indeed, alpine meadows are dominated by weaker silica accumulator species such as *Carex curvula*. Biogenic silica annual production by alpine meadows was estimated to be one order of magnitude lower than in subalpine grasslands (i.e. 1.2 g m^2 y^{-1} for *Carex curvula* alpine sward and 10.3 g m^2 y^{-1} for *Festuca scabriculmis* subalpine swards) (Carnelli et al., 2001).

The phytoliths occurring in the uppermost part of the soil are the result of the combination of inheritance and dispersal mechanisms (Fredlund and Tieszen, 1994; Barboni et al., 1999; Alexandre et al., 1997). Inheritance refers to decay-in-place mechanisms: decomposition of plant litter releases phytoliths that are incorporated in the soil. The assemblage should be interpreted as representative of the average grassland composition over hundreds of years**,** a time span in which local and regional composition of plant communities may vary considerably (Fredlund and Tieszen, 1994). A fraction of litter does not decay in place, but is subjected to dispersal mechanisms, such as eolian, fire-eolian, herbivory, fluvial and colluvial (Fredlund and Tieszen, 1994). The dominance of one or more of these mechanisms of transport is likely to be different according to the environmental setting. In the American Great Planes fire-eolian dispersal is regarded as the most important mechanism of biomass removal and redistribution, because of high frequency of fires (5-10 years), prior to Euro-American settlement. Fredlund and Tieszen (1994) hypothesise, on the basis of existing models for charcoal dispersal (Clark, 1988), that burnt leaf fragments would be deposited mainly in a relatively close distance (1-5 km)**.** In the same area, herbivory was estimated to be responsible for local-regional dispersal of 25% of plant biomass. These authors estimated that for the American Great Plains between 30% and 70% of the annual budget of biogenic silica for grassland soils has an extra-local and regional origin. This scenario is probably not applicable to the European Alps, where grassland fires were not a traditional agricultural practice, and natural fires are rare. However, grazing can be an important factor of redistribution of biomass. In the study area, herds are moved daily from the valleys bottom to the pastures up slope. In addition to grazing, hay has always been a valuable resource, and its harvest caused a net loss of biomass. Colluvial and hydric (both by water and by avalanches) erosion may contribute to transport of phytoliths to a different extent according to the geomorphological setting, and it is likely to be of relevance on steep slopes, where part or all of the plant biomass is periodically removed by avalanches.

5.1.5.2 Al phytoliths (Fig. 5.1.3; Table 5.1. 1)

X-rays microanalysis was applied on plant silica extracted from 20 species of *Gramineae*, *Cyperaceae*, *Ericaceae*, and *Pinaceae,* sampled in the same area considered for the present research (Carnelli et al., 2002). Among the taxa investigated, only woody species produced high proportions of phytoliths containing aluminium (Carnelli et al., 2002). An average of 72% of the polyhedron phytoliths from alpine heaths and conifers contained aluminium. In contrast, Al polihedron phytoliths were rare or absent in alpine grasses and sedges, and represented only maximum of 10% the examined polyhedrons (e.g. *Carex curvula*). The content of Al in phytoliths is considered an important tool in palaeoecological investigations of terrestrial data sets. The potentials of the tecnique are here tested on soil-born phytoliths.

In the sites below 2600 m a.s.l., the percentage of polyhedron phytoliths containig Al is always higher than 60%, while, at higher altitude sites, Al phytoliths are only about 10% of the polyhedrons tested.

To allow the comparison between B.S. content and Al-phytoliths frequency in the soil horizons, the punctual concentrations of B.S. and Al-B.S. (aluminiuos biogenic silica) were estimated for each soil horizons taking into account soil bulk density. The ratio Al-B.S./B.S. was plotted (Figure 5.1.3). The higher values of this ratio are found in the sites below 2550 m a.s.l., in podzosols. A higher content in Al-silica should be due to higher presence of *Ericaceae* and *Pinaceae*. The high values in AR3 might be attributed to the input of scattered heaths, that are locally present.

5.1.5.3 Influence of the humus type (Table 5.1.1)

Top soil phytolith assemblages integrate the input of phytoliths over a relatively short time scale and should give the record of the recent vegetation history of a site. The extension of time recorded by modern phytolith assemblages, is function of the mean residence time of phytoliths in the holorganic and mineral-organic horizons of the soil. Two factors are relevant in this respect: first, the average life expectancy of phytoliths and, second, the time needed by phytoliths to be translocated to deeper soil horizons. Quantitive data on these issues are missing and simulation in experimentally controlled conditions should be performed. Few qualitative considerations about phytolith life span can be done on the basis of the existing literature.

The rate of weathering of phytoliths was shown to be related to their physical-chemical properties (e.g. hydration state, anticorrrelated with phytolith age, surface/volume ratio, aluminium content) and the rate of soil organic matter decomposition (Bartoli and Wilding, 1980). The latter is slower at high altitude, because of the delay in litter break down as consequence of low temperature and strong solar radiation that reduce microbial activity. The full structural decomposition of leaves may take 2 years in high alpine forbs, 5 years in sedges and 10 years or more in evergreen dwarf shrubs. At low altitude, on the contrary, leaf litter is mostly recycled within a year (Körner, 1999).

Three humus types, with decreasing biological activity, occur in the study area: *mull*, with strong earthworm activity leading to a rapid incorporation of organic matter, *moder*, in which the organic matter decay is slowed down by the absence of anecitic earthworm and by limited fungal activity; and *mor* in which soil fauna is negligible, fungal activity peaks and organic matter accumulates in thick black layers. After the organic matter from the plant tissues is decomposed, the released phytoliths are subjected to soil weathering processes. Phytolith life-span is different for different species and tissues: litter from dicotyledons and grasses with low C/N ratio (originating mull-humus) is more easily mineralised, phytoliths from these plants are also less resistent to dissolution (Bartoli and Wilding, 1980), therefore mull-type humus releases a great quantity of soluble silica which is recycled by the vegetation. Litter from conifers and heaths have a higher C/N ratio and is more slowly mineralised, therefore, release less readily biogenic silica. These species are weak silica accumulator, and have biogenic silica richer in aluminium than the one from herbaceous dycotiledons and grasses (Bartoli, 1985); (Carnelli et al., 2002), therefore, less soluble. These phytoliths are first accumulated in the organo-minerals layers (O and A), a fraction is then leached to the spodic horizons (BPh and BPs) in association with organo-metal complexes, which are typical podzsolisation products (Bartoli and Wilding, 1980). The content of silica in soil developed from rocks poor in weatherable minerals depends principally upon vegetation and humus-type (Duchaufour, 1998).

In general, grasses produce mull-type humus and heaths and conifers mor or moder type, however, in alpine conditions this generalisation is not always valid. For instance, intermediate litter type can act as acidificant or not, according to local conditions (Gobat et al., 1998). Insaturated mor is typical of strongly limited environments (climatically, physically or chemically), in which the biological activity is constrained, e.g. by harsh alpine climatic conditions. The studied podzosols contain moder-type humus, whereas, the alocrisols in general have mull-type humus (Table 5.1. 2). Exception are BA-LE7 and FK1, podzsols that contain dysmull (i.e. mull with slow biological activity) and mor, respectively. In all the soils examined the distribution of B.S. and Al phytoliths followed the same pattern: a maximum in the holorganic (O) and organic-mineral (A) layers, and a diminution, often abrupt, in mineral layers (Chapter 5.2).

5.1.5.4 Morphotype percentages in top soil (Fig 5.1.4; Tables 5.1.5-5.1.8)

In soil samples both idioblastic and irregular phytoliths occur. The idioblastic types most frequently recovered are short cells. Short cells are regularly silicified in grasses and can be easily identified in soil assemblages. Short cell phytoliths show to be well preserved in the top horizons and are accumulated with depth in the organo-mineral horizons A. The presence of other distinctive grass morphotypes, however, is remarkably low (Tables 5.1.5- 5.1.8). Conical types from sedges are also very rarely recovered, despite being produced in some of the stand by true dominant species (*Carex*). The conical types are weakly silicified and seem to have low resistence to taphonomical processes already in the top soil. Silicified trichomas were also recovered frequently, these types are produced both by grass and dicotyledons, and showed to be well preserved both in O and A horizons. Morphotypes originated from dicotyledons (jigsaw cells, circular stomata, vessels with spiral thickening) were present, but with low frequency. It is to note that the frequency of jigsaw cells, that are distictive of dycotiledon species, decreases with increasing altitude (Figure 5.1.3), showing the same pattern of aluminiuos rich biogenic silica (Figure 5.1.4): these result are consistent with the higher frequency of heaths in the subalpine belt.

The production of polyhedral phytoliths in the Plant Kingdom is multiple (of different istological origin) and redundant (from different species). They are the dominant typology in Conifers and *Ericaceae* but they also occur in many monocotyledons (Carnelli et al., in press; Chapter 4.2). This might explain the high frequency of polyhedrons recorded in the top soil.

The PCA ordination of phytolith assemblages grouped either several horizons of the same soil, or horizons of similar type (e.g. A horizons), and in same cases the groups did not seem to show any logical association. No correspondence could be found with the ordination of grasslands based on species presence (Figure 5.1.1), or with the ordination based on the set of dominant species (Figure 5.1.2).

It is to note that even if only the phytolith assemblages of the horizon O (that showed to be the most rapresentative of the plant stand) are included in the analysis, it is not possible to recognise any significant trend. Alpine grasslands do not seem to be distinguishable in ecological meaningful groups on the basis of their phytolith assemblages. This result was, however, expected from the reference collection data that showed that the six dominant grass species occurring in the research area cannot be distinguished on the basis of their phytolith typologies (Carnelli et al., in press; Chapter 4.2). Only grasses belonging to the Festucoideae subfamily occur inside the area, and they all produce similar short cells (e.g. Twiss et al., 1969; Fredlund and Tieszen, 1994). Since examined grasslands have different frequency of grasses and sedges, it was expected, that a distinction might have been possible on the basis of sedge conical morphotypes. Indeed, cone morphotypes are clearly identifiable in reference material (Carnelli et al., in press; Chapter 4.2), but their presence in the phytolith assemblages is minimal or they are totally lacking (e.g. in BA-HO1 and BA-LE6 *Carex sempervirens* turvs are dominant, but cones are not recovered from soils). These typologies are probably too weakly silicified to be preserved in the soil.

5.1.5.5 Theoretical input of phytoliths (Tables 5.1.5-5.1.8; Figure 5.1.6)

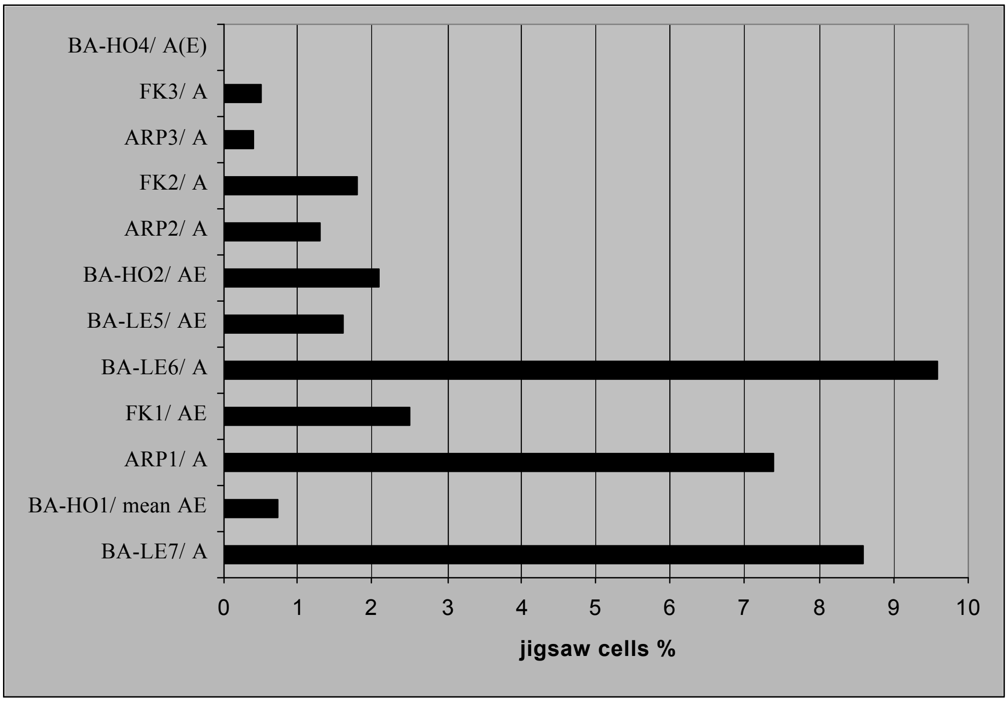
Species cover (Table 5.1.1) was employed to calculate the theoretical input of phytoliths of the alpine and subalpine swards, with the aim of testing the phytolith assemblage predictability on the basis of present vegetation. For the calculation of this estimate plant productivity, biogenic silica content and frequency of morphotypes in plants were taken into consideration (Carnelli et al., 2001, Carnelli et al., 2002).

The agreement between predictions and findings was different for the different typology of phytoliths and in general there was a stronger agreement in the uppermost horizons (O). In the holorganic horizons the deposition process appear to be dominant and P_{THEO} reflects plant stand composition. Deeper in soil, in the horizon A, phytolith concentrations do not reflect present plant stand composition, and they are the result of time integrated dissolution and translocation that overwhelm the deposition process. It is to note that the fate of phytolith morphotypes is different: some typology are accumulated (e.g. short cells), others are not recovered being probably not resistent to taphonomical processes (e.g. cones).

Rod types are present in the soil assemblages in lower percentages than expected: these types are probably not well preserved. Indeed, rods are only herratically silicified, and have a high surface/volume ratio, which makes them fragile and easy to dissolve. After fragmentation in soil, they are likely to be identified as polyhedrals. Conical morphotyphes were nearly absent in the soil assemblages, while they are produced in high quantities from plant stand (e.g. in BA-LE6 (A) 54.75% is the theoretical production, while only 0.1% occur in soil). They must be dissolved already in the top horizons.

The agreement between expected values and findings was good for short cells in the majority of the sites in the holorganic horizons OH or OA, while in the deeper mineral-organic horizon A short cells show to be accumulated.

Figure 5.1.5 Frequency of jigsaw cells in the A horizons of the all the sites. Sites are displayed with incresing altitude.



Differences between predicted production of cork cells and observed phytoliths in soil assemblages were great. This might be due to an over estimated calculation, as *Nardus stricta* was used as a reference for the grasses with unknown phytolith frequency. *Nardus stricta* has high values of cork cells (33%) compared to many other alpine grasses (e.g. 0.2% in *Festuca melanopsis*, 17.2% in *F. halleri*).

The values for trichomas are regularly underestimated, possibly as consequence of neglecting herbaceous dicotyledon input in the calculations. Jigsaw morphotypes (typical of dicotyledons) were also regularly underestimated.

In the present estimate, some forms are over represented while others are under represented relatively to expectation based solely on stand biomass. In particular the major discrepancy concerns the frequency of polyhedrons. For these phytolith types, predicted values are remarkably smaller than the measured ones, most likely because of the production of secondary typologies due to taphonomical processes. In our model these processes are not taken into account, resulting in a weak prediction of secondary typologies, as well as of fragile ones that are recovered in low percentage or are absent in the real assemblages. No evidences of the occurrence of allochtonous input were detected.

A methodological question, to which the theoretical estimate of phytolith input may bring a contribution, concerns the selection of the most representative sampling depth for modern analogs. According to the estimated values, the holorganic horizons O are the ones that give P_{THEO} frequencies closer to the predictions based on plant stand data. In the organic-mineral horizon A, instead, the influence of soil processes is already detectable. Phytoliths are accumulated from O to A (e.g. short cell percentage increases 2 times) and, weathering processes are more active as shown by the diminution of total biogenic silica content from OF to A .

The comparison of the groups individuated by the multivariate ordinations of phytolith assemblages (Figure 5.1.5) versus the groups based on grasslands composition (both of complete relevés Figure

5.1.1 and reduced relevées Figure 5.1.2) showed that there is no correspondence between the two groups. Thus, the information on species carried by the phytoliths of alpine grasslands is limited, and do not have the potential for distinguishing between grass- and sedge-dominated swards. Such a lack of sensitivity is mainly due to the fact that in alpine grass species short cells are only of a single type, and to the fragility of cone types phytolithy in soil.

5.1.6 Summary of conclusions

Phytolith production, transportat, deposition and preservation are issues that were investigated in this work: a better knowledge of these processe in modern analogs will allow to base plant history reconstructions on a stronger actualistic basis.

The present study enlighted that:

1. Biogenic silica extracted from soil was higher below 2600 m a.s.l., showing a direct relationship with the biogenic silica production of plant stands. Highly productive termophilous grasslands, dominated by *Festuca scabriculmis* and *Carex sempervirens,* have a content of B.S. in topsoil between 5.2 to 16%, while at higher altitude less productive *Carex curvula* swards contained only 1.5% to 3.9% of biogenic silica.
2. The ratio of Al-biogenic silica and total biogenic silica was higher at lower elevation: it is argued that the source should be the local input of Al phytolith from scattered woody species (alpine heaths and trees) more frequent in the subalpine belt.
3. The comparison between the frequency of phytoliths recovered in soil and the estimated theoretical input showed that frequency of some morphotypes (short cells) can be predicted on the basis of plant stand. However, for more fragile or secondary morphotypes the theoretical input was a very weak predictors, as the effect of taphonomical processes were not taken into account.
4. In an exploratory framework, several samples at increasing depth were analysed to verify the more representative sampling depth for modern analogs. It was put in evidence that the phytolith assemblages of the topmost holorganic horizons O seems to be dominated by

deposition processes while, in the deeper mineral-organic horizon A translocation and dissolution processes already play a role in determinig the assemblage composition. O horizons seem to give a snapshot of plant stand composition, A horizons are rather the result of time-integrated processes.

5. Phytolith assemblages showed a lack of sensitivity in distinguishing between alpine grasslands. This is because all the grass species occurring in the alpine ecosystem belong to the C_3- group and therefore produce the same short cells types, and because sedge distinctive morphotypes are poorly preserved.
6. Total content in silica, Al phytolith frequency and percentages of morphotypes (measured and estimated), suggest that the formation of phytolith assemblages in alpine grassland is dominated by a mechanism of in situ inheritance, although loss of biomass due to grazing and avalanches may play some role in the redistribution of phytoliths.

This work aims to supply a contribution to the understanding fundamental issues about the processe that rule the formation of phytolith assemblages in soil: key questions still awaits an explanation, such as migration time of phytoliths, life-span of biogenic silica and differential preservation of typologies. A better knowledge of phytolith signature given by present vegetation is the basis to improve fossil record interpretations.

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5.2 TREELINE RECONSTRUCTION BASED ON SOIL BIOGENIC SILICA EVIDENCES (SWISS VALAISIAN ALPS)

5.2.1 Abstract

In this study the elevation of the treeline during the Holocene is inferred on the basis of soil type, biogenic silica content and frequency of aluminium phytoliths in five soil transects located above the present treeline in the Central Swiss Alps. The curves of biogenic silica and aluminium rich phytoliths followed two main trends according the soil type: the PODZOSOLS were characterised by an anticorrelation of biogenic silica mass and the frequency of aluminium phytoliths in the deep soil horizons. In the ALOCRISOLS the two curves were correlated.

The co-existence of (1) PODZOSOLS, (2) low biogenic silica content and (3) high frequency of aluminium phytoliths is interpreted as signal of past occurrence of woody vegetation, (ericaceous heaths or conifers woodlands) producing acidificant humus to trigger the podzolisation, low amount of silica and high percentage of aluminium phytoliths. Such conditions characterised the soils located up to 2500-2550 m a.s.l.: this altitude is thought to be the higher matched by the treeline in the study area.

A correlation between variations in biogenic silica budget in soil and climatic fluctuations for the recent part of the Holocene is suggested: changes between cycles of accumulation-dominated and dissolution-dominated processes in soil may be the cause of variations in the stock of biogenic silica.

5.2.2 Introduction

The transition of dominant plant life form from tall trees of conifer forest in the subalpine vegetation belt, to dwarf shrubs, swards, and occasional stunted trees in the alpine belt, marks a striking biogeographical altitudinal boundary in the alpine landscape. Treelines are acknowledged to be the result of stress gradients of ecological factors. At mid latitudes, the decrease of air temperature of 0.55K° per 100 meters of elevation creates an altitudinal thermal gradient that is acknowledged to be the main factor regulating the altitudinal zonation of alpine vegetation. However, air and soil temperatures, are not the only determinants since meso- and micro-climate, slope processes, species ecophysiological traits, and ecosystems' resistance and resilience**,** interact in locally shaping the altitude of the forest limit (Brady, 1990). Moreover, in the European Alps the strong impact of human activities have heavily influenced even the highest elevation ecosystems. Pollen and plant macrofossil data record a 100-200 m receeding timberline after the Atlantic optimum, probably related to both climatic deterioration and intensive human activity (see for instance: Burga, 1988; Wick and Tinner, 1997).

A regional record of past altitudinal fluctuations of treeline is given by palynological investigations (Burga, 1991; Haas *et al.*, 1998), these data, however lack of spatial resolution and can be refined by other proxies (e.g. plant megafossils, plant macrofossil, charcoal analysis and phytolith analysis) that supply more spatially precise estimate (e.g. Eronen and Huttunen, 1993; Tinner *et al.*, 1996; Hormes *et al.*, 2001).

Soil born phytoliths have been employed in palaeoecology as tracer of past vegetation dynamics (e.g. Fredlund and Tieszen, 1997; Alexandre *et al.*, 1997b), and biogenic silica analysis may supply a new perspective to complete the scenario drawn on the basis of classical palaeoecological investigations.

In the present research, five altitudinal soil transects above the present treeline have been studied. Soil analysis, biogenic silica (B.S.) content, the rate of aluminious phytoliths and the frequency of phytoliths are combined to investigate the fluctuations of the forest limit during the Holocene.

Soils are palaeoecological archives highly suitable to detect gradients because, being largely available, they allow sampling along transects, thus providing spatially precise data.

Also, a screening of B.S. production of the dominant plant species and communities in the area, has shown that B.S. input is one order of magnitude higher in subalpine grassland than in alpine meadows, subalpine heaths and forest (Carnelli *et al.*, 2001). Such different production should be traceable in fossil B.S. record in soil. Moreover, B.S. input of woody species should be identified by the presence of aluminious phytoliths (Carnelli *et al.*, 2002).

The reconstruction of the altitudinal limit matched by the forest in a period of high climatic variability such as the Holocene, may enlighten the future response of alpine ecosystems at the subalpine-alpine ecocline. If the forecasted upwards migration of forest, triggered by global warming, take place, the expanding woody species would get in contact with less competitive communities at the upper alpine belt shifting existing species equilibrium (Theurillat *et al.*, 1998).

5.2.3 Methods

5.2.3.1 Site locations

Five altitudinal transects situated in lateral valleys of the upper Rhône valley (47°N, Central Swiss Alps, the Valais region) were investigated (Figure 2.1; Table 2.1). In each transect soil profiles were excavated at regular altitudinal interval of 200 meters, between about 2400 m and 2800 m a.s.l., above the present potential treeline. Present vegetation consists of acidic grasslands in all the sites. Sampling sites, altitude, coordinates, aspect, topography, dominant species and acronyms are listed in Table 2.1.

The transects from West to East are the following:

1) The most western transect is situated in Val d'Arpette (AR) (eastern limit of Mt. Blanc massif) on the S-slope (30-40°) of the Mt. Clochers d'Arpette (2810 m a.s.l.), it was sampled in three points.

Three transects were sampled in the Aletsch Glacier region:

2) Belalp_hofathorn (BA-HO), along the Mt. Hofathorn (2845 m a.s.l.) southern slope (25-30°) four soil profiles were sampled;

3) Belalp-Lengi Egga (BA-LE), on the S-E slope of Mt. Sparrhorn (3020 m a.s.l.) three soil profiles were selected, the highest of them in proximity of the peat bog Lengi Egga (see also: Tinner and Theurillat, unpublished);

4) Aletsch (HT), alongside the eastern side of the Aletsch glacier, along the S-slope of Mt. Hindererhinertüre in which two sites were sampled.

5) Finally, the most eastern transect, Furka (FK), is located in proximity of the Furka Pass, on the S slope of Tällisegg -Tällisgrat- Tällisker peaks, where three soils were sampled.

The parent rock material is acidic (granite in Val d'Arpette and gneiss in the other sites). Val d'Arpette and Belap transects are situated in proximity of the study sites of two long-term research projects investigating plant responses to environmental and climatic change ("ECOCLINE project": Theurillat *et al.*, 1996).

The present-day timberline (also forest line or forest limit) is located respectively at 2200 m in Val d'Arpette, at 2060 m a.s.l. at Belalp and Lengi Egga area, and at 2000 m a.s.l. at Furka (although *Alnus viridis* is present in the area up to 2200 m a.s.l.). Near the upper part of the Aletsch glacier, e.g. in the Märjelensee, the timberline does not exist as the glacier comes at or higher than the potential timberline, i.e. 2200-2250 m a.s.l. Potential timberline is estimated in Val d'Arpette around 2250-2300 m a.s.l., at Belalp and Lengi Egga around 2250-2300 m, and, at Furka 2200 m.

5.2.3.2 Climate and vegetation

Climatic conditions and dominant plant communities for the study sites are described in Chapter 2.

5.2.3.3 Soil analysis

Soil profile locations and acronyms are reported in Table 2.1. Field work was carried out during summers 1998 and 1999; soil profiles were described first in situ; then air-dried soil samples were sieved at 2 mm, and pH was measured for each layer, both in deionised water and KCl 1 M (volume ratio 1:2.5) (AFES, 1998). When necessary for soil identification, organic carbon content was determined (Anne method, AFES, 1998) and saturation rate was measured "at the pH of the soil" (percolation by KCl 1 M or NH_4Cl 0.5 M) (Baize and Jabiol, 1995). The soil classification follows AFES (1998). Soil types are listed in Table 3.2.

5.2.3.4 Biogenic silica extraction

More than 20 g of soil were sampled for the extraction of B.S.. Samples were collected from each soil horizon, and, for thicker horizons, several samples at regular intervals of 2-3 cm were taken. Further samples were collected in correspondence of pedogenetic discontinuities (e.g. colour or granulometry). Dried soil samples were sieved at 1 mm to discard roots and gravel; B.S. was extracted from about 5 g of sieved soil by successive wet oxidation and floatation in heavy liquid (Madella *et al.*, 1998). All the floating fraction was collected to measure the total content of B.S. in each sample.

5.2.3.5 X-rays microanalysis of polyhedral phytoliths

Subsamples of the biogenic silica residue were mounted on aluminium stubs, coated with gold and examined in a JEOL JSM 6400 scanning electron microscope. A sample on average of 60 irregular polyhedral phytoliths was checked by X-ray microanalysis for the presence of aluminium in the biogenic silica reticule. The procedure is described in Carnelli *et al.*, (2002) (Chapter 4.3). The standard deviation rate was calculated with the binomial distribution (Tables 5.2.1-5).

5.2.3.6 Phytolith counts

A subsample of B.S. extracted from each soil sample was mounted on a permanent microscope slide (in EUKITT; refractive index 1.5 at 20°C). Silica bodies were observed at a magnification of 504x with an optical microscope equipped with phase contrast optic and polarised illumination. A standardised scanning of the slide was performed according to Albert *et al.* (2000). The number of phytoliths counted per sample was on average 1200. Monocotyledon phytoliths were counted: nearly all the monocotyledon phytoliths were short cells, in lower proportions bulliform cells and cyperaceae-type cones were present. The frequency of monocotyledon phytoliths is expressed as percentage on the total of the phytolith counted. Counts were not performed on samples from the sites: BA-HO3, HT1 and HT2.

5.2.3.7 Calculation of the punctual mass of biogenic silica in soil

To avoid relative values, the mass of biogenic silica and of the Al-biogenic silica was estimated for each soil horizon (Table 5.2.6).

The mass of the soil horizon is given by its thickness (m), multiplied for the bulk density of the horizon (Kg m^{-3}). The average bulk density of the soil horizons considered (taken from literature) is approximately as follows (Kg m^{-3}): O= 100, OA= 250, A=800, AB= 1000; B, Sal and C =1300.

To calculate the total weight of B.S. per horizon: the mass of the soil horizon has to be multiplied for the percentage weight of B.S.. Here, for a more accurate comparison of the curves of the mass of B.S. and Al-B.S., the values were then reported to punctual values: punctual mass of B.S.= B.S.% * soil horizon bulk density; and Al-phytoliths punctual mass= Al-phytolith%* punctual mass of B.S.. The ratio of punctual mass of Al-B.S. and total B.S. in all the sites is plotted in Figure 5.2.6.

An estimate of the expected mass of B.S. in the soil was calculated for some of the sites (Figure 5.2.7-10).

In these sites, to calculate the average annual B.S. input, the daily biogenic silica input of the present vegetation (g m^{-2} d^{-1}) (Carnelli, *et al*. 2001) was multiplied for the length of the growing season (d). Then, the mass of B.S. in the horizon was divided for the annual input: in this way we obtain an "equivalent of the annual production (Eq.an.pr.)" that is gives an estimate of the number of years necessary to accumulate the B.S. measured in the whole soil. In this way, the expected the time-length necessary to produce the silica stock found in soil could be estimated.

5.2.4 Results

The soils investigated belong to three major types: PODZOSOL, ALOCRISOL, and BRUNISOL (Table 3.2). Soil descriptions and analysis are given in Chapter 3. B.S. content (percentage on dry soil mass), the frequency of Al phytoliths and of monocotyledon phytoliths are listed in Tables 5.2.1-5; plots and line drawings of soil profiles are displayed in Figures 5.2.1-5.

52.2.4.1 Arpette

a) Soils: In Val d'Arpette the soil profiles show a marked decrease of the podzolic activity with the increasing altitude: the sequence being as follows:

- at 2375 m PODZOSOL OCRIQUE (AR1)
- at 2565 m ALOCRISOL TYPIQUE (AR2)
- a shallow soil near the crest at 2720 m BRUNISOL OLIGOSATURÉ (AR3).

b) Biogenic Silica: In AR1 the horizon OH contains up to 10.8% of B.S., while in A and ABPh the content decreases to an average of 3.6%. In the underlying horizon BP, opal silica ranges from 1 to 2.6 %, with a tendency to accumulation with depth that is present also in C (up to 2.7%).

In AR2 the average content of B.S. in the profile is 3.3%. Silica is highly concentrated in A (7.2%), but drops abruptly in the deeper horizons (0.7% in Sal, and 0.4% in C1, C2, C3 and C4). The buried horizon BPh contains about 3 times B.S. than the horizons in which it is included (2.83%).

In AR3 B.S. is on average 3.8%. In the top horizons OH and A, B.S. is between 3% and 4.9%, and it is up to 7.5% in SC. Towards the deepest horizons the content decreases to 0.5%.

c) Al phytoliths: In AR1 the highest percentage of Al phytoliths occurred in the top soil (up to 70%), in deeper horizons the percentage decreases: in the illuvial horizons to 30%, and, furthermore in C to 20%. A peak of 60% was detected in the "pocket" of a discontinuous horizon [C1].

In AR2, Al-phytolith frequency are between 41.7% and 43.3% in the top horizons. They show a slight tendency to the accumulation in the illuvial horizons B (50.8%-53.3%) of the profile. In contrast Al phytoliths were nearly absent (1.6%) in the buried horizon BPh. In the same sample a peak of B.S. was detected.

In AR3 the frequency of Al phytoliths was constantly high: in top horizons it varied between 54.9% and 64.5%, with the minimum in BPh (29%). In this undeveloped shallow soil on the crest, the deeper sample at the contact with bedrock yielded a peak of Al phytolith (75%).

d) Monocotyledon phytoliths: In AR1 the frequency of monocotyledon phytoliths is rather constant along the profile, varying only between 53.7% in the top soil, to 27.4% at the basis of the profile. In the profile AR2 the frequency of monocotyledon phytoliths is high along all the profile: ranging only from 27.5% in A, to 23.6% in Sal, and about 27% in C1. A diminution is recorded in the buried horizon [BPh], in which the percentage is 17.2. In the deeper horizons monocotyledon phytoliths seem to be well preserved and accumulate to 38.3% at about 70 cm depth.

Table 5.1.1 Arpette transect. Sampled horizons; sampling depth; B.S. % (on dry soil weight basis); Al-phytoliths % and related standard deviation rate (S.D.), frequency of monocotyledon phytoliths (%).

ARP1 (PODZOSOL)						ARP2 (ALOCRISOL)						ARP3 (BRUNISOL)					
Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)
OH	5.5-10	10.8	63.5	6.1	53.7	A	5-2	7.2	41.7	6.4	27.5	OA	0-2	3	54.9	7	36.1
A	10-12	3.5	71.7	5.8	49.8	Sal	10-15	0.7	43.3	6.4	23.6	A	7-2	4.9	64.5	6.1	53.2
ABPh	12-16	3.8	31.8	5.7	39.3	C1	10-20	0.3	44.8	6.1	27.5	SC	16-7	7.5	61.7	7.1	46.7
BPh	16-20	1	63.3	6.2	45.9	C1	20-30	0.3	50.8	6.4	27.2	C1	22-16	3.3	29.1	6.1	51.2
BPsBPh	20-28	1.2	29.2	5.6	41.1	[BPh]	30-40	2.8	1.6	1.6	17.2	C2	25-30	0.5	75	5.6	41.9
BPs1	28-40	1.7	39.3	6.2	31.1	C2	30-40	0.4	52.2	6.1	34.9						
BPs2	40-53	2.6	22.6	5.3	34.3	C3	40-50	0.6	53.3	6.4	31.9						
[C1]	50-70	2.7	61.6	5.7	45.7	C3	50-60	0.3	39.4	6	41.8						
C2	53-80	2.2	26.4	6.1	27.4	C4	60-70	0.2	61.7	6.3	30.9						
						C4	>70	0.9	48.4	6.3	38.3						

52.2.4.2 Belalp-Hofathorn

a) Soils: In soils at Belalp-Hofathorn the podzolic activity was detected up to 2550 m a.s.l.; Belalp-Hofathorn soils appear undisturbed and do not present any evidences of colluvial activity.

- BA-HO1 (2385 m a.s.l.) PODZOSOL MEUBLE
- BA-HO2 (2570 m a.s.l.) PODZOSOL OCRIQUE
- BA-HO3 (2665 m a.sl.) and BA-HO4 (2830 m a.s.l.) are ALOCRISOL TYPIQUES

b) Biogenic silica: In BA-HO1, the organic horizons contained percentage of B.S. between 1.3% and 0.4% of B.S.. At the transition horizon AE, B.S. is 0.7%. From EH, down to the spodic horizons B, there was a tendency to the accumulation of B.S. (3.2%). In C the average content of B.S. decreases to 2.3%.

In BA-HO2, the top organic horizon OF1 yielded only 2.1% B.S.; while in the underlying horizons OF2 and AE, B.S. content was up to 9.7%. In the eluvial horizon EH and in the illuvial BPH, B.S. diminished to 3.4% and 2.7%, respectively. Towards the basis of the profile B.S. is accumulated: in BPsC is up to 5.5% and decreased slightly in C (4%).

In BA-HO3, B.S. increases from the top horizon OF (0.4%) to the underlying AH horizons (4%). The accumulation is rather constant also in the deeper horizons Sal and C (from 7.4% in Sal1, to 8.5% in C).

In BA-HO4, the holorganic horizon OF yielded 5.4% of B.S., the content decreased abruptly in the horizons A(E) and A (2.1 and 2.3%). The concentration in Sal was rather constant varying only from 1.7% to 2.2%. B.S. increases in the deeper horizons, being on average 4.7% in SalC and, up to 6% in C.

c) Al phytoliths: In BA-HO1, Al phytoliths were up to 73.3% in the OH/OF horizon, and decreased to 63.3% at the contact with AE. They decrease to 31.7% at the base of AE. In the eluvial horizon Eh, values are rather constant, while in the illuvial horizon B, a neat decrease is recorded: 18.6% at the top of B, while is 13.8% at the base of this horizon. Deeper in BPsC, the frequency of Al-phytoliths is on average 10%. In the C horizon there is a neat increase, up to 51.6% at 75-80 cm depth.

In BA-HO2 the top horizons contained up to 77.6% of Al phytoliths, in the illuvial horizon about the 30% of phytoliths contained Al; their frequency decreases to 13% at the basis of the profile.

In BA-HO3, Al phytoliths are extremely abundant in the OF horizon (91.7%), and decrease to 53.3% and 52.5% in Ah and Sal1. From Sal2 to R they are only about 3%-5%.

In BA-HO4 the percentages of Al phytoliths were never more then 11.7%, and no regular variation with depth is shown.

d) Monocotyledon phytoliths: In BA-HO1 monocotyledon phytoliths are only 15.1% in the top holorganic horizon OF/OH, but they increase already in OF to 32.35% and, up to 72% at the basis of AE. In the eluvial horizon Eh a decrease to 36.1% is recorded, becoming more marked with depth (Al phytoliths are only 13.3% at the basis of BPs). The horizon BPsC and C show a wide variability: with values ranging from 18.3% to 2.9%.

In BA-HO2 monocotyledon phytoliths are accumulated in the top horizond (from 17.3% in OF1, to 46.7% in AE) and then decrease steadily in the deeper horizons (only 1% in C).

In BA-HO4 monocotyledon phytolith decrease with depth: top horizons contain 24.2% to 25.1%, then a slight increase it is recorded in the top sample of Sal (28.1%); in the deeper horizons values ranges between 0 and 4.1%.

Table 5.2.2 Belalp-Hofathorn transect. Sampled horizons; sampling depth; B.S. % (on dry soil weight basis); Al-phytoliths % and related standard deviation rate (S.D.), frequency of monocotyledon phytoliths (%).

BA-HO1 (Podzosol)						BA-HO2 (Podzosol ocrique)						BA-HO3 (Alocrisol)				
Horizon	Depth (cm)	B.S. (%)	Al (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S (%)	Al (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. %	Al (%)	S.D. (%)
OF/OH	0-1	1.3	73.3	5.7	15.1	OF1	1-2	2.1	37.9	6.4	17.3	OF	0-3	0.4	91.7	1.1
OF	2-3	0.4	61.3	6.2	32.3	OF2	2-3	9.7	75	5.6	43.4	AH	3-6	4.4	53.3	5.4
AE	3-4	0.8	63.3	6.2	69.2	AE	3-6	8.2	77.6	5.5	46.7	Sal1	6-10	7.4	52.5	6.2
AE	5-6	0.7	30.6	5.8	62.9	(Eh)	6-7	3.4	54.5	6.7	42.5	Sal2	11-12	7.6	31.7	8.8
AE	8-9	0.7	31.7	6	72.1	BPh	7-8	2.7	25.8	5.7	29.1	Sal2	17-18	6.9	1.7	11.8
Eh	9-10	0.4	31.7	6	41.4	BPsC	8-17	3.3	30	6.5	7.4	SalC	20-25	6.3	4.8	15.3
Eh	12-13	0.5	34.4	6.1	47.3	BPsC	17-24	5.5	5.2	2.9	8.4	C	25-32	8.5	3.1	12.1
Eh	16-17	0.4	46.7	6.4	36.1	C	24-40	4	13.1	4.3	1.0	R	>32	7.2	5.0	14.3
EhBPs	18-19	1.8	18.6	5.1	18.4											
BPs	20-21	2.3	16.7	4.8	15.7											
BPs	26-27	3	13.8	4.5	13.3											
BPsC	27-28	3.8	16.7	4.8	4.0											
BPsC	33-34	3.7	10	3.9	13.2											
BPsC	38-39	2.9	10	3.9	4.3											
BPsC	43-44	3.4	16.7	4.8	12.7											
C1	44-45	2.1	38.7	6.2	16.8											
C1	46-47	2.5	39.3	6.2	11.5											
C2	52	2.1	53	6.1	11.9											
C2	53-54	2.3	44.3	6.4	2.9											
C2	60-70	2	51.4	6	5.0											
C2	75-80	2.7	51.6	6.2	15.5											

BA-HO4 (Podzosol)					
Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)
OF	0-3	5.4	6.2	3	24.2
A(E)	3-4	2.1	10	3.9	26.9
A	4-7	2.3	6.8	3.3	25.1
Sal	7-8	1.7	11.7	4.1	28.1
Sal	12-13	2.2	7.9	3.4	11.6
Sal	19-20	1.7	8.3	3.6	1.7
SalC	24-25	4.6	6.9	3.3	0.9
SalC	30-31	4.9	0	0	1.4
C	34-50	6	11.7	4.1	0.8

5.2.2.4.3 Belalp-Lengi Egga

a) Soils: Belalp-Lengi Egga transect showed the maximum of podzolic activity in the soils at 2451 m a.s.l.; at 2550 m a.s.l. the podzolic activity is weaker.

-BA-LE7 (2305 m a.s.l.) is a PODZOSOL developed on a palaeosoil.

-BA-LE5 (2550 m a.s.l.) and BA-LE6 (2451 m a.s.l.) are similar to the PODZOSOLS in Belalp transect.

b) Biogenic silica: In BA-LE7, the horizon A contained 13% of B.S.. In Eh and BPh the content was only 2.4%. In BPs biogenic silica is slightly accumulated (4%). In the same horizon BPs, a minimum was recorded in correspondence of the buried soil (2%).

In BA-LE6, the mineral-organic horizon A contained 11.5% to 14.5% of B.S. Biogenic silica decreases abruptly to 2.2% in Eh. In the horizon B, B.S. content is variable: it is accumulated up to 4.7% at the basis of the illuvial horizon (BpsC) and in C (4.5%). B.S. content decreased to about 2% towards the bottom of the soil profile.

BA-LE5 contained 4.6% of B.S. in OHA. The content diminished abruptly in the illuvial horizons (0.9 and 0.5% in AE and Eh respectively). In the BP horizons and in C biogenic silica is accumulated to 2.2%. In the deeper horizons the content is at maximum 2.3%.

c) Al phytoliths: In the top horizons of BA-LE7 the frequency of Al-phytoliths reached 100%. A slight decrease is recorded in the illuvial horizon (76.7%), the trend is steady in the BPs horizon (min. 0%). At the basis of the profile the percentage of Al phytoliths is variable (between 63.3% and 15%).

BA-LE6 the top horizons contained as much as 88% of Al-polyhedrons, the value decreased to 70% at the basis of the spodic horizon with a wide variability (35-76%). In C Al phytoliths were nearly the total (up to 98.3%).

In BA-LE5, in the top horizons OHA, Al-polyhedral phytoliths were 83.3%; the content decreases in the eluvial horizon to 29.2% and, furthermore, in the illuvial one (values between 3.2 and 5%). In C values are up to 32.3%.

d) Monocotyledon phytoliths: Monocotyledon phytoliths increase steadily from the top sample (25.2%) to the underlying Eh horizons (59.4%). In the illuvial horizon BPh the content is more variable, ranging from 44.7% to 29.6%. Towards the deeper horizons the content ranges only from 57.1% to 53.1%.

Table 5.2.3 Belalp-Langi Ëgga transect. Sampled horizons; sampling depth; B.S. % (on dry soil weight basis); Al-phytoliths % and related standard deviation rate (S.D.), frequency of monocotyledon phytoliths (%).

BA-LE7 (PODZOSOL)						BA-LE6 (PODZOSOL)						BA-LE5 (PODZOSOL)					
Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)
A	1.5-3	11.2	80	5.2	25.2	A	3-4	11.5	65	6.2	51.4	OHA	1.5-3.5	4.6	83.3	3.8	38.7
A	3-4	14.5	100	0	44.9	Eh	6-7	2.1	88.3	4.1	65.5	AE	2-6	0.9	27.5	4.7	66.0
Eh	8-9	2.2	76.7	5.5	59.4	BPh	12-13	4.7	65	6.2	20.4	[Eh]	5-8	0.5	29.2	3.4	77.4
BPh	13-14	2.7	41.5	6.1	27.6	BPh	17-18	1.7	35	6.2	54.0	BPh	8-11	2.2	6.7	19.2	37.8
BPs	16-17	2.4	31.7	6	44.7	BPs	18-19	1.9	70	5.9	50.3	BPs	12-13	1.6	3.3	26.2	48.1
BPs	22-23	4.0	28.3	5.8	29.6	BPs	24-25	2.7	76.7	5.5	58.2	BPs	24-25	1.9	5	22	17.2
BPs	28-29	2.5	0	0	46.2	BPsC	26-27	2.5	41.7	6.4	52.8	BPsC	25-26	1.1	3.2	27.1	18.9
BPs	29-30	1.9	63.3	6.2	57.2	BPsC	33-34	1.3	73.3	5.7	44.5	BPsC	32-33	1.5	3.3	26.4	16.6
BPsC	38-39	4.7	15.0	4.6	55.6	C	39-40	2.2	98.3	1.6	30.5	C	33-34	2.3	29	7.1	16.1
IIC	39-45	4.5	30	5.9	53.2	C	50-51	1.7	96.8	2.2	26.8	C	40-41	1.6	32.3	5.6	27.4

Table 5.2.4 Aletsch transect. Sampled horizons; sampling depth; B.S. % (on dry soil weight basis); Al-phytoliths % and related standard deviation rate (S.D.), frequency of monocotyledon phytoliths (%).

HT1 (ALOCRISOL)					HT2 (ALOCRISOL)				
Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)
OH	2-4	11	-	-	A	2-3	5.6	57.4	6.3
A	7-8	6.1	53.6	6	A	5-10	6.8	66.7	6.1
A	14-15	8.4	66.7	6.1	ASal*	12	4.1	61.7	6.3
Sal	20-21	2.8	41.7	6.4	ASal	10-15	4.2	19.4	5
Sal	30-31	5.5	25	5.6	S1	15-20	3.4	20	5.2
Sal	35-40	4.5	11.7	4.1	S2	20-25	3.3	11.7	4.1
Sal	40	4.8	44.4	6.3	S2	25-35	4.2	15	4.6
SC	42	1.9	11.7	4.1	SC	30-35	4	8.3	3.6
SC	50	5.2	36	5.5	SC	40-45	5.2	8.3	3.6
SC/C	60	1.7	11.7	4.1	C	45-50	6.4	6.7	3.2
C	80	2.4	9.2	3.6	C	55-50	4.4	6.7	3.2
					C	55-60	5.4		6.7

(*) layer of charcoals

5.2.2.4.4 Aletsch

a) Soils: In Aletsch transect the podzolisation is absent,

-HT1 (2580 m a.s.l.) and HT2 (2710 m a.s.l.) are ALOCRISOLS TYPIQUE

b) Biogenic silica: Top samples of HT1 contained between 6.1 and 8.4% of B.S.. In the underlying horizon Sal the content decreased to 2.85%. Deeper, an accumulation of up to 4.8% at the base of the Sal horizon is recorded. Towards the bottom of the profile, in the SC horizon, B.S. values ranged between 1.9% and 5.2%. In the C horizon, B.S. was 2.4%.

In HT2, B.S. content was 4.8% on average. In A the content was between 5.6 and 6.8%; in ASal it decreased to 4.1%, and in S1-S2 to 3.3%. Towards the deeper horizon B.S is slightly accumulated (up to 6.4%).

c) Al phytoliths: The top horizons of HT2 contained between 53.6% and 66.7% of Al phytoliths. In the horizon Sal the concentration decreased although with a wide variability (from 11.7% to 44.4%). In the horizon SC, towards the base of the profile, values are again varying widely (between 36% and 1.7%).

In HT2, Al-polyhedrons were up to 66.7% in the top horizons, but the percentage decreased abruptly at 10-15 cm of depth (19.4%-20%). Toward the base of the profile, the frequency of Al-phytoliths ranged between 15% and 6.7%.

5.2.2.4.5 Furka

a) Soils: In the sites at Furka, altitude, soil and, humus type were correlated: podzolic activity was detected only in the low altitude soil at 2403 m a.s.l., but was absent at 2618 m and 2785 m a.s.l.

- FK1 is a PODZOSOL MEUBLE (2403 m a.s.l.),

- FK2 (2618 m a.s.l.) and FK3 (2785 m a.s.l.) are ALOCRISOLS.

b) Biogenic silica: In FK1 the highest concentration of B.S. was recorded in the organic episolum (25% in OH). Silica is depleted in the horizons A, E, with values as low as 0.4% in EBPh. In BPh there is a weak accumulation of B.S. (2%). B.S. content decreases again (0.8%) in the deeper horizons. In the horizon A of the profile FK2, the content of B.S. 1.2%. B.S. content is nearly constant along the profile, with only a slightly increasing trend from Sal1 (1.6%) towards the base of the profile (2.2%). In FK3, B.S. extracted from the A horizon was 5.4%. The content in B.S. decreased in SalC1 and SalC2 (about 0.8%). In the C horizon, at the base of the profile, B.S. is accumulated up to 3.2%.

c) Al phytoliths: In the soil profile FK1 the higher frequency of Al phytoliths was recorded in the top horizon (up to 96.8%). The frequency of Al phytoliths decreased in the eluvial horizon. In the upper part of the illuvial horizon the percentage was 57%, towards the bottom of the profile it decreased to 3.3%.

In FK2 the highest concentration was recorded in the top soil (56.7%), while in the lower part of Sal, the frequency of Al phytoliths diminished to 6.2%. They are accumulated up to 20% in the horizon C. In FK3 the content decreased from 22.4% in the top horizons, to 6.7% at the base of the soil.

d) Monocotyledon phytoliths: The frequency of monocotyledon phytoliths in FK1 was 41.4% in OH, and it increased slightly in AE (55.4%). Deeper on, in the horizons EBPh and BPhBPs the frequency of monocotyledons phytoliths ranged between 29.5% and 35.2%. In BPsC and C values are between 34.7% and 20.1%.

Table 5.2.5. Furka transect. Sampled horizons; sampling depth; B.S. % (on dry soil weight basis); Al-phytoliths % and related standard deviation rate (S.D.), frequency of monocotyledon phytoliths (%).

FK1 (PODZOSOL)						FK2 (ALOCRISOL)						FK3 (ALOCRISOL)					
Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)	Horizon	Depth (cm)	B.S. (%)	Al-phy. (%)	S.D. (%)	Mon. Phy. (%)
OH	1.5-3	25.5	78.3	5.3	41.4	A	0-3	1.2	56.7	6.4	45.9	A	0-3	5.4	22.4	5.5	30.9
AE	3-6	6.8	96.8	2.2	55.4	Sal1	3-7	1.6	20	5.2	39.6	Sal	3.5-11	0.9	16.7	4.8	28.4
E	4-10	0.2	86.7	4.4	30.3	Sal2	7/17-10	2.3	11.7	4.1	27.1	Sal C1	7-17	1	1.7	1.6	11.5
EBPh	10-13	0.4	30	5.9	29.5	Sal2	7-17>15	2.3	6.2	3	29.9	SalC2	17-28	0.7	15	4.6	12.5
BPh	13-17	2	57.4	6.3	35.2	C	17-50	2.2	19.3	5	28.3	[C1]	27-40	1	18.3	5	7.3
BPhBPs	17-22	1.2	25	5.6	32.3							C2	30-40	1.2	6.7	3.2	12.2
BPs	22-32	1.7	20.6	5.1	19.6							C3	>40	3.2	6.7	3.2	5.4
BPsC	32-40	1	11.1	4	34.4												
C	40-50	0.8	3.3	2.3	20.1												

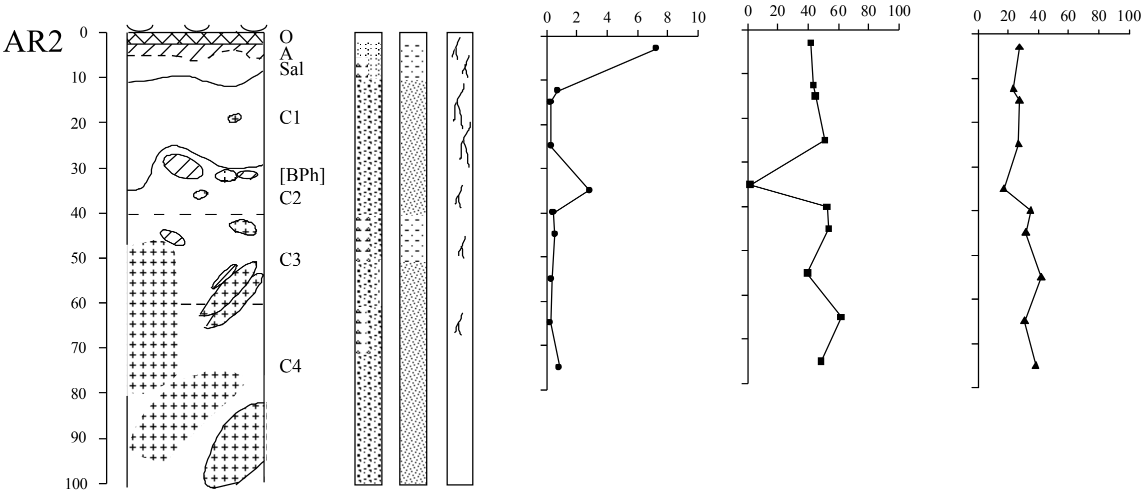
Table 5.2.6
Values of punctual B.S. mass and punctual Al-B.S. mass, in all the samples. Values are calculated considering BS%, thickness and bulk density of the horizons (see Methods).
The values here displayed are plotted in Fig. 5.7-10. In Fig.5.6 the ratio between punctual Al-BS and BS is diyplayed.

Site	Horizon	Horizon thickness (m)	BS%	Al%	Horizon bulk density (kg/m^{-3})	Total B.S. (kg m^{-2})		Total Al (kg m-2)		**punctual BS (g/dm3)**	**punctual Al- BS (g/dm3)**
AR1	OH	0.045	0.108	0.635	100	0.486		0.309		**10.800**	**6.858**
	A	0.020	0.035	0.717	800	0.560		0.402		**28.000**	**20.076**
	ABPh	0.020	0.038	0.318	1000	0.760		0.242		**38.000**	**12.084**
	BPh	0.040	0.010	0.633	1300	0.520		0.329		**13.000**	**8.229**
	BPsBPh	0.080	0.012	0.292	1300	1.248		0.364		**15.600**	**4.555**
	BPs1	0.120	0.017	0.393	1300	2.652		1.042		**22.100**	**8.685**
	BPs2	0.130	0.026	0.226	1300	4.394		0.993		**33.800**	**7.639**
	[C1]	0.200	0.027	0.616	1300	7.020		4.324		**35.100**	**21.622**
	C2	0.270	0.022	0.264	1300	7.722	18.342	2.039	5.719	**28.600**	**7.550**
AR2	A	0.030	0.072	0.417	800	1.728		0.721		**57.600**	**24.019**
	Sal	0.050	0.007	0.433	1300	0.455		0.197		**9.100**	**3.940**
	C1	0.100	0.003	0.448	1300	0.390		0.175		**3.900**	**1.747**
	C1	0.100	0.003	0.508	1300	0.390		0.198		**3.900**	**1.981**
	[BPh]	0.100	0.028	0.016	1300	3.640		0.058		**36.400**	**0.582**
	C2	0.100	0.004	0.522	1300	0.520		0.271		**5.200**	**2.714**
	C3	0.100	0.006	0.533	1300	0.780		0.416		**7.800**	**4.157**
	C3	0.100	0.003	0.394	1300	0.390		0.154		**3.900**	**1.537**
	C4	0.100	0.002	0.617	1300	0.260		0.160		**2.600**	**1.604**
	C4		0.009	0.484	1300		4.913		2.292	**11.700**	**5.663**
AR3	OA	0.020	0.030	0.549	250	0.150		0.082		**7.500**	**4.118**
	A	0.050	0.049	0.645	800	1.960		1.264		**39.200**	**25.284**
	SC	0.090	0.075	0.617	1300	8.775		5.414		**97.500**	**60.158**
	C1	0.060	0.033	0.291	1300	2.574		0.749		**42.900**	**12.484**
	C2	0.050	0.005	0.750	1300	0.325	13.784	0.244	7.754	**6.500**	**4.875**
BA-OH1	OF/OH	0.020	0.013	0.733	100	0.026		0.019		**1.300**	**0.953**
	OF	0.010	0.004	0.613	100	0.004		0.002		**0.400**	**0.245**
	AE	0.020	0.008	0.633	1000	0.160		0.101		**8.000**	**5.064**
	AE	0.030	0.007	0.306	1000	0.210		0.064		**7.000**	**2.142**
	AE	0.010	0.007	0.317	1000	0.070		0.022		**7.000**	**2.219**
	Eh	0.030	0.004	0.317	1300	0.156		0.049		**5.200**	**1.648**
	Eh	0.030	0.005	0.344	1300	0.195		0.067		**6.500**	**2.236**
	Eh	0.020	0.004	0.467	1300	0.104		0.049		**5.200**	**2.428**
	EhBPs	0.020	0.018	0.186	1300	0.468		0.087		**23.400**	**4.352**
	BPs	0.060	0.023	0.167	1300	1.794		0.300		**29.900**	**4.993**
	BPs	0.010	0.030	0.138	1300	0.390		0.054		**39.000**	**5.382**
	BPsC	0.060	0.038	0.167	1300	2.964		0.495		**49.400**	**8.250**
	BPsC	0.050	0.037	0.100	1300	2.405		0.241		**48.100**	**4.810**
	BPsC	0.050	0.029	0.100	1300	1.885		0.189		**37.700**	**3.770**
	BPsC	0.010	0.034	0.167	1300	0.442		0.074		**44.200**	**7.381**
	C1	0.020	0.021	0.387	1300	0.546		0.211		**27.300**	**10.565**
	C1	0.060	0.025	0.393	1300	1.950		0.766		**32.500**	**12.773**
	C2	0.010	0.021	0.530	1300	0.273		0.145		**27.300**	**14.469**
	C2	0.070	0.023	0.443	1300	2.093		0.927		**29.900**	**13.246**
	C2	0.150	0.020	0.514	1300	3.900		2.005		**26.000**	**13.364**
	C2	0.050	0.027	0.516	1300	1.755	21.790	0.906	6.772	**35.100**	**18.112**
BA-OH2	OF1	0.010	0.021	0.379	100	0.021		0.008		**2.100**	**0.796**
	OF2	0.010	0.097	0.750	100	0.097		0.073		**9.700**	**7.275**

	AE	0.030	0.082	0.776	1000	2.460		1.909		**82.000**	**63.632**
	(Eh)	0.010	0.034	0.545	1300	0.442		0.241		**44.200**	**24.089**
	BPh	0.010	0.027	0.258	1300	0.351		0.091		**35.100**	**9.056**
	BPsC	0.090	0.033	0.300	1300	3.861		1.158		**42.900**	**12.870**
	BPsC	0.070	0.055	0.520	1300	5.005		2.603		**71.500**	**37.180**
	C	0.160	0.040	0.131	1300	8.320	20.557	1.090	7.172	**52.000**	**6.812**
BA-OH3	OF	0.030	0.004	0.917	100	0.012		0.011		**0.400**	**0.367**
	AH	0.030	0.044	0.533	800	1.056		0.563		**35.200**	**18.762**
	Sal1	0.050	0.074	0.525	1300	4.810		2.525		**96.200**	**50.505**
	Sal2	0.060	0.076	0.317	1300	5.928		1.879		**98.800**	**31.320**
	Sal2	0.030	0.069	0.017	1300	2.691		0.046		**89.700**	**1.525**
	SalC	0.050	0.063	0.048	1300	4.095		0.197		**81.900**	**3.931**
	C	0.070	0.085	0.031	1300	7.735		0.240		**110.500**	**3.426**
	R		0.072	0.050	1300		26.327		5.460	**93.600**	**4.680**
BA-OH4	OF	0.030	0.054	0.062	100	0.162		0.010		**5.400**	**0.335**
	A(E)	0.010	0.021	0.100	800	0.168		0.017		**16.800**	**1.680**
	A	0.030	0.023	0.068	800	0.552		0.038		**18.400**	**1.251**
	Sal	0.050	0.017	0.117	1300	1.105		0.129		**22.100**	**2.586**
	Sal	0.070	0.022	0.079	1300	2.002		0.158		**28.600**	**2.259**
	Sal	0.050	0.017	0.083	1300	1.105		0.092		**22.100**	**1.834**
	SalC	0.060	0.046	0.069	1300	3.588		0.248		**59.800**	**4.126**
	SalC	0.040	0.049	0.000	1300	2.548		0.000		**63.700**	**0.000**
	C	0.160	0.060	0.117	1300	12.480	23.710	1.460	2.151	**78.000**	**9.126**
BA-LE7	A	0.015	0.112	0.800	800	1.344		1.075		**89.600**	**71.680**
	A	0.050	0.145	1.000	800	5.800		5.800		**116.000**	**116.000**
	Eh	0.050	0.022	0.767	1300	1.430		1.097		**28.600**	**21.936**
	BPh	0.030	0.027	0.415	1300	1.053		0.437		**35.100**	**14.567**
	BPs	0.060	0.024	0.317	1300	1.872		0.593		**31.200**	**9.890**
	BPs	0.060	0.040	0.283	1300	3.120		0.883		**52.000**	**14.716**
	BPs	0.010	0.025	0.000	1300	0.325		0.000		**32.500**	**0.000**
	BPs	0.090	0.019	0.633	1300	2.223		1.407		**24.700**	**15.635**
	BPsC	0.010	0.047	0.150	1300	0.611		0.092		**61.100**	**9.165**
	IIC	0.060	0.045	0.300	1300	3.510	21.288	1.053	12.437	**58.500**	**17.550**
BA-LE6	A	0.030	0.115	0.650	800	2.760		1.794		**92.000**	**59.800**
	Eh	0.060	0.021	0.883	1300	1.638		1.446		**27.300**	**24.106**
	BPh	0.050	0.047	0.650	1300	3.055		1.986		**61.100**	**39.715**
	BPh	0.010	0.017	0.350	1300	0.221		0.077		**22.100**	**7.735**
	BPs	0.060	0.019	0.700	1300	1.482		1.037		**24.700**	**17.290**
	BPs	0.020	0.027	0.767	1300	0.702		0.538		**35.100**	**26.922**
	BPsC	0.070	0.025	0.417	1300	2.275		0.949		**32.500**	**13.553**
	BPsC	0.060	0.013	0.733	1300	1.014		0.743		**16.900**	**12.388**
	C	0.110	0.022	0.983	1300	3.146		3.093		**28.600**	**28.114**
	C		0.017	0.968	1300		16.293		11.664	**22.100**	**21.393**
BA-LE5	OHA	0.020	0.046	0.833	250	0.230		0.192		**11.500**	**9.580**
	AE	0.030	0.009	0.275	1000	0.270		0.074		**9.000**	**2.475**
	[Eh]	0.030	0.005	0.292	1300	0.195		0.057		**6.500**	**1.898**
	BPh	0.040	0.022	0.067	1300	1.144		0.077		**28.600**	**1.916**
	BPs	0.120	0.016	0.033	1300	2.496		0.082		**20.800**	**0.686**
	BPs	0.010	0.019	0.050	1300	0.247		0.012		**24.700**	**1.235**
	BPsC	0.070	0.011	0.032	1300	1.001		0.032		**14.300**	**0.458**
	BPsC	0.010	0.015	0.033	1300	0.195		0.006		**19.500**	**0.644**
	C	0.070	0.023	0.290	1300	2.093		0.607		**29.900**	**8.671**
	C		0.016	0.323	1300		7.871		1.140	**20.800**	**6.718**
HT1	OH	0.050	0.110	-							
	A	0.070	0.061	0.536	800	3.416		1.831		**48.800**	**26.157**
	A	0.060	0.084	0.667	800	4.032		2.689		**67.200**	**44.822**
	Sal	0.100	0.028	0.417	1300	3.640		1.518		**36.400**	**15.179**
	Sal	0.050	0.055	0.250	1300	3.575		0.894		**71.500**	**17.875**

	Sal	0.050	0.045	0.117	1300	2.925		0.342		**58.500**	**6.845**
	Sal	0.020	0.048	0.444	1300	1.248		0.554		**62.400**	**27.706**
	SC	0.080	0.019	0.117	1300	1.976		0.231		**24.700**	**2.890**
	SC	0.100	0.052	0.360	1300	6.760		2.434		**67.600**	**24.336**
	SC/C	0.200	0.017	0.117	1300	4.420		0.517		**22.100**	**2.586**
	C		0.024	0.092	1300		31.992		11.010	**31.200**	**2.870**
HT2	A	0.030	0.056	0.574	800	1.344		0.771		**44.800**	**25.715**
	A	0.050	0.068	0.667	800	2.720		1.814		**54.400**	**36.285**
	ASal*	0.020	0.041	0.617	1000	0.820		0.506		**41.000**	**25.297**
	ASal	0.050	0.042	0.194	1000	2.100		0.407		**42.000**	**8.148**
	S1	0.050	0.034	0.200	1300	2.210		0.442		**44.200**	**8.840**
	S2	0.050	0.033	0.117	1300	2.145		0.251		**42.900**	**5.019**
	S2	0.100	0.042	0.150	1300	5.460		0.819		**54.600**	**8.190**
	SC	0.050	0.040	0.083	1300	2.600		0.216		**52.000**	**4.316**
	SC	0.100	0.052	0.083	1300	6.760		0.561		**67.600**	**5.611**
	C	0.100	0.064	0.067	1300	8.320		0.557		**83.200**	**5.574**
	C	0.050	0.044	0.067	1300	2.860		0.192		**57.200**	**3.832**
	C	0.050	0.054	0.067	1300	3.510	40.849	0.235	6.772	**70.200**	**4.703**
FK1	OH	0.015	0.255	0.783	100	0.383		0.299		**25.500**	**19.967**
	AE	0.030	0.068	0.968	1000	2.040		1.975		**68.000**	**65.824**
	E	0.060	0.002	0.867	1300	0.156		0.135		**2.600**	**2.254**
	EBPh	0.030	0.004	0.300	1300	0.156		0.047		**5.200**	**1.560**
	BPh	0.040	0.020	0.574	1300	1.040		0.597		**26.000**	**14.924**
	BPhBPs	0.050	0.012	0.250	1300	0.780		0.195		**15.600**	**3.900**
	BPs	0.100	0.017	0.206	1300	2.210		0.455		**22.100**	**4.553**
	BPsC	0.080	0.010	0.111	1300	1.040		0.115		**13.000**	**1.443**
	C	0.100	0.008	0.033	1300	1.040	8.845	0.034	3.853	**10.400**	**0.343**
FK2	A	0.030	0.012	0.567	800	0.288		0.163		**9.600**	**5.443**
	Sal1	0.040	0.016	0.200	1300	0.832		0.166		**20.800**	**4.160**
	Sal2	0.050	0.023	0.117	1300	1.495		0.175		**29.900**	**3.498**
	Sal2	0.050	0.023	0.062	1300	1.495		0.093		**29.900**	**1.854**
	C	0.330	0.022	0.193	1300	9.438	13.548	1.822	2.419	**28.600**	**5.520**
FK3	A	0.030	0.054	0.224	800	1.296		0.290		**43.200**	**9.677**
	Sal	0.050	0.009	0.167	1300	0.585		0.098		**11.700**	**1.954**
	Sal C1	0.090	0.010	0.017	1300	1.170		0.020		**13.000**	**0.221**
	SalC2	0.130	0.007	0.150	1300	1.183		0.177		**9.100**	**1.365**
	[C1]	0.130	0.010	0.183	1300	1.690		0.309		**13.000**	**2.379**
	C2	0.100	0.012	0.067	1300	1.560		0.105		**15.600**	**1.045**
	C3		0.032	0.067	1300		7.484		0.999		

[redacted]


AR2
0
10
20
30
40
50
60
70
80
90
100
O
A
Sal
C1
[BPh]
C2
C3
C4
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100

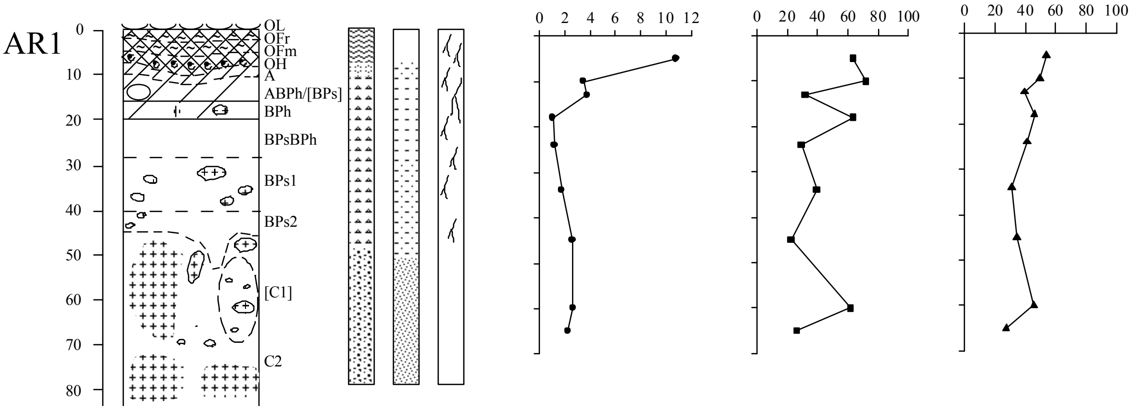

AR1
0
10
20
30
40
50
60
70
80
OL
OFr
OFm
OH
A
ABPh/[BPs]
BPh
BPsBPh
BPs1
BPs2
[C1]
C2
0 2 4 6 8 10 12
0 20 40 60 80 100
0 20 40 60 80 100

Figure 5.2.2

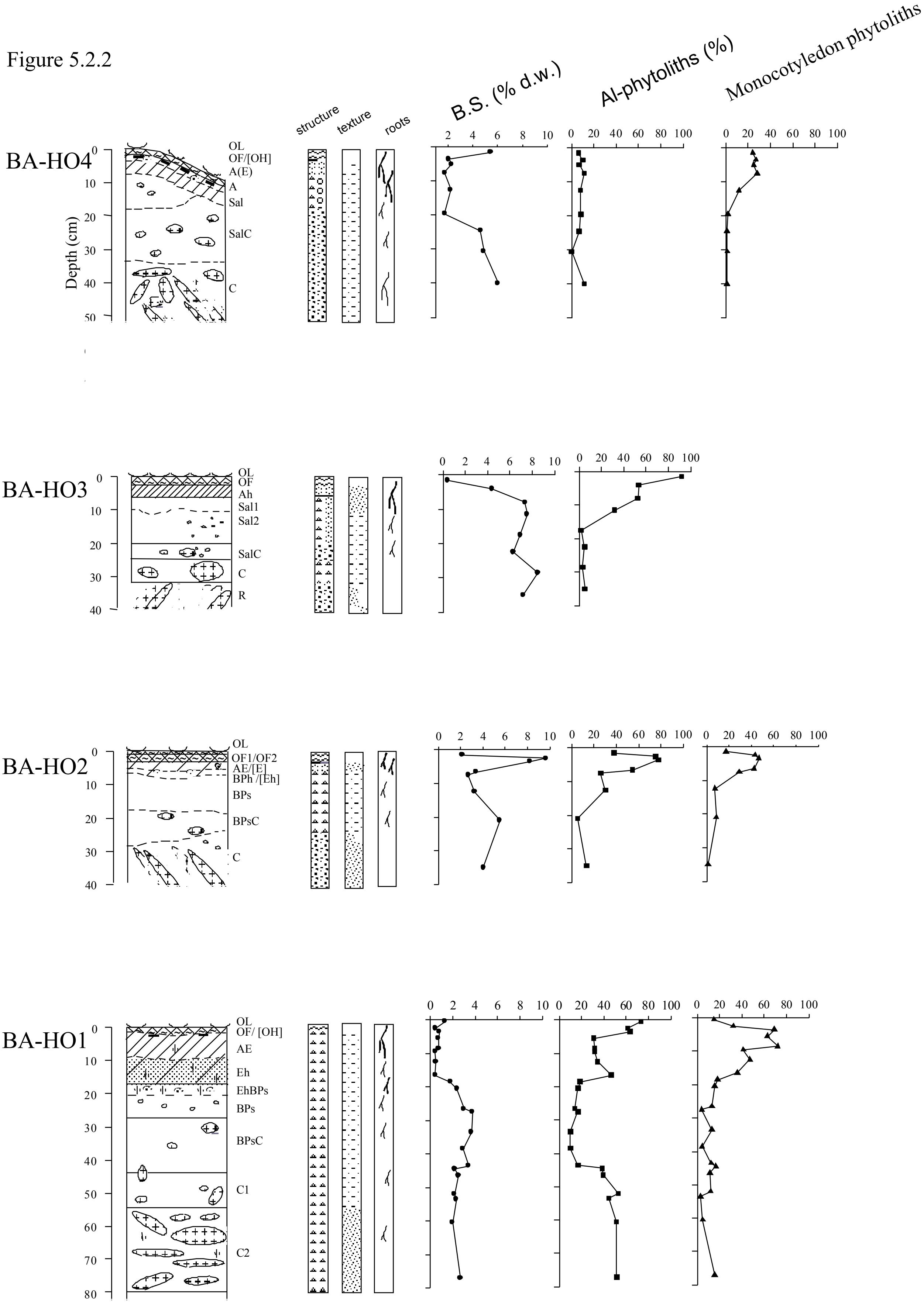

structure
texture
roots
B.S. (% d.w.)
Al-phytoliths (%)
Monocotyledon phytoliths
Depth (cm)
BA-HO4
OL
OF/[OH]
A(E)
A
Sal
SalC
C
2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
0 10 20 30 40 50
BA-HO3
OL
OF
Ah
Sal1
Sal2
SalC
C
R
0 2 4 6 8 10
0 20 40 60 80 100
0 10 20 30 40
BA-HO2
OL
OF1/OF2
AE/[E]
BPh /[Eh]
BPs
BPsC
C
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
0 10 20 30 40
BA-HO1
OL
OF/ [OH]
AE
Eh
EhBPs
BPs
BPsC
C1
C2
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
0 10 20 30 40 50 60 70 80

Figure 5.2.3

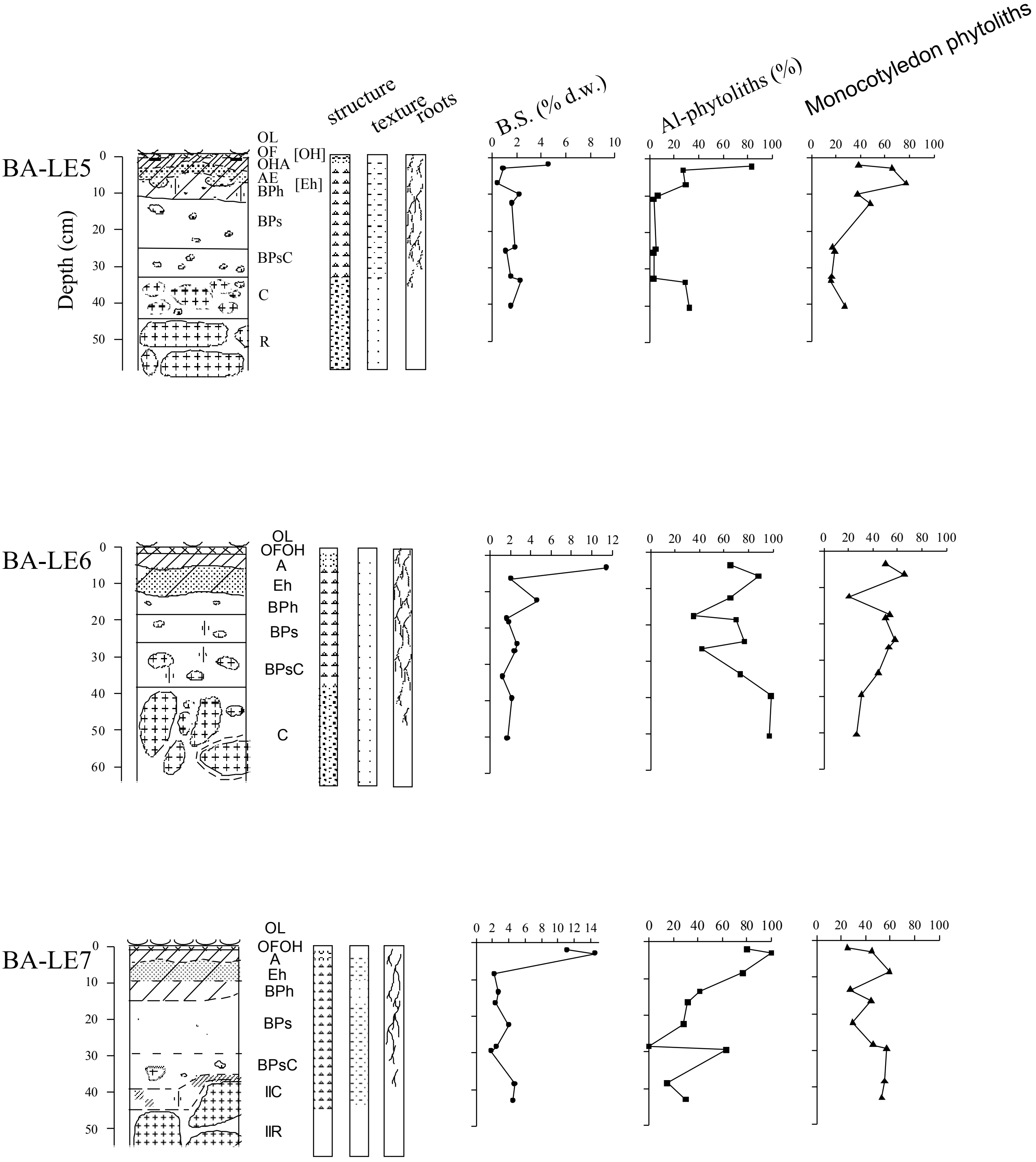
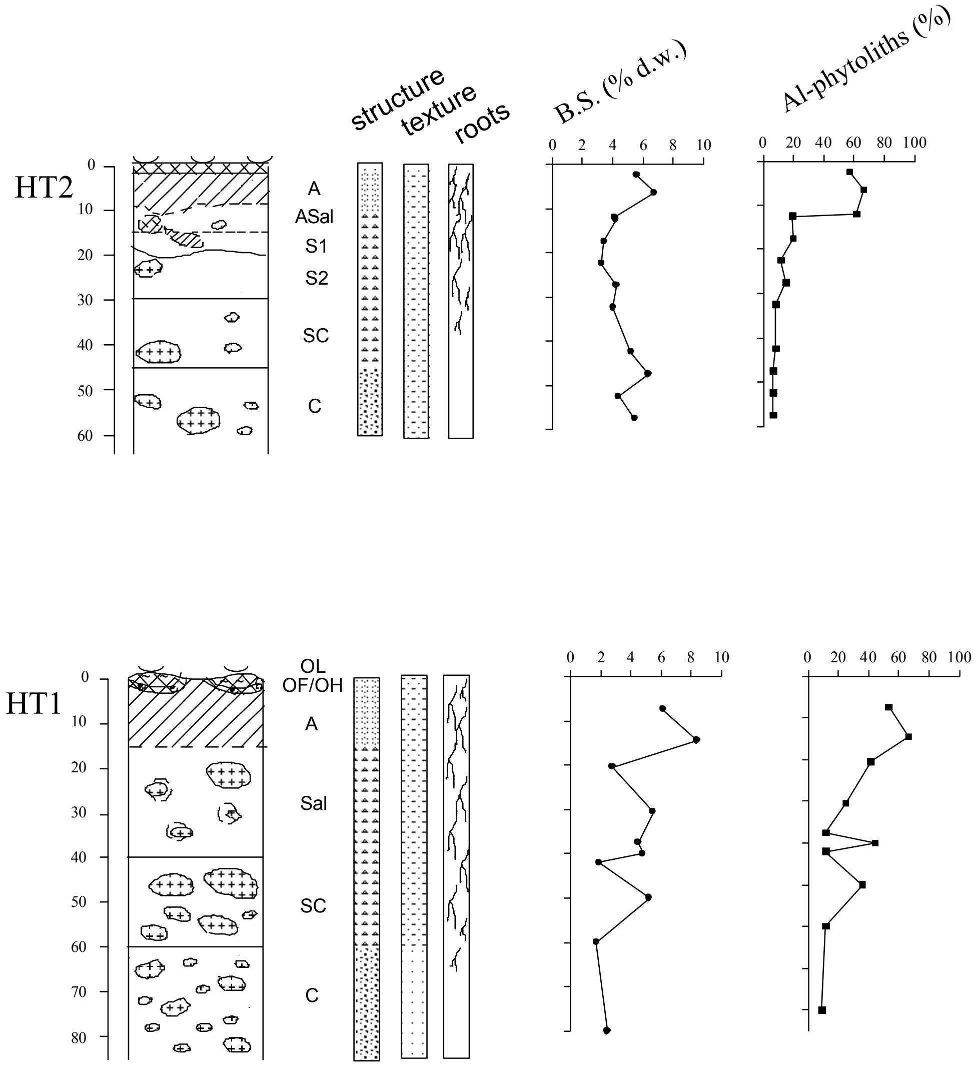

structure
texture
roots
B.S. (% d.w.)
Al-phytoliths (%)
Monocotyledon phytoliths
Depth (cm)
BA-LE5
OL
OF
OHA
AE
BPh
[OH]
[Eh]
BPs
BPsC
C
R
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
BA-LE6
OL
OFOH
A
Eh
BPh
BPs
BPsC
C
0 2 4 6 8 10 12
0 20 40 60 80 100
0 20 40 60 80 100
BA-LE7
OL
OFOH
A
Eh
BPh
BPs
BPsC
IIC
IIR
0 2 4 6 8 10 12 14
0 20 40 60 80 100
0 20 40 60 80 100
0
10
20
30
40
50
60

Figure 5.2.4



HT2
HT1
structure
texture
roots
B.S. (% d.w.)
Al-phytoliths (%)
0 2 4 6 8 10
0 20 40 60 80 100
0
10
20
30
40
50
60
70
80
A
ASal
S1
S2
SC
C
OL
OF/OH
A
Sal
SC
C

Figure 5.2.5

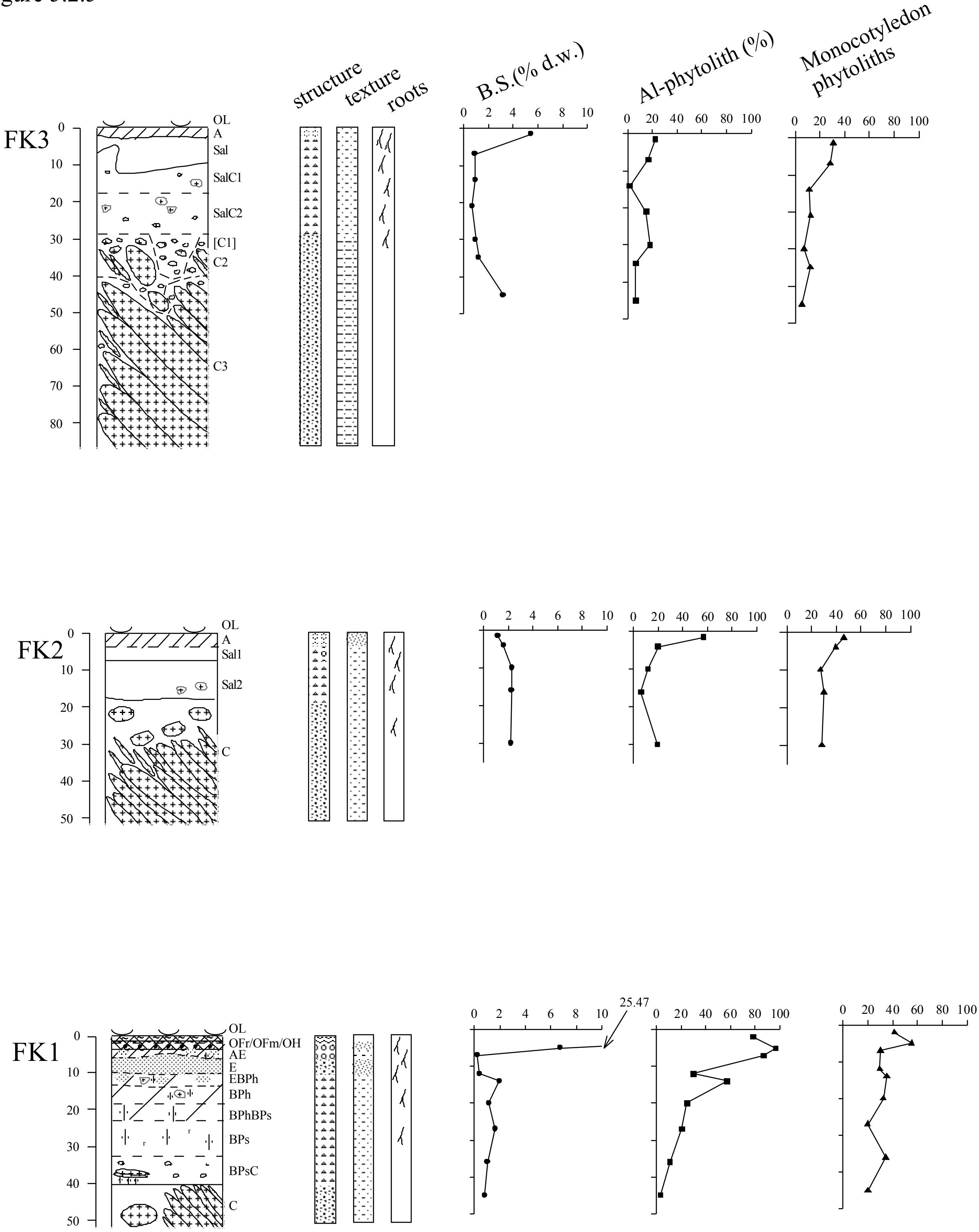

structure
texture
roots
B.S.(% d.w.)
Al-phytolith (%)
Monocotyledon phytoliths
FK3
0
10
20
30
40
50
60
70
80
OL
A
Sal
SalC1
SalC2
[C1]
C2
C3
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
FK2
0
10
20
30
40
50
OL
A
Sal1
Sal2
C
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100
FK1
0
10
20
30
40
50
OL
OFr/OFm/OH
AE
E
EBPh
BPh
BPhBPs
BPs
BPsC
C
25.47
0 2 4 6 8 10
0 20 40 60 80 100
0 20 40 60 80 100

Figure 5.2.6
Ratio of Aluminous B.S and total B.S.in the study sites (Bars). Sites are displayed with increasing elevation (Table 5.2.7). If the ratio Al-B.S. / tot.B.S. < 0.2 (dotted line) the persistence of grasslands is hypothesised. If the ratio Al-B.S./ tot.B.S. > 0.3 (solid line) the former presence of heathlands is argued, for the sites at higher elevation (AR3, HT1, AR2), the presence of scattered krummholtz may be hypothesised.
Buried horizons were not included in the calculation

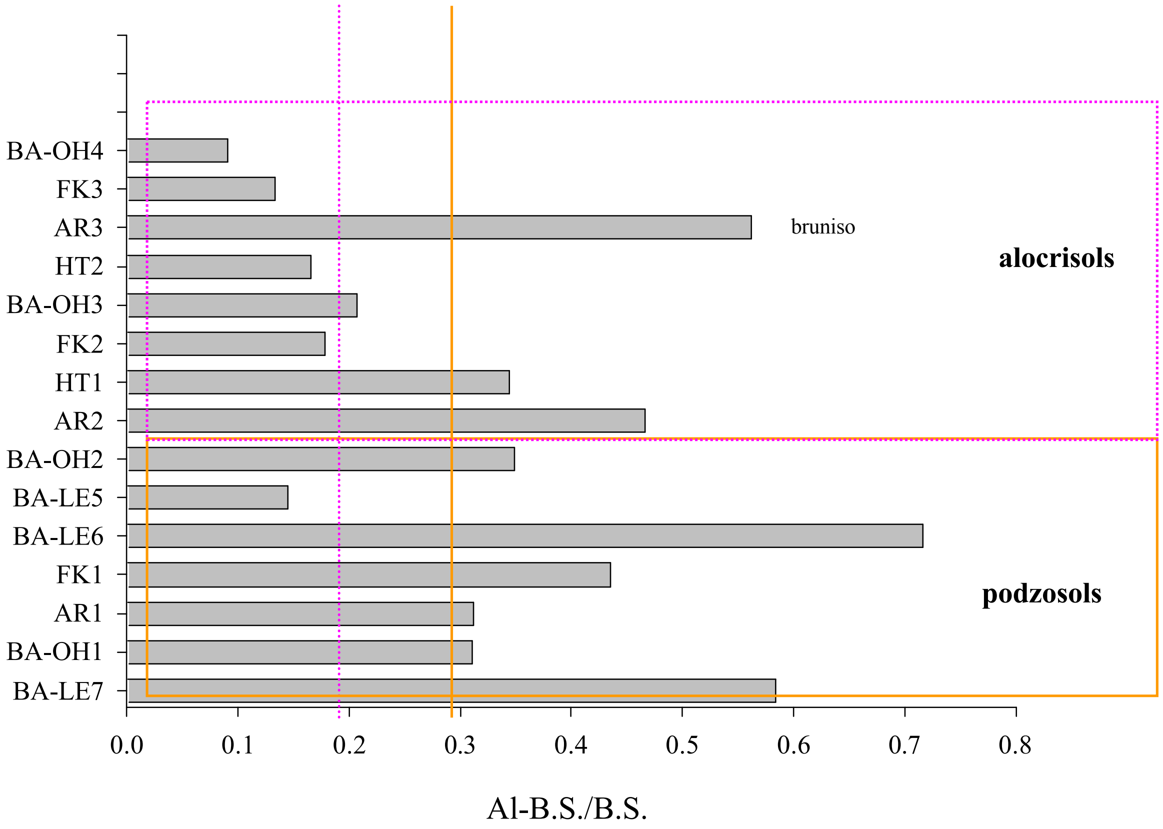


Figure 5.2.7 The variations in B.S. and Al-B.S. in the podzosol BA-HO1 are correlated with climatic variations during the last 3350 years. It is here hypothesised that that the low content of B.S. in the horizons O and AE is due to the strong grazing pressure during the last 300-400 years plus, possibly, the lost of biomass due to avalanches.
Data used for the calculations are: growing season 110 days; productivity is 3.3 g $d^{-1}m^{-2}$; average content of B.S. in the vegetation is 2.29%; total average production of B.S. 8.31 g $d^{-1}m^{-2}$; total content of B.S. in the horizon O 0.03 kg= 3.6 equivalent of the annual productivity (Eq. an. pr.); total B.S. in A 0.44 kg=1084 Eq. an. pr.; total B.S. in E: 0.455 kg=55 Eq. an. pr.; total B.S. in BP 10.348 kg=1245 Eq. an. pr; total B.S. in C 7.748 kg=932 Eq. an. pr.; total B.S. in the soil is ca. 3220 Eq. an. pr.. = 0.28 the time length considered (3350 years).
Dots: punctual B.S.; squares: punctual Al-B.S.; ascisse axis is soil depth in centimeters.

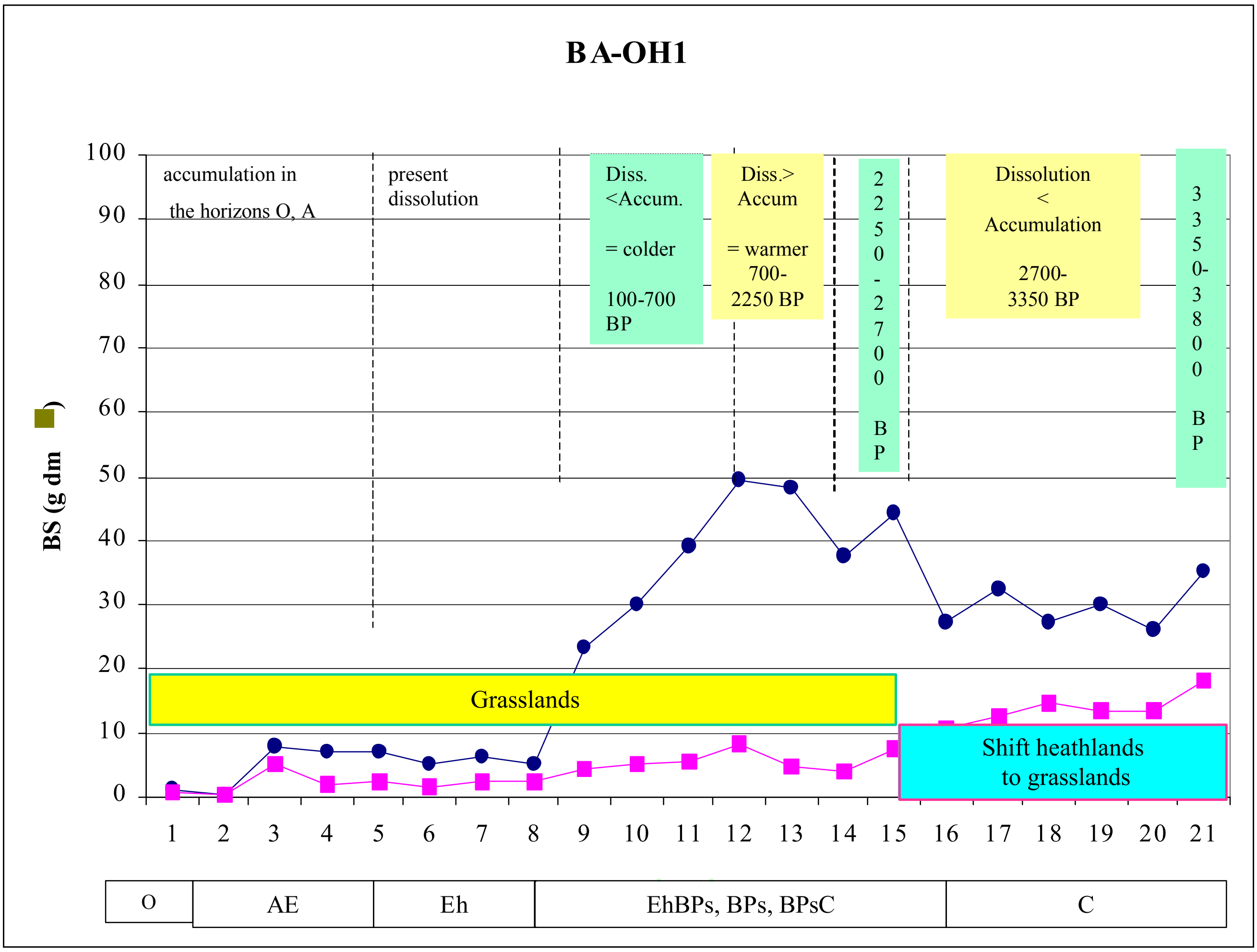


Figure 5.2.8 The variations of B.S. and Al-B.S. in the PODZOSOL BA-HO2 are correlated with climatic variations in the last 2250 years. The variations of B.S. and Al-B.S. are parallel: vegetation has always been of grassland type.

Data used for the calculations are: growing season 90 days; productivity is 1.3 g $d^{-1}m^{-2}$; average content of B.S. in the vegetation is 0.99%; total annual average production of B.S. 1.12 g $d^{-1}m^{-2}$; total content of B.S. in the horizon O 0.118 kg= 105 equivalent of the annual productivity (Eq. an. pr.); total B.S. in A 2.640 kg=2196 Eq. an. pr.; total B.S. in E: 0.442 kg=395 Eq. an. pr.; total B.S. in BP 9.217 kg=8229 Eq. an. pr; total B.S. in C 8.320 kg=7429 Eq. an. pr.; total B.S. in the soil is ca. 18 350 Eq. an. pr.= 3.3 the time length considered 2250 years).

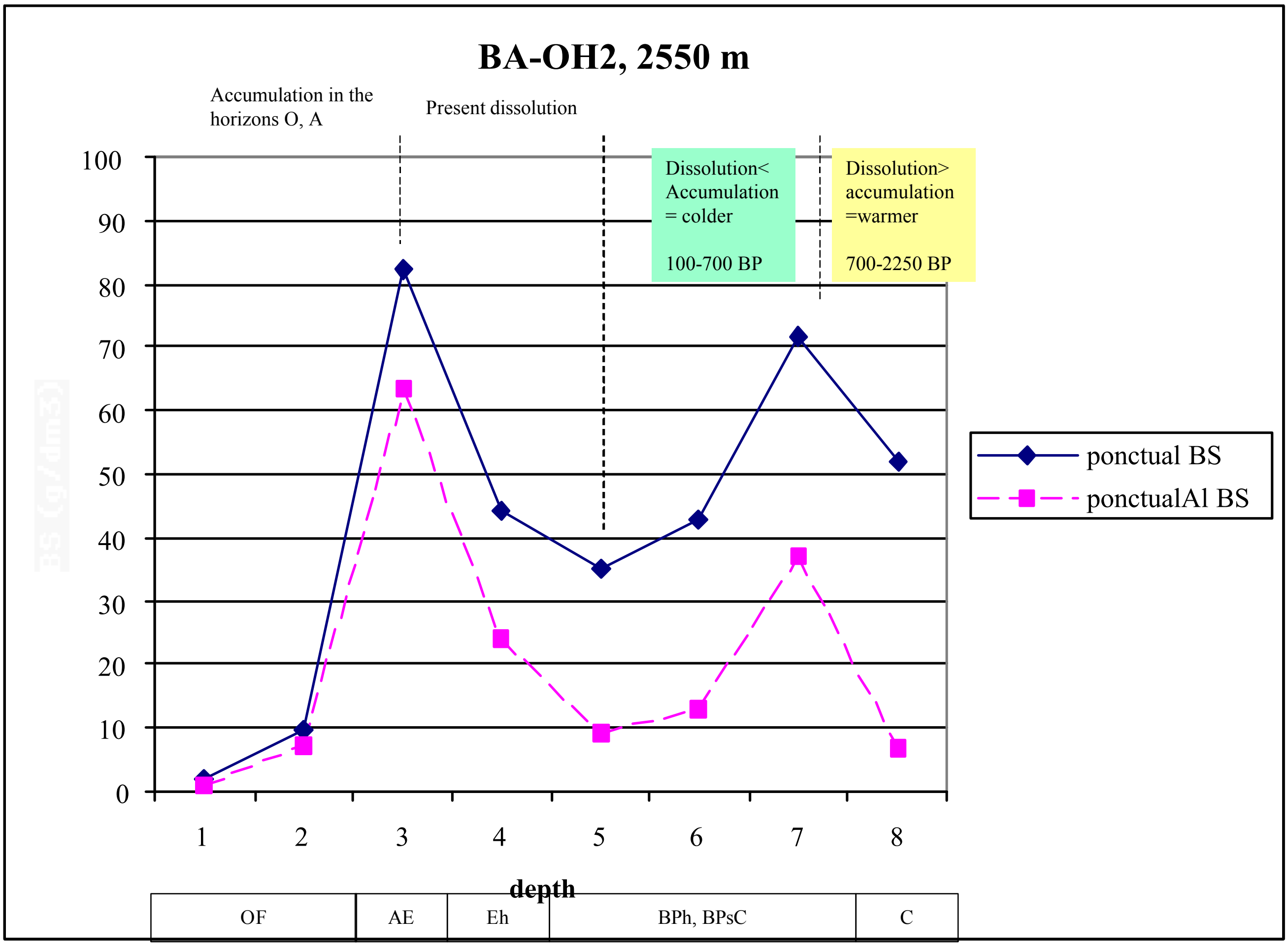


Figure 5.2.9 The variations in B.S. and Al-B.S. in the PODZOSOL BA-LE6 are correlated with climatic variations during the last 3800 years. The hypothesis is made that B.S. in solution in the soil is leached or recycled by the vegetation; in the horizon A Al-B.S. is more accumulate than B.S.; in the horizon Eh both Al-B.S. and B.S. are dissolved. During cold phases the dissolution is weaker than the production producing an accumulation. Biogenic silica is translocated downwards the illuvial horizons with a migration rate proportional to the dissolution rate.
Data used for the calculations are: growing season 101 days; productivity is 3.3 g d^{-1}m^{-2}; average content of B.S. in the vegetation is 2.29%; total average production of B.S. 7.63 g d^{-1}m^{-2}; total content of B.S. in the horizon O 0.03 kg= 3.6 equivalent of the annual productivity (Eq. an. pr.); total B.S. in A 2.760 kg=361 Eq. an. pr.; total B.S. in E: 1.638 kg=215 Eq. an. pr.; total B.S. in BP 8.749 kg=1147 Eq. an. pr; total B.S. in C 2.288 kg=300 Eq. an. pr.; total B.S. in the soil is ca. 2023 Eq. an. pr.. = 0.5 the time length considered (3800 years).

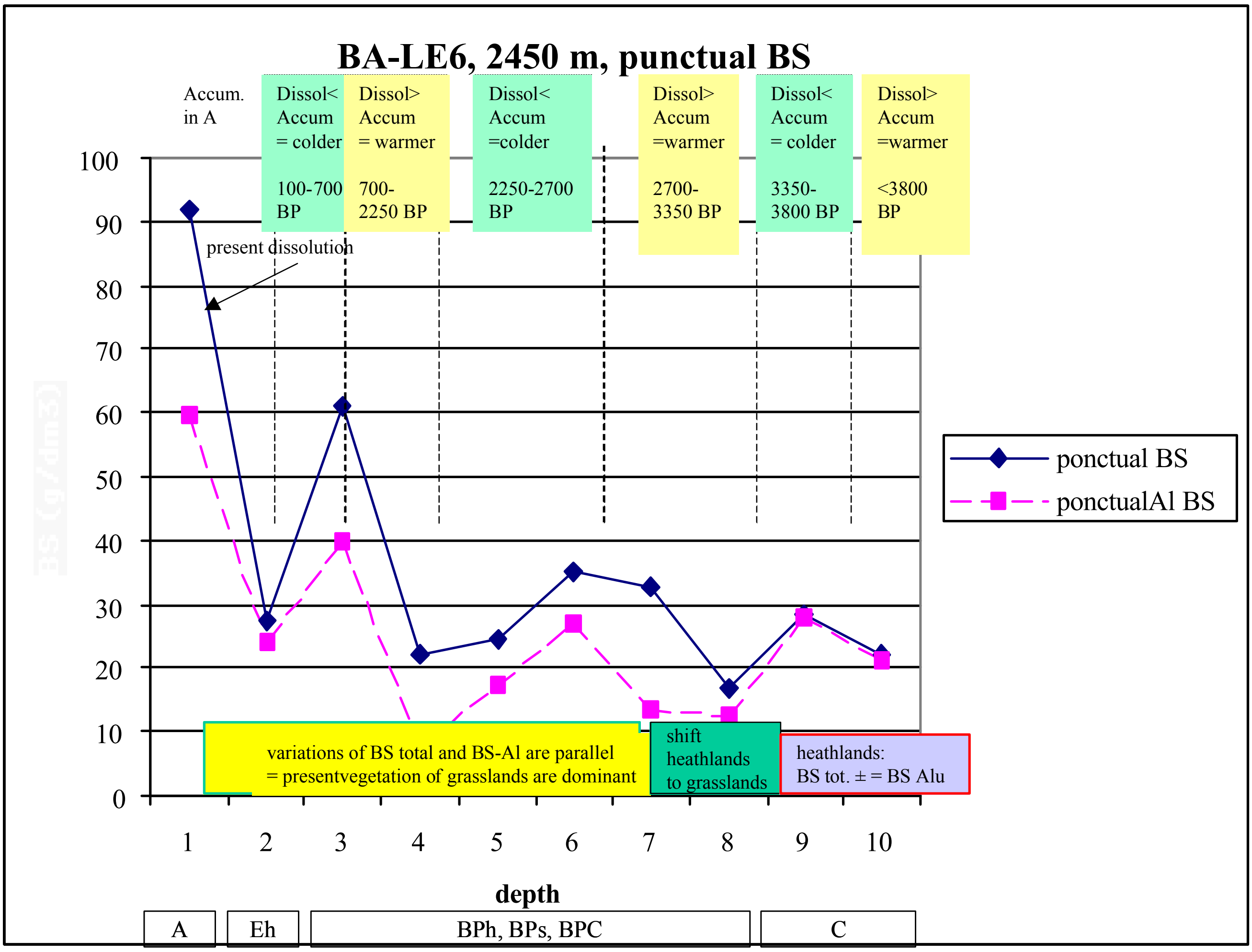
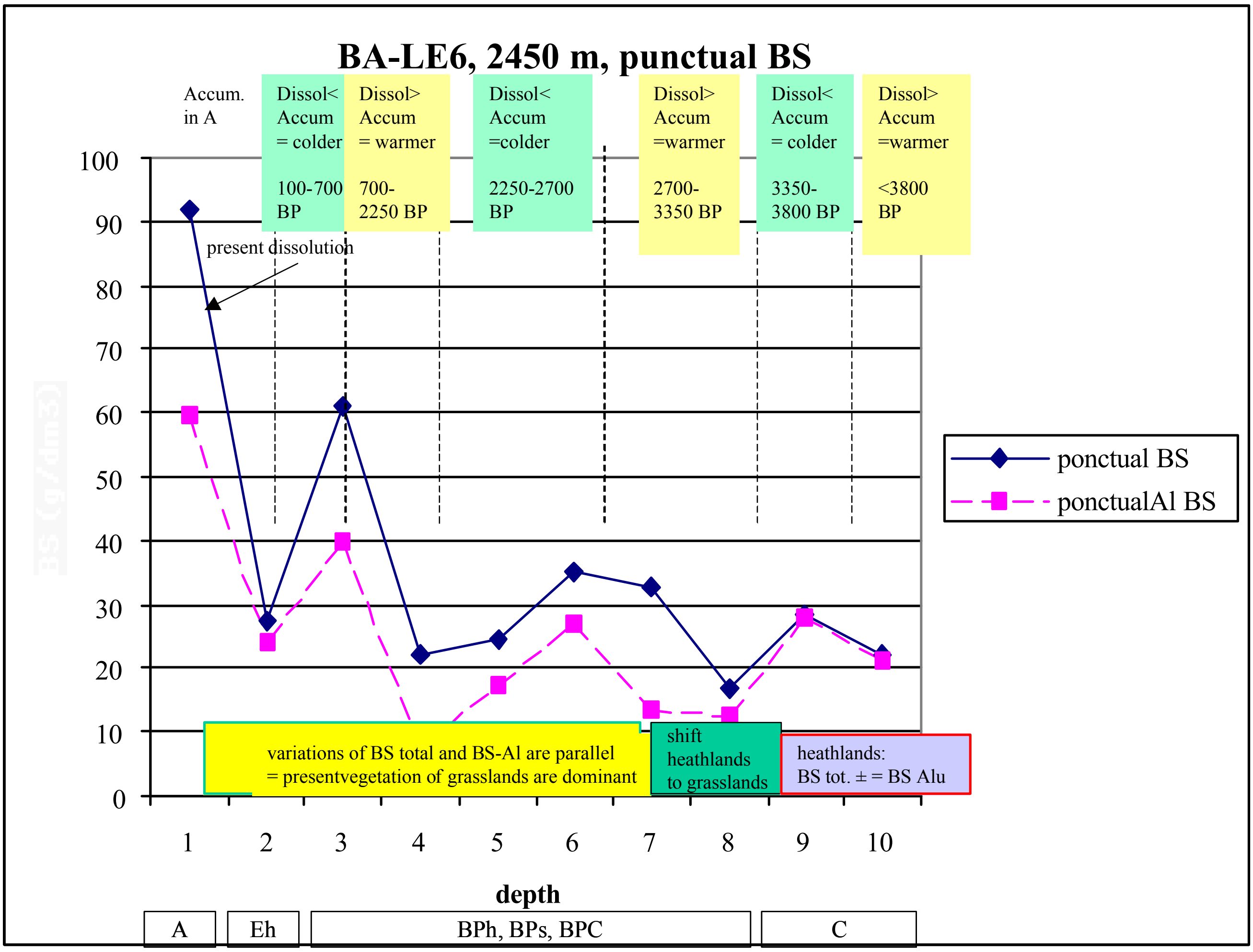


Figure 5.9.10 The variations of B.S. and Al-B.S. in the ALOCRISOL HT1 are correlated with climatic variations during the last 4800 years.

Data used for the calculations are: growing season 91 days; productivity is 3.3 g d^{-1}m^{-2}; average content of B.S. in the vegetation is 2.29%; total average production of B.S. 6.87 g d^{-1}m^{-2}; total B.S. in A 7.448 kg=1084 Eq. an. pr.; total B.S. in Sal 24.544kg=3573 Eq. an. pr.; total B.S. in the soil is ca. 4657 Eq. an. pr.. = 0.97 the time length considered (4800 years).



5.2.5 Discussion

5.2.5.1 Soil-type altitude correlation

A strict correlation between soil-type and altitude was detected in all the sites (Chapter 3 and 5). Indeed, the upper limit of the podzolic activity is located in a narrow altitudinal belt comprised between 2500 m (at Furka and in Val d'Arpette) and 2570 m (at Belalp). At higher elevation the dominant soil types were alocrisols.

The knowledge of alpine and sub-alpine soils dynamics in the Central Alps is limited to few studies (Paternoster, 1981; Spaltenstein, 1984; Keller, 1991; Fierz and Gobat, 1996; Theurillat *et al.*, 1998). A study of soil biosequences in a site in the Central Valais found an altitudinal zonation of soil types similar to the one observed in the present study. In transects between 1780 m and 2600 m a.s.l. the upper limit of podzolic activity was detected at 2450 m (Tinner *et al.*, 1996).

In all the sites a transition of soil type from PODZOSOLS to ALOCRISOLS is recorded in a narrow altitudinal belt, at about 2550 m a.s.l..

It is hypothesised that the upper limit of the PODZOSOLS MEUBLE represents an ancient vegetation border: conifer woodlands and/or close heathlands would have been dominant at least up to 2400 m a.s.l.. These communities supply acidic litter and have high net primary production and therefore can lead to a fully developed PODZOSOL MEUBLES soil type (Duchaufour, 1998). The present vegetation consisting of meadows is unable to drive pedogenesis to this stage.

The podzolic activity in soils blurs with altitude, giving origin to weakly podzolised soil types, i.e. PODZOSOLS OCRIQUES. This belt should be origineted under a less prooductive vegetation type, and should correspond to the treeline ecocline. This transition zone was located between 2400 and 2570 m a.s.l..

At higher altitude (above 2500-2550 m a.s.l.) the dominant soil types are ALOCRISOLS. Their genesis is consistent with the persistence of less productive plant community and with less acidificant humus types: this belt it is argued to be the result of the presence and persistence of grasslands during the Holocene. In the sites close to the Aletsch Glacier podzolisation did not occur.

5.2.5.2 Biogenic silica in soil top horizons

Phytoliths occurring in the uppermost part of a soil are mainly the result the decomposition of plant stand litter on a relatively short time scale (see for instance: Fredlund and Tieszen, 1994). For this reason, the content of B.S. of topsoil horizons is not employed for palaeoecological reconstruction and is discussed elsewhere (Chapter 5.1). The amount of biogenic silica in topsoil varies consistently with present plant stand composition: in the sites below 2600 m, where silica accumulator species grow, B.S. in top soils is 5.2% to 16% of dry soil mass. In the sites at higher altitude, dominated by weak silica producers, B.S. in top soil is only 1.5% to 3.9% of soil mass. Al phytoliths in top soil were more abundant at low elevation (up to 70%). The study of modern analogs of phytoliths assemblages showed that an *in situ* mechanism of deposition of phytoliths in subalpine-alpine grasslands is dominant (Chapter 5.1). On the basis of the principle of the actualism, it can be inferred that the same mechanism was at the origin of the formation of past assemblages in the subalpine-alpine ecosystems.

5.2.5.3 Biogenic silica in deeper soil horizons

a) Patterns of phytolith distribution in soil

Soil mineral horizons integrate on a longer time scale, vegetation input and soil processes (Alexandre *et al.*, 1997a). Phytoliths in soil are subjected to dissolution processes (Alexandre *et al.*, 1997a). The abrupt decrease of biogenic silica recorded in the top portion of all the podzosols (Chapter 5.1) shows that B.S. is partially ricycled by the vegetation already in the mineral organic fraction of the soil.

The fraction of phytoliths resistant to dissolution migrates downwards in the soil profile, with a distribution curve called "phytolith profile" (PhP). Soil texture was shown to exert a considerable effect on the PhP: for instance, it was evidenced that the removal of phytoliths by capillary waters is negligible in a loamy podzosol, while, in contrast, the migration of phytoliths in sandy podzosols is relevant (Gol'yeva, 1997). Soil micromorphology also plays a role in the downward migration process of phytoliths: it was shown that the content of phytoliths was higher in fissures and pores of the illuvial horizon, than in the bulk soil. This distribution points to the role of pores in the downwards migration of phytoliths together with soil skeleton material (Gol'yeva, 1997).

- Undisturbed soil profiles

Soil texture in all the studied soils was sandy-silty and can be approximately considered constant in all the profiles. In these conditions, if the input from the vegetation is constant, phytoliths should migrate downwards the bottom of the profile linearly, following the pattern of soil particles of the same size-class.

For undisturbed soil profiles five typical patterns of migration of phytoliths could be identified (Figures 5.2.1-5.2.5):

a) B.S. decreases regulary from the top towards the base of the soil;
b) B.S. decreases with an irregular pattern towards the base of the soil;
c) B.S. decreases in the upper part of the profile and is accumulated in the deeper part;
d) B.S. is constant, or nearly constant, along all the profile;
e) B.S decreases in the upper part of the soil, followed by a neat peak of B.S., and than by a decrease in the deepest part of the soil.

The aluminious phytoliths showed two patterns of distribution that appear to be correlated with altitude. Below 2600 m a.s.l. the types b) and c) occur in the PODZOSOLS. Above this altitude, the patterns a) and d) characterize the ALOCRISOLS, while the type e) occurs in the BRUNISOL.

In the PODZOSOLS, a decrease in the eluvial horizon (E) is followed by an accumulation in the illuvial horizons (B). At the top of the horizon C the content of biogenic silica decreases again, and it may slightly increase towards the basis of C. The behaviour of B.S. in the PhP of PODZOSOLS is in accordance with published literature (e.g.: Gol'yeva, 1997; Kamanina, 1997).

In the ALOCRISOLS biogenic silica decreases from the organic horizons O to the Sal horizons, towards the bottom of the profile the migration is linear.

For the ALOCRISOLS no comparative data is available.

-Discountinuous pedogenesis and bioturbation

Some of the soils examined presented discontinuous pedogenesis: they either have undergone colluvial activities (AR1 and AR2), or were developed on residual palaeosoils (BA-LE7 and HT2). It is to note that the colluvial activity and the residues of palaeosoils were consistently detected by peaks in the B.S. and Al phytoliths records. This result is remarkable as it shows that alpine soils are highly conservative media, and soil re-mixing processes are faithfully recorded in the PhP. Analogous considerations can be made concerning the effect of bioturbation on the PhP in subalpine-alpine soils. The persistence of peaks of biogenic silica inside the buried horizons seems to show that the biological activity in soil does not strongly affect the PhP profile, and it does not erase major variations of biogenic silica content.

b) Distribution of monocotyledon phytoliths

The distribution of monocotyledon phytoliths shows a clear repetitive distribution pattern in PODZSOLS and ALOCRISOLS. Very good examples are in the BA-HO1 and BA-HO2 profiles: in the horizons O, A and E the majority of phytoliths are from monocotyledons (i.e. nearly all short cells), deeper on monocotyledon phytoliths show a sharp decrease, and then in the underlaying horizons their concentration is rather constant. This distribution can be intepreted as the result of a simply gravitative migration of the small monocotyledon phytoliths (mainly short cells) that have a size of about 10 µm.

c) Dissolution processes

Biogenic silica turnover in soil is little known. Investigations in tropical soils evidenced the importance of opal in determining soil silicon weathering budget (Lucas *et al.*, 1993; Alexandre *et al.*, 1997a; Meunier *et al.*, 1999). Biogenic silica distribution in tropical soils follows a bicompartimental model, similar to the decomposition pattern followed by soil organic matter: a fraction of the phytolith input released after the mineralisation of litter is dissolved in the soil, while a pool of phytoliths is dislocated along soil profile to form a stock of more durable phytoliths (Alexandre *et al.*, 1997a).

In all the soils here examined, the distribution of B.S. followed a similar pattern: a maximum was recorded in the holorganic (O) and organo-mineral (A) layers, followed by a decrease, often abrupt, in the mineral layers with rate of loss of B.S. between 60 and 97%. The majority of phytoliths are dissolved in the eluvial horizon where the weathering is more active, and the dissolved opal is recycled by the vegetation or leached by percolating waters. A pool of more resistant phytoliths, however, is translocated to the deeper horizons.

Litter of heaths and conifers yields little biogenic silica in respect to grassland.It has been estimated that the B.S. input of a stand of *Larix decidua* is 2.4 g m^{-2} y^{-1}, while a grassland with *Festuca scabriculmis* produces 10.3 g m^{-2} y^{-1}(Carnelli *et al.*, 2001). Moreover, grassland and forest produce also different humus forms that influence the fate of phytoliths in soil. Indeed, the content of silica in soil developed from rocks poor in weatherable minerals depends principally upon vegetation and humus-type (Duchaufour, 1998). Phytoliths easier to dissolve occur in litter from dicotyledons and grasses which has a low C/N ratio (originating humus of mull-type). In contrast, conifers and heaths producing litter with a higher C/N ratio (originating humus of mor- or moder-type), contain phytoliths more resistent to dissolution (Bartoli, 1980).

Thus, mull-type humus releases a great quantity of soluble silica, while, moder and mor humus release very little soluble silica, and phytoliths are accumulated in the organic layers (O and A). A fraction can be leached in the spodic horizons (BPh and BPs) in association with dispersed clays and organo-metallic complexes, which are typical podzolisation products (BARTOLI, 1981). In podzolic soils, under thick humus releasing great quantities of organic acids, B.S. is badly recycled by the vegetation and is accumulated in the soil. It follows that podzosol should act as valuable archives of phytolith and especially of Al phytoliths.

-Stock of biogenic silica in soil

The soils at about 2400 m a.s.l. in Belalp and Val d'Arpette contain on average 2% of B.S., while at higher altitude in the same transects, the content is around 5%. Grassland input calculated for modern vegetation in the same area is not consistent with these figures: subalpine grasslands growing at 2400 m are about 10 times more productive of B.S. than the alpine meadows dominant at 2800 m a.s.l. (Carnelli *et al.*, 2001).

The lower content of B.S. at 2400 m may be the result of the interaction of two causes:

1) B.S. is dissolved more actively at lower elevation (2300-2400m);
2) in the sites at lower elevation a vegetation shift occurred, from a plant community producing low B.S., to present day grasslands that are silica accumulators.

The first hypothesis is formulated for analogy to weathering of primary minerals in alpine soils. Along an altitudinal transect between 400 and 2400 m a.s.l. in the Southern Swiss Alps (Ticino) it was shown that crystalline silica weathering decreases exponentially with altitude (Drever and Zorbrist, 1992). However, the present study refer to a smaller altitude gradient (2400-2800 m) and are not directly comparable. Moreover, a clear correlation between the rate of dissolved B.S., altitude and, soil type was not observed. Regardless of elevation and soil type, the content of biogenic silica is high in the top horizons and it drops abruptly in the eluvial horizons, with a rate of loss varying between 60% and 97%. Therefore, it could be argued that crystalline silica and opal silica may behave differently in respect to dissolution processes, and more investigations are needed to evaluate the role of biogenic silica as a sink or as a pool for silicon (Meunier *et al.*, 1999).

The second hypothesis, discussed in the following paragraph, would explain the lack of B.S. at the basis of the profile in the soils at about 2400 m a.s.l..

5.2.5.4 Palaeoecological reconstruction inferred from soil biogenic silica

The study of biogenic silica in soil has a potential for palaeoenvironmental reconstructions. This methodology has been successfully employed in tropical ecosystems, and it is here applied to alpine ecosystems for the first time.

In this study the amount of B.S. and the frequency of Al-B.S. are put in comparison. The percentages of Al phytoliths are here interpreted as proxy-data of presence of heaths and conifers (Carnelli *et al.*, 2002), this approach is here tested for the first time.

The distribution curves of Al phytoliths for the deeper portion of the soil profiles mainly followed five types of trends (Figures 5.2.1-5): either they showed an accumulation towards the deeper horizons, or, in contrast, a steady decrease with depth is recorded.

At lower elevation, in soils between 2400 and 2550 m, in Val d'Arpette, at Belalp and Belalp Lengi Egga, Al phytoliths accumulate towards the deeper part of the profile [i.e. AR1 (60%), AR2 (50%), BA-HO1 (60%), BA-LE6 (98%), BA-LE7 (63%), and in lower in FK3 (33%)]. The increasing of Al phytolith percentage at the basis of the profile, is anticorrelated with the B.S. curve: this is interpreted as signal of the former presence of plant communities richer in this "chemotype", Ericaceae and conifers.

When the aluminium PhP is not changing with depth, or a steady decrease is present, a monogenic origin of phytoliths can be argued: this is the case for instance of the ALOCRISOL at higher elevation: BA-HO4, BA-HO3, HT2, FK2 in which the phytolith curve is linear and does not show any peak: this trend can be interpreted as given by a monogenic origin, i. e. herbaceous vegetation was always dominant.

For the sites at about 2400 m, that showed a clear anticorrelation between Al phytoliths and B.S. content (i.e. BA-HO1, AR1, AR2, BA-LE7, BA-LE6, and FK3), we make the hypothesis that a vegetation shift from woody vegetation (low silicon producer but high Al-phytoliths producer) to grasslands had occurred.

In the soils above 2550 m a.s.l. (with the exception of AR3), the percentage of Al phytoliths in the deep horizons is always very low (less than 20%). In these sites the Al-phytolith curves and B.S. curves are generally correlated: it is hypothesised that both Al-phytolith, and B.S. content, are in equilibrium with present physical-chemical processes of dissolution and translocation in soil, and with present vegetation. In these sites no vegetation shift has occurred, and grasslands dominated all along the phytolith record.

The high content of Al phytoliths at 2720 m in Val d'Arpette still awaits an explanation: it can be speculated that in this shallow soil near the crest, the dissolution rate of Al phytoliths was very low, leading to such an accumulation, but further evidences should be gathered for a more accurate interpretation.

A synthesis of these results is displayed in figure 5.2.6, where the ratio between punctual values of Al-B.S. and B.S. is showed. The majority of the sites in which this ratio is less than 0.2, are situated above 2500 m: for these sites the persistence and dominance of grasslands is hypothesised. In the sites in which this ratio is higher we may speculate that woody vegetation occurred at least for a period of time. We suggest that the values higher than 0.3 might be indicative of the past occurrence of woody species. The soils for which this ratio is higher than 0.3 are generally PODZOSOLS.

We speculate that in the sites at higher elevation in which this ratio is more that 0.3, the input of Al-phytoliths may be the result of the presence of dwarf alpine heaths, and/or isolated krummholtz of conifers.

5.2.5.5 Changes in biogenic silica cycle are climatically driven?

Models for the Si biocycle in alpine soils are lacking. The evaluation of the silica budget in soil goes beyond the purposes of this work, nevertheless it can be hypothesised that in temperature-limited ecosystems, such as the alpine ones, B.S. biocycle must be linked to climatic fluctuation, mainly temperture. Indeed, although in the alpine environments water availability is generally large, however, temperature determines the availability of liquid water during the different seasons influencing the rate of soil leaching. Some perspectives for a correlation between climatic fluctuations and the record of B.S. are here suggested.

It is here assumed that since phytoliths migrate in the sandy-silty horizons linearly, peaks of punctual B.S. and Al-B.S. (Table 5.2.6) should mark a different rate between dissolution and accumulation processes. During the colder periods of the Holocene the dissolution in soil must have been lower, as a consequence of the slowing down of the biochemical processes and therefore phytoliths must have been accumulated in larger quantity, although the input from vegetation was reduced. During warmer periods plant productivity and the production of phytoliths increased, but, at the same time the soil activity was stronger and dissolution rate higher, leading to a decrease of the stock.

In figures 5.2.7-10 the variations of punctual B.S and Al-B.S. in some of the sites are tentatively correlated with the climatic fluctuations known for the last part of the Holocene.

The hypothesis of a mechanism of alternance of accumulation and dissolution dominated periods, is slightly modified for the site HT1 (Figure 5.2.10). This site is located at a close proximity to the glacier, where it is argued that even during warmer periods the temperature never raised remarkably: in this case in both warmer and colder periods the accumulation has always been higher than the dissolution. These speculations should be tested by investigating several issues: for instance by evaluating the migration speed of phytoliths in the profile to have an indirect measure of the age of phytoliths at the basis of the profile.

5.2.5.6 History of vegetation

In Val d'Arpette, Belalp-Hofathorn, Belalp-Lengi Egga, and Furka the upper limit of the podzolisation, B.S. content and, aluminium phytolith frequency, consistently suggest that the treeline might have been between 2500 and 2550 m (Fig. 5.2.6). Above this elevation, alpine meadows were dominant along the Holocene, although very likely, scattered heaths and conifer krummholtz trees occurred as well.

In the Aletsch transect both soil types and phytolith contents seem to exclude past occurrence of woody species, and swards appear to be constantly dominant during the Holocene.

The now existing treeline in the Central Swiss Alps matches locally different altitude, being inversely correlated with the degree of oceanicity and snow persistence. Indeed, present treeline attains 2400 m a.s.l. in the more continental central Valais (Zermatt region), while in the S. Gotthard region, in proximity of Furka, it is 200 meter lower (Eggenberg, 1995). Less favourable conditions for conifer establishment in the S. Gotthard region, are reflected by the lack of *Pinus cembra* and the scarcity of *Larix decidua* pollen during the postglacial in the area (Burga and Perret, 1998). In contrast, the stronger oceanicity favours at Furka, the upwards expansion of green alder (*Alnus viridis*). The low Al phytolith percentages recorded at Furka may reflect less favourable condition for conifers.

Indipendent evidences for the reconstruction of the uppermost limit of the treeline are supplied by soil charcoal analysis (Chapter 5): results of pedoanthracology were largely in accordance with present findings. Indeed above 2500 m a.s.l., the anthracomass was negligible, consistently with the absence of podzosols.

In the same direction point the results of the analysis of plant macrorests and pollen fluxes from a peat-bog located at Lengi Egga, at 2557 m a.s.l. (nearby BA-LE5), where the occurrence of the forest in the peat-bog catchment area during the Holocene is to be excluded (Tinner and Amman, 2001).

The knowledge of the altitudinal range of Holocene treeline fluctuations is limited to a few site in the European Alps. The treeline was 100-150 m higher in Austrian Alps (Patzel, 1975). In the Swiss Central Alps the treeline was 80-100 m higher (Tinner *et al.*, 1996), and in the Eastern Swiss Alps the 120-150 m higher (Wick and Tinner, 1997); it was 300 m higher in the Italian Southern Western Alps

(Burga, 1991). The majority of the authors estimates that forest fluctuations caused by climatic causes did not exceed 100 or maximum 150 m (Wick and Tinner, 1997).

Present data suggest that, in Val d'Arpette and in the Belalp region the treeline was at 2450-2550 m, i.e. 250-300 m higher than present potential treeline. At Furka it reached about 2400 m, i.e. it was 200 m higher then present potential one.

5.2.6 Summary of conclusions

The uppermost position of the treeline was reconstructed on the basis of phytolith content and chemistry.Biogenic silica and Al phytolith frequency showed to be suitable to investigate dry terrestrial ecosystems along transitional gradients.

In the five soil transects situated above present day treeline, the upper limit of the podzolic activity in the soil occurs at 2500-2550 m a.s.l.. This limit corresponds to low content of B.S. and high content of Al-B.S. in the deeper part of the soil. Since the selected sampling sites were homogeneous for aspect, slope and bedrock: this transition is attributed to the past occurrence of a vegetation border between herbaceous and woody vegetation of ericaceous heaths and/or conifer woodlands. The former having high production of silica, low amount of Al phytoliths and the latter producing low amount of silica and high percentage of Al phytoliths.

In the transect "Aletsch" the persistence of alpine swards during the Holocene can be argued.

The soil profile distribution of biogenic silica records mixing phenomena, discontinuous pedogenesis and palaeohorizons. These evidence suggests that alpine soils, in spite of being highly dynamic systems, are conservative media, that act as reliable palaeoecological archives.

It is essential for a better understanding of the mechanisms and rates of weathering of silicon to determine the role of biogenic silica as a sink or as a pool in soil. However, it is here suggested that in temperature-limited ecosystems, the fluctuations in B.S. frequency in the soil deeper horizons may reflect climatic fluctuations. The alternance of accumulation vs. dissolution cycles in the study area should correspond to late Holocene colder and warmer periods, respectively.

The taxonomical value of aluminium rich phytoliths has been applied for palaeoecological reconstruction using soil-born phytolith assemblages. Al phytolith frequency in soil has been shown to be consistent with the soil type and with other independent palaeocological evidences (charcoals in soil and plant macrorest in a peat-bog). This methodology has proved to be valuable in alpine ecosystems.

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CHAPTER 6: SOIL CHARCOAL ANALYSIS

In this Chapter the problem of the position of the uppermost limit attained by the forest during the Holocene is addressed by means of two methodologies: soil and charcoal analysis in the same sites investigated for the study of biogenic silica in Chapter 5.

Ancient vegetation should have left fingerprints in alpine soils, both under the form of traces of pedological processes, and of remains of charred wood. Soil and charcoal analysis should be considered as complementary: soil study allows a virtually complete spatial and temporal continuty, while the study of soil charcoals, on the other hand, focus on the result of punctual fire events, limited in time and space. Neverthless, pedoanthracological studies allow high taxonomic resolution that allows to inferre the taxonomical composition of woody vegatetion. Moreover charcoals supply material for absolute chronology.

6.1 PAST UPPERMOST TREE LIMIT IN THE CENTRAL EUROPEAN ALPS (SWITZERLAND) BASED ON SOIL AND SOIL CHARCOAL*

Adriana L. Carnelli[1], Jean-Paul Theurillat[2], Michel Thinon[3], Gaëlle Vadi[4] and Brigitte Talon[3]

[1]Institut F.-A. Forel, Université de Genève, 10 route de Suisse, CH-1290 Versoix, Switzerland; [2]Centre Alpien de Phytogéographie, Fondation J.-M. Aubert, CH-1938 Champex, Switzerland and Laboratoire de Biogéographie, Département de Botanique et de Biologie végétale, Université de Genève, 1 ch. de l'Impératrice, CH-1292 Chambésy, Switzerland; [3]Institut méditerranéen d'Ecologie et de Paléoécologie (IMEP, UMR CNRS 6116), Case 461, FST Saint-Jêrome, Université d'Aix-Marseille III, F-13397 Marseille cedex 20, France; [4]Institut de Botanique, Université de Neuchâtel, rue Emile-Argand 11, CH-2007 Neuchâtel, Switzerland.

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6.1 Abstract

The uppermost limits of past treelines in the Alps are established using soil type and soil charcoal mass. In all the studied sites, a sharp decrease of soil charcoal mass is correlated with the upper altitudinal limit of PODZOSOLS. On the basis of this evidence, the uppermost tree limit reached 2500±100 m a.s.l. in the Valaisan Alps during the Holocene, i.e., it was 250±100 m higher than today's potential treeline. Consequently, the timberline would have reached 2400±100 m a.s.l.. From the presence of charcoals above the treeline we infer that a belt of alpine meadows, dotted with scattered conifers, was present throughout the Holocene in the alpine belt. Podzolic activity and soil charcoal mass are considered to be reliable indicators of the ancient uppermost limit of treeline in the European Alps.

6.2 Introduction

Tree survival at the alpine treeline (or tree limit) is mainly limited by cold-stressed conditions that cause a shift of the dominant life-form. Stress gradients of climatic, edaphic and biotic factors are shown to be involved in determining treeline position (e.g. for a review Körner, 1998). Nevertheless, evidence exists for a valid, world wide correlation between the maximum altitude attained by treelines, mean air temperature (between 5.5 and 7.5 °C), and soil temperature (about 7 °C) during the growing period (Körner, 1999; Paulsen, 2000).

Regionally, mesoclimatic factors determine treeline position: the degree of hygric continentality is directly correlated with present day treeline positions in the Swiss Alps (Gams, 1931; 1932; Pache *et al.*, 1996; Eggenberg, 1995; Theurillat *et al.* , 1998). Locally, topography (aspect and slope) plays a role in shaping the forest upper limit. Where edaphic or topographic factors change abruptly, a sharp boundary may be present (ecotone) while, if the stress gradient is mainly climatic, the transition of dominant plant life-form is gradual and a transition zone (ecocline) of heaths, shrubs, stunted trees and meadows can occur between the forest limit and the treeline (e.g. Theurillat *et al.* , 1998). Past treelines may be indicators of regional and local palaeoclimatic conditions. Forest fluctuations in response to climatic changes, however, are not easily triggered. Indeed, ecosystem resilience and the magnitude of climatic changes have to be taken into account when climatic reconstructions are attempted on the basis of past altitudinal or latitudinal fluctuations of treelines (Payette *et al.*, 1989; Holtmeier, 1994; Lavoie and Payette, 1996; Theurillat *et al.*, 1998).

Right up to the present day, human activities have dictated the altitudinal extension of the treeline ecocline (also the “kampfzone” or “krummholz zone”) in the Alps. It is very likely that this was one the first ecosystems in the area to be cleared and grazed during the Neolithic Age (4000-3000 yr BC) (Burga, 1988). Alpine meadows were extended downwards, directly by slash-and-burn practices and, indirectly, by artificially extending the habitat of herbivores, e.g. Capra ibex L. (Wiersema, 1989). In natural conditions, the treeline ecocline has an altitudinal extension of (50-) 100-150 m above the forest limit (e.g.: Ozenda, 1985; Favarger, 1995; Burga and Perret, 2001).

To reconstruct both natural and anthropogenic fluctuations of the treeline, spatially-precise contributions from palaeobotanical data are needed. Thus, in this paper, soil and soil charcoal analysis are paired to determine the upper tree limit during the Holocene in five sites in the Swiss Alps. Soil-charcoal analysis, or pedoanthracology, (Thinon, 1978) can supply such palaeobotanical data in areas where peat bogs are lacking (Payette and Gagnon, 1985; Thinon, 1992; Carcaillet and Brun, 2000) and can contribute to multidisciplinary studies (Tessier *et al.* , 1993).

Soil is a highly conservative medium and horizon features are the result of long-lasting climatic factors and vegetation input on a mesoclimatic scale through time. Soil analysis can, therefore, supply independent evidence to complete the scenario inferred from temporally and spatially limited palaeobotanical records, such as soil charcoal (Tinner *et al.* 1996).

6.3 Methods

6.3.1 Study area

The study area is located in the upper Rhone river valley (46°N, Central Swiss Alps) between 2300 m and 2800 m a.s.l. (Figure 2.1). Five sites were sampled for soil and soil charcoal. The westernmost site is in Val d'Arpette (eastern limit of the Mt. Blanc Massif) on the south slope of the Clochers d'Arpette (2810 m a.s.l.). Three sites were selected in the Aletsch region: two of them at Belalp, one on the south-east slope of Hofathorn (2845 m a.s.l.), one at "Lengi Egga", on the south-east slope of Sparrhorn (3020 m a.s.l.), and one on the east side of the Aletsch Glacier, at "Hindererhinertüre", along a south-west slope at the bottom of Gross Wannenhorn (3905 m a.s.l.). The fifth, easternmost site, is located near the Furka Pass, on the S-W slope of Tällistock (2861 m a.s.l). The range of mean daily temperature in summer, mean annual precipitation and snowmelt period are, respectively, 9.8-12.3°C, 1524 mm yr $^{-1}$, April-May in Val d'Arpette, 8.6-11.7C°, 908 mm yr^{-1}, May-June at Belalp and 7-10°C, 1500 mm yr^{-1}, late June at Furka. Parent rock material is acidic; soil classification corresponds to AFES (1998). Present vegetation in all the sites consists of acidic alpine swards (Table 6.1).

The present uppermost forest limit, or timberline, is located respectively at 2200 m a.s.l. in Val d'Arpette, at 2060 m a.s.l. at Belalp (area), and at 2000 m a.s.l. at Furka (although *Alnus viridis* is present in the area up to 2200 m). Except in Val d'Arpette, these limits result from secular human activity. The position of the potential treeline (in absence of human disturbance) can be estimated locally on the basis of the occurrence of plant communities of forest substitution: i.e. subalpine vegetation of mixed heaths, pastures, and conifers (spruce, larch, Arolla pine), together with leafy shrubs (green alder, birch, willows).

In Val d'Arpette, where the human activities have been limited by very steep slopes, the uppermost treeline reaches at present ca. 2300 m a.s.l.. At Belalp the uppermost potential treeline is estimated at ca.

2300 m a.s.l., and at ca. 2200 m a.s.l. at Furka. Near the upper part of the Aletsch glacier (e.g. in the Märjelensee, 2300 m a.s.l.) the glacier is present at or higher than the potential treeline, which is estimated at 2200 m. These elevations are in accordance with the potential forest limit given by Landolt (1992) for the Swiss Alps.

The definition of the "treeline" is a controversial issue (see for instance: Körner, 1999), but many authors agree upon 2-3 m as minimum size for a "tree" (e.g. Slayter and Noble, 1992; Körner, 1998; Theurillat *et al.*, 1998; Paulsen, 2000; Burga and Perret, 2001).

The upper limit reached by a tree species above the treeline is referred to as "tree species limit" or "lethal limit" (Burga and Perret, 2001; Callaghan *et al.*, 2002).

6.3.2 Soil sampling

Fifteen soil profiles were dug along five altitudinal transects in the study area, and soil features (horizon, texture, structure, skeleton, colour, root presence) (see Figures 6.1-6.6) were described following Baize and Jabiol (1995). Soil samples were air-dried and sieved at 2 mm, and pH was measured for each layer, both in deionized water and KCl 1 M (volume ratio 1:2.5) (AFES, 1998). When necessary for soil identification, organic matter content was measured by loss on ignition at 450°C, organic carbon content was determined (Anne method, AFES, 1998) and saturation rate was measured "at the pH of the soil" (percolation by KCl 1 M or NH_4Cl 0.5 M) (Baize and Jabiol, 1995). Soil classification follows AFES (1998); correspondence with Soil Taxonomy (USDA, 1999) are PODZOSOLS: Humic Cryothord, and ALOCRISOLS: Typic Dystrochrept. In each transect, three to four soil pits were excavated at an altitudinal interval of 200 meters above present potential treeline (Table 6.1). Acronyms, elevation, soil taxonomy, location, slope, aspect and topography are listed in Table 6.1 for each of the fifteen soils.

6.3.3 Charcoal study and radiocarbon dating

Sampling and processing were carried out following the pedoanthracological method (Thinon, 1992; Carcaillet and Thinon, 1996; Talon, 1997b; Carcaillet, 2001). Sampling sites were selected in flat areas, not subject to active erosion. The soil trench was dug down to the bedrock and sampling was conducted in layers of about 30 cm, starting from the deepest horizon to prevent contamination from upper layers during sampling. Samples of 7 to 15 kg of dry soil were taken at each layer.

The extraction was performed by floatation with a defloculant ($Na_4P_20_7$), followed by wet sieving, densimetric sorting by water flow and manual sorting under a binocular microscope. Only charcoal particles larger than 400 µm were extracted. The charcoal mass (= specific anthracomass, AM) is expressed as mg of extracted charcoal per kg of dry soil fraction finer than 5 mm to exclude stones. Charcoal from HT2 (1-2 cm size) was cleaned by defloculant and an ultrasonic wave generator; smaller, more fragile microcharcoal was treated with HF (70%) and HCl (35%) to destroy clays. Charcoal was observed under an incident light microscope with differential interference contrast (Thinon, 1988) and identified with reference to the literature (e.g.: Schweingruber, 1990; Talon, 1997a) and to a charred wood reference collection. *Larix decidua* and *Picea abies* wood was shown to be identifiable on the basis of miscrosopical anatomical features (Talon, 1997a). However, it is not always possible to identify fragments smaller than 1 mm. Dubious samples of charcoal of conifers or dicotyledons for which it is impossible to positively identify either species or genus, were described as "conifers n.id." or "dicotyledons n.id.". All other non-identified material was ascribed to "n.id.". Seven samples were dated by AMS ^{14}C. The majority of charcoal extracted was below the minimum mass required for measurement (about 2 mg). Thus, when necessary, charcoal extracted from the same soil layer was grouped. AMS ^{14}C dating was carried out at the Ångström Laboratory, Division of Ion Physics, in Uppsala (Sweden). The ^{14}C dates were calibrated as AD/BC by the program OxCal.

6.4 Results

6.4.1 Soil descriptions

Soils were classified in three main groups: PODZOSOLS, ALOCRISOLS and BRUNISOLS (see Table 6.1, Figures 6.1-6.6). PODZOSOLS are characterized by the presence of the diagnostic eluvial E and/or illuvial BPh, BPs horizons, pH in water always lower than 5, texture silty-sandy to sandy-silty, and organic matter content higher in the illuvial BPh horizons than in the other mineral horizons. Two sub-types were distinguished: TYPICAL PODZOSOLS with well developed eluvial horizons, and OCHRIC PODZOSOLS with less developed or discontinuous eluvial horizon.

TYPICAL ALOCRISOLS correspond to a very early stage of podzolic activity; they are characterized by the occurrence of the aluminious horizon Sal (2-8 mol+/kg of Al 3+ extracted by KCl), and pH in water lower than 5.

DESATURATED BRUNISOLS have a structural horizon S with a blocky structure and a pH in water around 5.

In Val d'Arpette soil profiles show a marked decrease of podzolic activity with increasing elevation (Table 6.1, Figure 6.2) in the profile AR1 the sequence of horizons O-A-BPh-BPs-C yields a PODZOSOL OCRIQUE; the soil AR2 is described as ALOCRISOL TYPIQUE (O-A-Sal-C) and AR3 is a DESATURATED BRUNISOL (OA-A-SC-C). Podzolic activity is evident at 2375 m a.s.l. (AR1), but in AR2, colluvial activity and solifuction have brought to surface traces of a discontinuous colluvial horizon (BPh) that testify to past podzolic activity up to 2565 m a.s.l..

Along the Belalp-Hofathorn transect (6.1, Figure 6.2), podzolic activity was detected at 2358 m a.s.l. (BA-HO1) in a TYPICAL PODZOSOL (O-AE-Eh-BPs-C) and, although weaker, at 2570 m a.s.l. (BA-HO2) in an OCHRIC PODZOSOL (O-AE/E-BPh[Eh]-BPs-C). The two other soils at higher elevation (BA-HO3 at

2665 m a.sl. and BA-HO4 at 2830 m a.s.l.) were described as TYPICAL ALOCRISOLS (O-Ah-Sal-C respectively O-A(E)-A-Sal-C).

In Belalp-Lengi Egga transect (Table 6.1, Figure 6.3) podzolization is present all along the transect with TYPICAL PODZOSOLS. At 2305 m a.s.l. (BA-LE7), the profile is developed on a truncated soil and the sequence of horizons is O-A-Eh-BPh-BPs-C. At 2451 m a.s.l. (BA-LE6), the sequence is O-A-Eh-BPh-BPs-C and at 2550 m a.s.l. (BA-LE5) it is O-OHA-AE-[Eh]-BPh-BPs-C.

In the Aletsch transect (Figure 6.4), PODZOSOLS are absent. There are ALOCRISOLS both at 2580 m a.s.l. (HT1) and at 2710 m a.s.l. (HT2) with the respective sequence of horizons O-A-Sal-SC-C and O-A-ASal-S-SC-C. HT3 and HT4 were not described.

At Furka (Figure 6.5), podzolic activity was detected at 2403 m a.s.l. (FK1) in the TYPICAL PODZOSOL (O-AE-E-BPh-C), but was absent higher at 2618 m a.s.l. (FK2) and at 2785 m a.s.l. (FK3) were TYPICAL ALOCRISOLS occur (O-A-Sal-C and O-A-Sal-SalC-C, respectively).

6.4.2 Charcoals

Charcoal mass (= specific anthracomass, AM) and charcoal identification are listed in Figures 6.1-6..5. In general, the majority of charcoal was extracted from the topsoil. Only in Belalp-Hofathorn, in BA-HO1 (Figure 6.3) charcoal was concentrated deeper, at 65-85 cm. The majority of soil profiles yielded conifer charcoal (*Pinus cembra, Larix decidua, Picea/Larix, Juniperus sp.*). Dicotyledon charcoal was abundant in AR1 (mainly *Ericaceae* family), one charcoal of *Rosa* sp. was recovered in the profile HT4, one of birch (*Betula* sp.) was found at FK1, and two of alder (*Alnus* sp.) and heather (*Calluna vulgaris*) in BA-LE5.

In Val d'Arpette (Figure 6.1), the soil at 2375 m a.s.l. (AR1) yielded the highest AM (19.35 mg kg^{-1} in the top layer); the charcoal record consists of dwarf shrubs (*Ericaceae* and *Juniperus sp.*), and conifers (*Picea/Larix* and *Pinus cembra*). Charcoals were seldom found higher than 2720 m a.s.l..

Along the Belalp-Hofathorn transect (Figure 6.2), soils at 2358 and 2570 m a.s.l. (BA-HO1, BA-HO2) yielded respectively 2.89 and 1.75 mg kg^{-1} of charcoal. At 2665 and 2830 m a.s.l. (BA-HO3, BA-HO4) charcoal was rarely present. At Belalp-Lengi Egga (Figure 6.3), AM was low all along the transect (0.62 to 0.32 mg kg^{-1}).

Table 6.1 Soil profile acronyms, elevation, soil taxonomy, location, slope, aspect and topography for the five study sites. (*) in close proximity to HT2

Site	Altitude m a.s.l.	Soil type	Coord.	Slope degrees	Aspect	Topography
Val d'Arpette						
AR1	2375	OCHRIC PODZOSOL colluvial,	46° 01.714' N 7° 04. 409' E	33	S	Small saddle
AR2	2565	ALOCRISOL Colluvial, leached	46° 01.714' N 7° 04. 409' E	33	S	Flat area
AR3	2720	DESATURATED BRUNISOL	46° 01.714' N 7° 04. 210' E	32	S	Flat area
Belalp- Hofathorn						
BA-HO1	2358	TYPICAL PODZOSOL	46° 22.129' N 7° 56.980' E	18	E-SE	Small saddle
BA-HO2	2570	OCHRIC PODZOSOL	46° 21.779' N 7° 56.762' E	3	84° N	Flat area
BA-HO3	2665	TYPICAL ALOCRISOL	46° 22.154' N 7° 57. 370' E	15	235°N	Flat area
BA-HO4	2830	TYPICAL ALOCRISOL	46° 22.398' N 7° 57. 236' E	20	98° N	Slope near the crest
Belalp- Lengi Egga						
BA-LE7	2305	TYPICAL PODZOSOL superposed on buried soil	46° 23.087' N 7° 58.530' E	20	171°N	Flat area
BA-LE6	2451	TYPICAL PODZOSOL	46° 23.289' N 7° 58.551' E	12	189°N	Flat area
BA-LE5	2550	TYPICAL PODZOSOL	46° 23.587' N 7° 58'.389' E	12	148°N	Proximity of flat area
Aletsch Glacier						
HT1	2580	TYPICAL ALOCRISOL	46° 28.498' N 8° 04.853' E	12	197°N	Saddle, solifluction terrace
HT2	2710	TYPICAL ALOCRISOL on truncated BRUNISOL	46° 28.558' N 8° 04. 893' E	0	SW	Large saddle
HT3	2740	-	(*)	-	-	-
HT4	2710	-	(*)	-	-	-
Furka Pass						
FK1	2403	TYPICAL PODZOSOL	46° 32. 529' N 8° 23.213' E	12	134°N	Flat area at the base of a slope
FK2	2618	ALOCRISOL	46° 32. 962' N 8° 23.671' E	2	231°N	Flat
FK3	2785	ALOCRISOL	46° 33.230' N 8° 23.981' E	16	243°N	Slope near the crest

Charcoal of conifers (*P._cembra, Picea/Larix,* conifers n.id.) was ubiquitous, and one piece of charcoal of dwarf shrubs and five of "dicotyledons n. id." were extracted from BA-LE5 at the top of the transect. It should be noted however, that the lower point of the transect (BA-LE7, 2305 m a.s.l.) is a truncated soil and that solifluction might be responsible for the low AM. In both transects, no charcoal of ericoid dwarf shrubs was found except for *Calluna vulgaris* in BA-LE5.

Soil AM was low all along the transect Furka (Figure 6.5): only 1.57 mg kg^{-1} at 2403 m a.s.l. (FK1), and negligible at 2618 m a.s.l. (FK2) and 2785 m a.s.l. (FK3).

In all the transects, in the belt between 2305 and 2570 m a.s.l. (in which PODZOSOLS are present) soil AM varied between 0.1 and 19.6 mg kg^{-1}. At a higher elevation, i.e. between 2570 and 2830 m a.s.l. (where ALOCRISOLS are the dominant soil types) AM was in general lower than 0.1 mg, or no charcoal was extracted.

The Aletsch glacier transect (Figure 6.4), HT2 (2710 m a.s.l.) is an exception as a layer of charcoal, with fragments of up to a few centimeter was detected at a depth of about 12 cm, hence with AM greater than 1 g. However, this layer was absent a few meters from the profile (HT3 and HT4) where less than 0.1 mg of charcoal was found in shallow soils (not described).

6.4.3 Radiocarbon dating

The results of ^{14}C AMS dating are reported in Table 6.2. In AR1, in the same layer (10-30 cm depth), one piece of charcoal of *Vaccinium uliginosum* dates from the recent past (1400-1640 cal. AD; 430± 70BP uncal. yr.), and a pooled sample of charcoal of conifers dates 1010-750 cal. BC (2665±80 BP uncal.). In the site BA-HO1 two samples extracted from the same soil layer (65-85 cm depth) gave the following dates: 2310-1880 cal. BC (3715±70 BP uncal., one piece of charcoal), and 2700-2100 cal. BC (3955±85 BP uncal., pooled charcoal sample). In the Belalp-Langi Egga transect at BA-LE7, samples of pooled charcoal gave 3350-2500 cal. BC (4265±95 uncal.), and at BA-LE6 1150-750 cal. BC (2705±85 BP uncal.).

In the site HT2 one piece of charcoal of *Pinus cembra* was dated 550-100 cal. BC (2285±75BC uncal.).

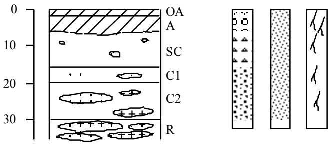
Charcoals recovered at Furka (FK1) were dated 600-980 cal. AD (1275±95 BP uncal., pooled sample).

Table 6.2 Radiocarbon-dated charcoals. Samples AR1 and AR1^{a} were extracted from the same soil layer. Idem for BA-HO1 and BA-HO1^{a} . Calibrated dating was computed using the calibration program OxCal (Stuiver and R. S. Kra. Eds., 1986 Radiocarbon 28 (2B): 805-1030). AR1^{a}, BA-HO1^{a}, BA-LE6, BA-LE7 and FK1 are pooled charcoals.

Sample Codes	Sample name and origin	Sampling Depth (cm)	delta $13C^{0}/_{00}$ PDB	Conventional radiocarbon date BP uncal. yr	Calibrated BC/AD yr	Mass (mg)	N. of Fragments	Charcoal identification
Ua-18125	AR1	10-30	-26,3	430±70	1400-1640 AD	2.8	1	*Vaccinium uliginosum*
Ua-18126	AR1^{a}	10-30	-23,7	2665±80	750-1010 BC (82.7%)	1.6	many	*Larix/Picea*, *P. cembra*, conifers n.id.
Ua-18127	BA-HO1	65-85	-23,9	3715±70	2310-1880 BC	4	1	*Larix/Picea*
Ua-18128	BA-HO1^{a}	65-85	-25,2	3955±85	2700-2100 BC (93.2%)	1.7	12	conifers n.id., *P. cembra*, *Larix/Picea*
Ua-18129	BA-LE6	0-20	-23,9	2705±85	1150-750 BC (92.8%)	0.9	17	conifers n.id., *P. cembra*
Ua-18130	BA-LE7	0-20	-24,9	4265±95	3350-2500 BC	2	11	conifers n.id., *P. cembra*
Ua-18131	FK1	0-15	-24,6	1275±95	600-980 AD	2.1	26	conifers n.id., *Larix/Picea*
Ua-18132	HT2	12	-22,8	2285±75	550-100 BC (92.7%)	70.8	1	*P. cembra*

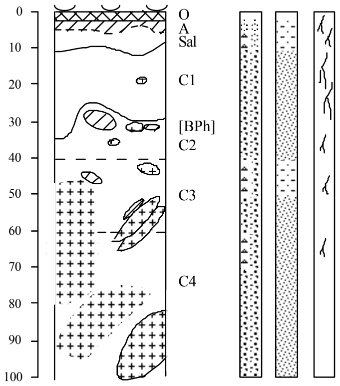
Figure 6.1 Val d'Arpette transect. Soil sketches and logs of soil structure, texture and roots. In the tables are given sampling depth (cm); anthrachomass per soil layer AM (mg of charcoal kg^{-1} soil); charcoals identifications and number of fragments recovered. (*) AM negligible (i.e. charcoal mass <1 mg). See Figure 6.6 for the symbolic for soil profiles.

AR3 2720 m a.s.l.; BRUNISOL



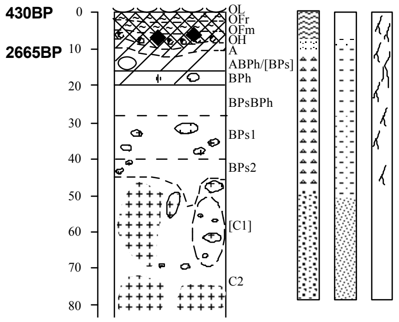
Depth (cm)	AM (mg kg^{-1})	*Larix/ Picea*
0-10	*	4
10-30	0	

AR2 2652 m a.s.l.; ALOCRISOL



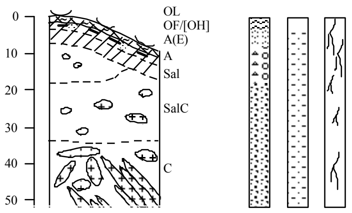
Depth (cm)	AM (mg kg^{-1})	*Larix/ Picea*	n.id.
5-18	*	3	
20-40	*	2	2
40-65	0.11	1	
65-95	*	5	
AM total	0.11		

AR1 2375 m a.s.l.; PODZOSOL



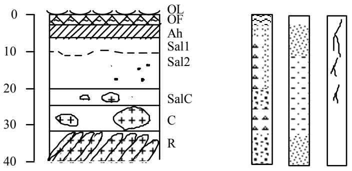
Depth (cm)	AM (mg kg^{-1})	Conifers n.id	*Pinus cembra*	*Larix/Picea*	*Juniperus communis* aggr.	*Vaccinium myrtillus*	*V.uliginosum*	*V.vitis-idaeus*	*Vaccinium* sp.	*Arctostaphylos uva-ursii*	*Calluna vulgaris*	*Loiseleuria procumbens*	*Ericaceae*	Dicotyledon n. id.	n.id.
10-30	19.35	4	1	2	5	6	17			3	2	1	10		23
35-55	0.28		2			2		1	2				5		6
60-85	*	1		1			2							1	
AM total	19.63														

BA-HO4 2830 m a.s.l.; ALOSCRISOL



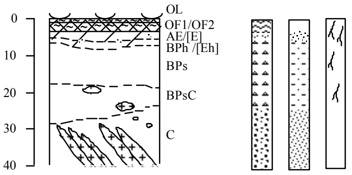
Depth (cm)	AM (mg kg^{1})	Conifers n.id	*Pinus cembra*	*Picea/Larix*
0-10	*			3
10-20	*	6	1	1
>25	*	2		
AM total	*			

BA-HO3 2665 m a.s.l.; ALOCRISOL



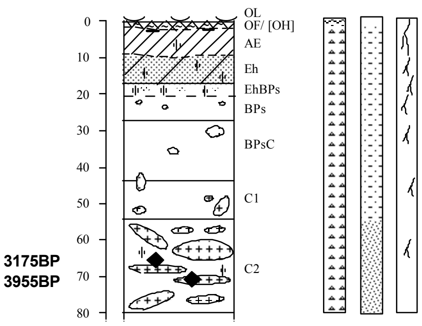
Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/ Picea*
0-10	*	2	1	5
10-35	0			
AM total	*			

BA-HO2 2570 m a.s.l.; PODZOSOL



Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/ Picea*	n. id.
0-7	1.75	8	2	4	1
7-30	0				
30-40	0				
AM total	1.75				

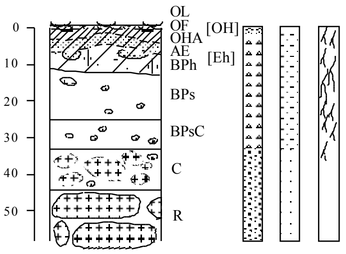
BA-HO1 2358 m a.s.l.; PODZOSOL



Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/ Picea*	n. id.
5-20	0.63	10	5	7	9
20- 45	0				
45 -65	0.08			2	
65- 85	2.18	7	1	9	
AM total	2.89				

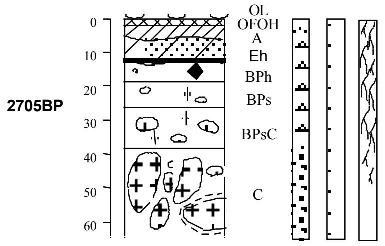
Figure 5.2 Belalp-Hofathorn

BA-LE 5 2550 m a.s.l.; PODZOSOL



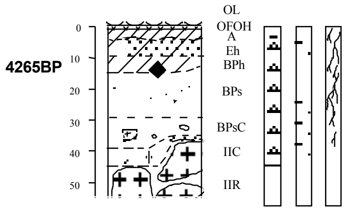
Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/Picea*	*Juniperus communis* aggr	*Alnus*	*Calluna vulgaris*	Dicotyledon n.id.
0-15	0.51	5	1	5	1	1	1	4
15-30	*			1				1
30-50	0							
AM total	0.51							

BA-LE6 2451m a.s.l.; PODZOSOL



Depth (cm)	AM (mg kg^{-1})	*Larix/ Picea*	n. id.
0-20	0.32	6	5
20-40	0		
40-60	0		
AM total	0.32		

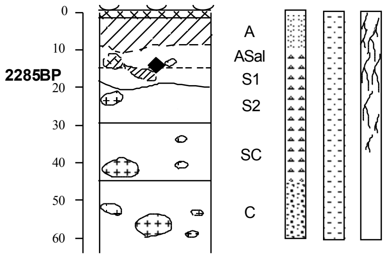
BA-LE7 2305 m a.s.l.; PODZOSOL



Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/ Picea*	Dicotyledonn .id.
0-20	0.62	8	6	1	2
20- 45	0				
AM total	0.62				

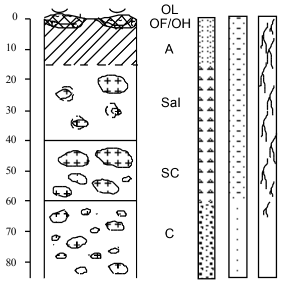
Figure 5.3 Belalp-Lengi Egga transect. Soil sketches and logs of soil structure, texture and roots. In the tables are given sampling depth (cm); anthrachomass per soil layer AM (mg of charcoal kg^{-1} soil); charcoals identifications and number of fragments recovered. (*) AM negligible (i.e. charcoal mass <1 mg). See Figure 5.6 for the symbolic for soil profiles.

HT2 2710 m a.s.l.; ALOCRISOL



Depth (cm)	AM (mg kg^{-1})	*Pinus cembra*	*Larix/ Picea*	*Juniperus sp.*	n.id.
0-25	90.3	18	50	26	
12	1274		44	1	3
25-45	9.83			51	
AM total	1374.13				

HT1 2580 m a.s.l.; ALOCRISOL



Depth (cm)	AM (mg kg^{-1})	*Juniperus sp.*	*Pinus cembra*
0-40	*	1	1
40- 85	0		

HT3 2740 m a.s.l.

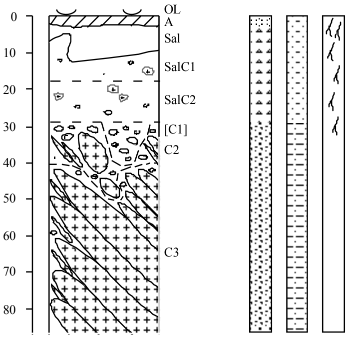
Depth (cm)	AM (mg kg^{-1})	Dicotyledon n. id.
0-15	*	1
AM total	*	

HT4 2710 m a.s.l.

Depth (cm)	AM (mg kg^{-1})	*Rosa* sp.	n. id
0-15	*		1
15-30	*	1	1
AM total	*		

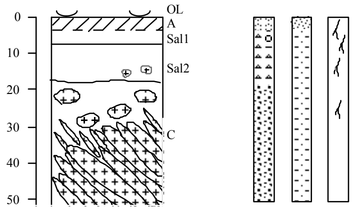
Figure 5.4 Aletsch glacier transect. Soil profiles and soil structure, texture and roots. In the tables are listed: sampling depth (cm), charcoal mass per soil layer AM (mg of charcoal kg^{-1} soil), charcoals identifications and number of fragments recovered. (*): AM negligible (i.e. charcoal mass <1 mg). See Figure 5.6 for the symbolic for soil profiles.

FK3 2785 m a.s.l.; ALOCRISOL



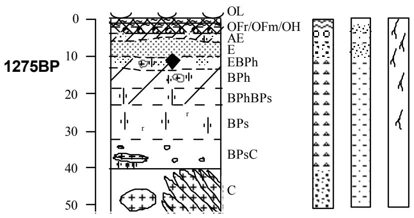
Depth (cm)	AM (mg kg^{-1})	*Pinus cembra*	*Larix/ Picea*
0-12	*	1	1
12-30	0		
30-50	0		
50-80	0		
AM total	*		

FK2 2618 m a.s.l.; ALOCRISOL



Depth (cm)	AM (mg kg^{-1})
0-17	0
17-50	0
AM total	0

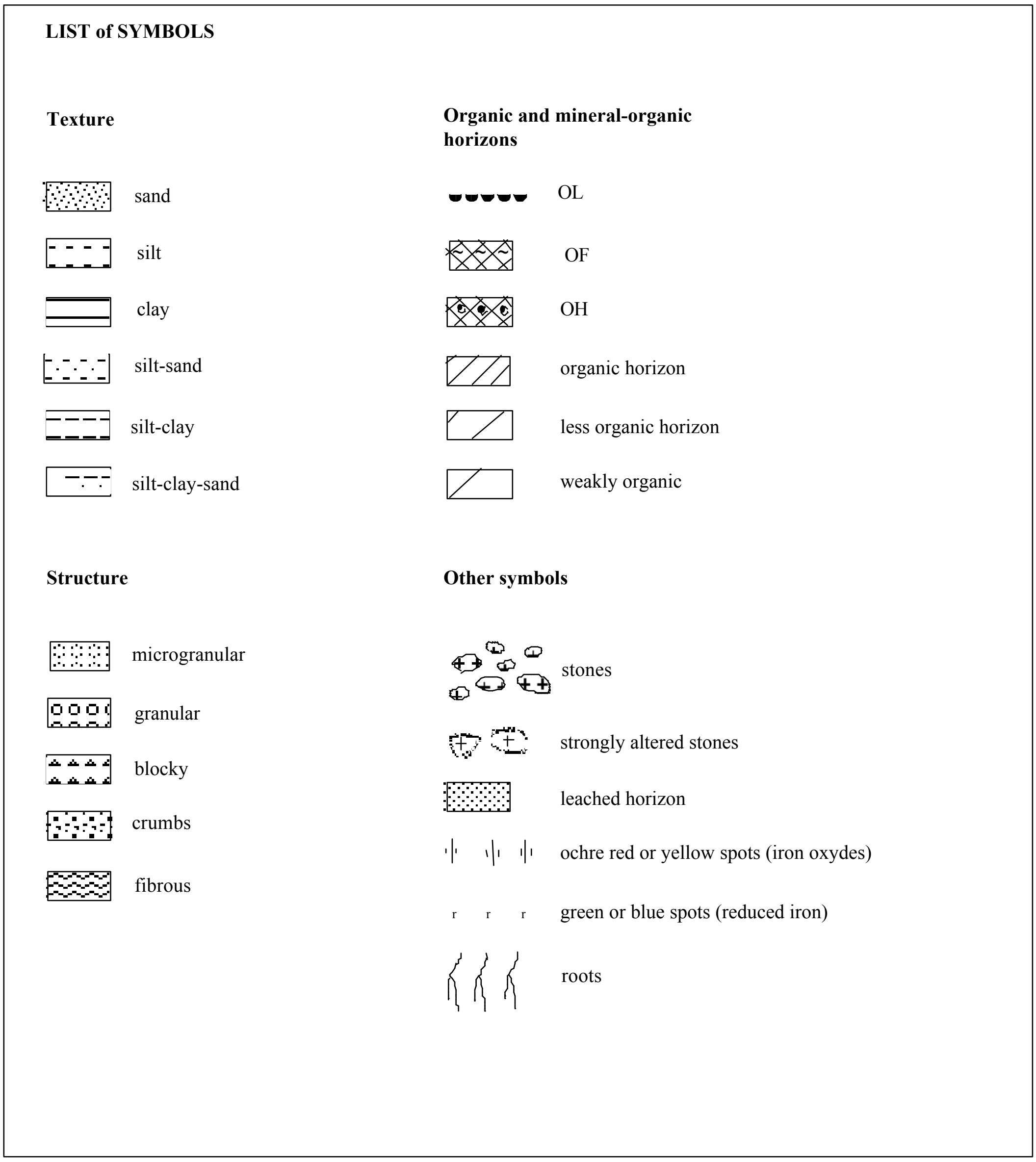
FK1 2403 m a.s.l.; PODZOSOL



Depth (cm)	AM (mg kg^{-1})	Conifers n.id.	*Pinus cembra*	*Larix/ Picea*	*Betula sp.*
0-15	1.57	18	2	14	1
15-40	0				
40-60	*			2	
AM total	1.57				

Figure 5.5 Furka transect. Soil sketches and logs of soil structure, texture and roots. In the tables are given sampling depth (cm); anthrachomass per soil layer AM (mg of charcoal kg^{-1} soil); charcoals identifications and number of fragments recovered. (*) AM negligible (i.e. charcoal mass <1 mg). See Figure 5.6 for the symbolic for soil profiles.

Figure 6.6 Symbolic used to represent soil profiles in Figures 6.1-6.5.



6.5 Discussion

6.5.1 Soils

Along the five altitudinal transects, evidences of podzolic activity was recorded up to 2570 m a.s.l.

No evidences were found at a higher elevation, where ALOCRISOLS are the dominant soil types. At the upper limit of the PODZOSOL belt, around 2550 m a.s.l., the eluvial horizons become gradually thinner and discontinuous, showing a weakening of the podzolic activity. However, in all the sampling sites, present vegetation, consisting of alpine meadows, is unable to drive pedogenesis to the stage of fully developed TYPICAL PODZOSOL (Duchaufour, 1998), and instead, BRUNISOLS would be expected to occur in all the sites.

Podzolization is a pedogenetic process characteristic of soils developed under a strongly acidic vegetation, in cold and humid climates. PODZOSOLS typically occur in the northern boreal conifer forest zone with an average annual temperature <8°C. However, over quartz-rich substrates which tend to rapid leaching, PODZOSOL can develop under all other humid climate and an acidic vegetation. In such conditions, leaching and translocation result from the very low buffer capacity of parent material, and PODZOSOLS may be found in arctic and antarctic environments, in warm and temperate climates, as well as in humid tropical areas (Duchaufour, 1998; Stützer, 1999).

In temperate regions, PODZOSOLS occur zonally in mountainous areas where boreal conditions prevail. Leaching and translocation are favoured by the marked seasonal temperature excursion and the slow melting of snow cover during spring (Duchaufour, 1998; AFES 1998; Stützer, 1999). At the subalpine and alpine belts of temperate regions, only conifer woodlands and/or heath communities may produce a sufficient biomass of acidic litter to trigger enough podzolic activity leading to the formation of the TYPIC PODZOSOL. Accordingly, ALOCRISOLS, which are a very early stage of the podzolization process, would develop under acidic swards. Therefore, along the altitudinal transects here considered, present vegetation, homogeneous substrate and climatic conditions do not explain the observed marked pedological transition PODZOSOL – ALOCRISOL at ca. 2550 m a.s.l. Only the presence of a former subalpine woody vegetation in the PODZOSOL zone, below 2550 m a.s.l., could account for such a transition. These PODZOSOLS persisted after the disappearance of the woody vegetation since climatic and edaphic conditions were not markedly different to develop backwards ALOCRISOLS or BRUNISOLS.

6.5.2 Soil anthracomass

In all five transects, there is a general trend towards AM diminishing with increasing elevation (Figure 6.7). Up to ca. 2400 m a.s.l., a mean anthracomass of 6.18 (0.62-19.63) mg kg^{-1} was found in the four profiles AR1, BA-OH1, BA-LA7, FK1. Between 2400 and 2570 m a.s.l., a mean AM of 0.67 (0.11-1.75) mg kg^{-1} was found in the four profiles AR2, BA-OH2, BA-LE6, BA-LE5. Above 2570 m a.s.l., AM is negligible in all profiles except HT2. Comparable values of anthracomass (i.e. between 2.29 and 0.08 mg kg^{-1}) were found in the southern French Alps (Briançonnais, Queyras, Ubaye valley and Haute Tinée) for 33 subalpine and alpine soils sampled along seven transects situated between 1950 and 2919 m a.s.l. (Figure 6.8) (Talon, 1997b), and 15 soils along two transects in the northern French Alps (Haute-Maurienne; Carcaillet, 1996). A correlation between elevation and AM was evidenced for these 48 soils (Carcaillet and Talon 2001). According to Figure 6.9, the highest AM values were recorded between 2000 and 2440 m a.s.l., sometimes with very high values (e.g. 3890 mg kg^{-1} at 2200 m a.s.l.). From 2440 to 2775 m a.s.l. the AM dropped to 0.1-4.1 mg kg^{-1}. At higher elevations, AM was between 0.1 and 1 mg.
The sharp decrease in AM at certain elevations in both Figures 6.7 and 6.8 would support the hypothesis that AM is produced "in situ" rather than transported. (For a discussion on airborne charcoal particles see: Benedict, 2002; SALTUS, 2001; Ohlson and Tryterud, 2000; Clark, 1988; Clark *et al.* , 1998; Thinon, 1992).

In this respect, it is worth to mention the historical records of two fires that occurred in 1896 and 1944 in the Aletschwald (only 3-4 km away of Lengi Egga) (Lüdi, 1946; Perrig, 1944). In particular, although the 1944 fire burnt for almost a whole month in late Spring, fought by more than 750 firemen, and destroyed 60-65 ha (10,000 m^3) of subalpine forest dominated by *Pinus cembra* (75%) with *Larix decidua* (20%) and *Picea abies* (5%), no particles that date to this period were found in the Belalp-Lengi Egga area. However, in spite of the fire extension, it is reported that for most of the tall trees, the burning was only superficial.

In the present study, as well as in the studies in the Southern French Alps, AM shows the same diminishing trend with increasing elevation (Figures 6.7 and 6.8). According to the distribution of woody biomass from timberline to treeline in today's natural conditions, it would appear as if AM may provide an indication of the mean woody stand biomass in the past, as suggested by Carcaillet and Talon (2001). In Figure 6.7, the group of AM > 1 mg would correspond to the woody biomass below the past timberline, the group with low AM (0.1-1 mg) to the woody biomass of the transition zone ("kampfzone") between timberline and past treeline, and the group with negligible AM to woody biomass above past treeline. The same applies in Figure 6.8. Here, the sampling went below present forest line where mean AM values are significantly higher then above 2440 m a.s.l. Then, higher up, mean AM is comparable with the Valaisan data as in Figure 6.7.

These values are in line with the sharp decrease in woody biomass that occurs at today's timberline in natural conditions. There, the reduced tree density and tree height (from 5-8 m to 2 m), results in a reduced woody biomass. Then, higher up at treeline, woody biomass is further reduced, and only rare prostrate trees lower than 2 m and sparse low shrubs occur**.** Low values of woody biomass near treeline are explained by the fact that growth, recolonisation process, and seed production slow down with increasing elevation. Therefore, when the woody biomass is partially or totally destroyed, e.g. by a fire, it may take a long time to rebuild it. Recurrent fire events, even at a pace of several hundred years

(Carcaillet *et al.*, 1998) may impede to build a sufficient biomass that, when burnt, would produce lasting soil charcoal, or could even prevent any tree regrowth. This is especially the case for *Pinus cembra* with its ornithochorous dispersion and its comparatively slow growth, all the more so with a less favourable climate. However, soil anthracomass depends on the intensity of the fire and, in some cases, may not truly reflect the standing woody biomass (Carcaillet and Talon, 2001). In the study region, this is exemplified by the important 1944 fire in the Aletschwald mentioned above (Lüdi; 1946; Perrig, 1944) in which tall trees biomass was not completely burnt. Indeed, it is reported that for most of the tall trees, the wood was untouched and still good enough to be used as firewood. On the other hand, dwarf shrubs (*Juniperus communis* subsp. *alpina, Rhododendron ferrugineum, Vaccinium* spp., *Calluna vulgaris*) were totally destroyed. Therefore, the total AM resulting from such a fire was probably not very high and would not reflect the much greater standing woody biomass.

Figure 6.7 Charcoal mass (AM, mg kg^{-1}) per soil profile with increasing elevation. The charcoal concentration drops significantly in correspondence of the upper limit of podzolic activity in soil (Wilcoxon ranked-sum test, two-tailed; p = 0.01). The AM decrease is significant with elevation (Kendall's rank correlation; p = 0.01).

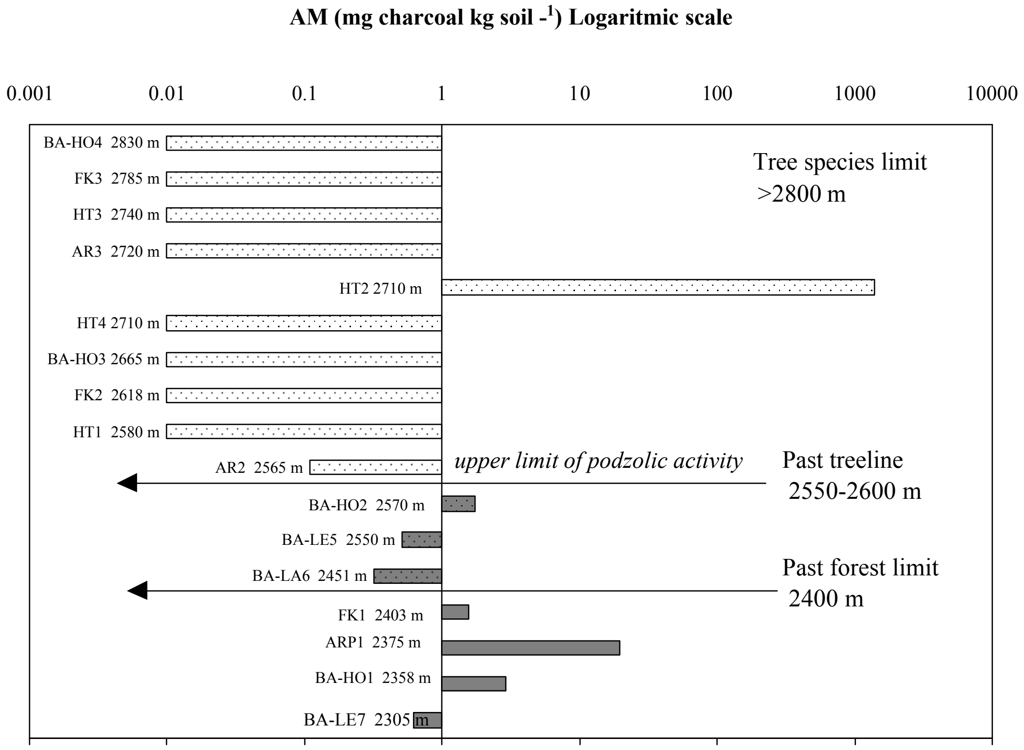
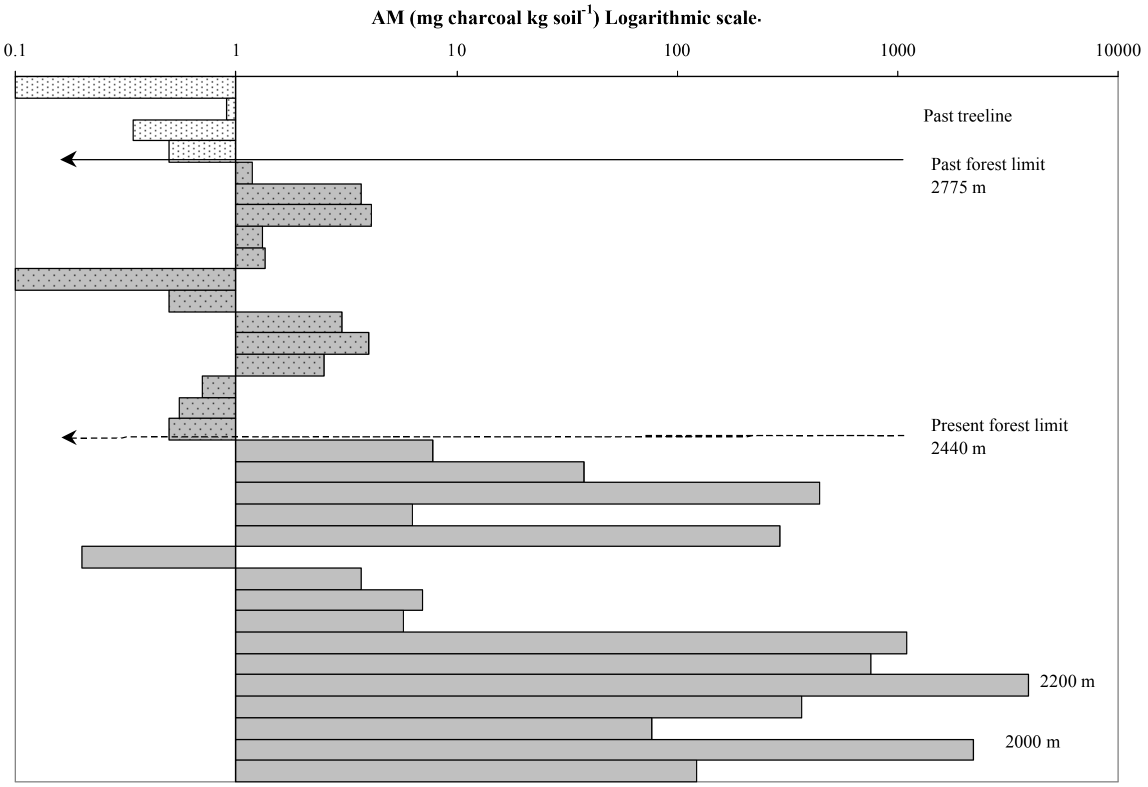


Figure 6.8 Specific soil charcoal mass (AM, mg kg^{-1}) per soil profiles with increasing altitude in 33 subalpine and alpine soils sampled along three altitudinal transects from 1950-2900 m a.s.l. from the southern French Alps (Briançonnais, Queyras, Ubaye valley and Haute-Tinée). Two marked, significant decreases in mean AM appear, a first one at 2440 m a.s.l. (Wilcoxon ranked-sum test, two-tailed; p = 0.01) and a second one at 2775 m a.s.l. (Wilcoxon ranked-sum test, two-tailed; p<0.1). The first zone, up to 2440 m a.s.l., with mean AM >> 1 mg corresponds to present forest. The second zone, between 2440 and 2775 m a.s.l., with a mean AM ≥1 mg corresponds to the past forest. The third zone, above 2775 m a.s.l., with a mean AM 0.1-1 mg corresponds to past treeline zone (past subalpine-alpine transition). (From Talon, 1997b).



6.5.3 Soil type versus anthracomass

In the present study, AM diminishes abruptly in all sites around 2550 m, corresponding to the pedological transition PODZOSOL – ALOCRISOL (Figure 6.8), with the exception of HT2 in the Aletsch glacier transect. Similar findings are available in the French Alps where AM consistently decreases above 2700 m a.s.l. (Talon, 1997b; 1998; Carcaillet and Talon, 2001).

We therefore suggest that both the upper limit of podzolic activity and the anthracomass diminution mark an ancient vegetation boundary, probably delimiting the uppermost elevation attained by a palaeo treeline. Weak podzolic activity sometimes results in presence of scattered heaths and isolated krummholtz of conifers, i.e. the treeline ecocline. Higher up, ALOCRISOLS or BRUNISOLS developed under herbaceous vegetation throughout the Holocene. This is supported by the negligible AM in all the sites at higher elevation.

A similar correspondence was found in a soil biosequence sampled for soil charcoal along a subalpine-alpine transect between 1780 and 2800 m a.s.l. in Val d'Hérémence (Swiss Central Alps, left hydrological side of Rhone river valley) (Tinner *et al.*, 1996). In 25 soil profiles sampled along two transects, the transition from soils with A-B-C horizonation (Cambic/ Ferric Podzol) to A-C soils (Regosol) was found to occur between 2400 and 2500 m a.s.l. (soil nomenclature according to UNESCO-FAO classification). In these transects, the highest macroscopic charcoal of *Pinus cembra* was found at 2380 m a.s.l.

6.5.4 Site variability

Although these general comments are valid for all transects, each site has local variations which could have modified the position of treeline. Indeed, thanks to warmer mean air temperature, due to the Massenerhebung effect (Brockmann-Jerosch, 1919), and to higher hygric continentality (Gams, 1931; 1932), present-day forest limit reaches 2400-2500 m a.s.l. in the central Valais (e.g. the Zermatt region), while in the S. Gotthard region (close to Furka) it is 200-300 meters lower (Eggenberg, 1995). In addition, treeline elevation is shown to be inversely correlated with snow cover duration (Eggenberg, 1995).

Meso- and microclimatic differences influence the position of the treeline in the different study sites. For instance, Val d'Arpette has a lower hygric continentality than Belalp, but it is warmer, more rocky, steeper and snow cover disappears rapidly in early spring. Compared to Belalp, Furka is cooler and has lower hygric continentality**.**

Arpette

At 2375 m a.s.l. (AR1, Figure 6.1), charcoal mass, charcoal taxa (*Arctostaphylos uva-ursi, Vaccinium myrtillus, V. uliginosum, V. vitis-idaea, Calluna vulgaris*), and podzolic activity suggest the presence in the past of a thermophilous woody vegetation around 1010-750 cal. BC (2665±80 BP uncal.), which is found 200-300 m lower down today. At present, grasses and sedges are the dominant species (*Festucetum variae* s.l.) with a cover (20%) of low shrubs (*Vaccinium myrtillus, V. vitis-idaea, V. uliginosum subsp. microphyllum, Rhododendron ferrugineum* and *Juniperus communis* subsp. *alpina*). At 2565 m and higher (AR2, AR3), the anthracomass decreases dramatically (19.63 mg in AR1 versus 0.11 mg in AR2), and podzolic activity is absent, although not totally, since traces of past podzolic activity are found in pockets of a buried horizon, redistributed along the slope by colluvial activity (e.g. AR2). The low mass of charcoals, including *Larix decidua*, and sporadic podzolic activity, suggest a past scenario with a low woody biomass, therefore a mosaic of alpine meadows, dwarf shrubs, with small, scattered conifers, within the zone of the tree species limit. Much as is the case today, although now there are probably many fewer heaths and conifers. Such vegetation did not produce sufficient biomass to trigger the formation of PODZOSOLS on steep slopes, except locally. Thus, the sharp decrease of AM between AR1 and AR2, the sporadic presence of podzolic activity, plus the steep and rocky slope, suggest a potential uppermost limit reached by treeline in Val d'Arpette around 2500-2550 m a.s.l., i.e. about 200-250 m higher than present uppermost treeline.

Belalp

In the PODZOSOL zone between 2305 and 2570 m a.s.l.(Figure 6.2-6.3), regular findings of conifer charcoals*, (P. cembra, L. decidua,* conifers n.id.) in all profiles suggest the presence of a woody vegetation in the past. Dwarf shrubs were also present, but not frequent. Charcoal of *Calluna vulgaris* was found only once. According to radiocarbon dates, this conifer formation dates at about 2310-1880 cal. BC (3715±70 BP uncal.), and 2700-2100 cal. BC (3955±85 BP uncal.). At present, there are mostly swards at these elevations, with *Carex sempervirens* being dominant in the lower part (BE-HO1) and *C. curvula* in the upper part (BA-HO2, BA-HO3) (see Guisan *et al.*, 1998; Theurillat, 1992). In the ALOCRISOL zone, conifer charcoal was also found, but the anthracomass was negligible (< 0.1 mg). This, together with the absence of podzolic activity, suggests that swards were always present in the past above ca. 2550-2600 m a.s.l. and were dominant over dwarf shrubs. Therefore, the uppermost treeline extended up to ca. 250-300 m higher than today. The extension up to 2570 m a.s.l. is probably the result of a local condition, as BA-HO2 is located on a crest that would have favoured the upward extension of the treeline.

At a very short distance from BA-LE5, the alpine peat-bog of Lengi Egga situated at 2557 m a.s.l. was investigated for pollen and plant macrorests (Tinner and Ammann, 2001; Tinner and Theurillat, in press). Macrorests clearly showed that throughout the whole Holocene period the forest never reached the peat-bog catchment area. Herb and dwarf shrub macrofossils were abundant in the sediments between 8500-4400 BP uncal. The last 3000 years were characterized by regular findings of *Salix herbacea* and *Carex*. In comparison with other macrofossils, tree remains were of marginal importance: single but regular findings of needles of *Larix decidua*, *Betula* "alba" fruits (both macrofossils suited to wind transportation) and charred needles of *Picea* and *Larix*, were recorded. It is worth mentioning here that no transport of particles, even the smallest, was found that could come from the two recent fires (1896, 1944) in the Aletschwald (Lüdi, 1946; see above). Combining these findings with the weak podzolic activity at about 2550 m a.s.l. and the low anthracomass, we argue that treeline did not exceed this elevation in the past. Thus, timberline was possibly situated around 2400 m, corresponding to the upper limit of well developed PODZOSOLS.

Aletsch

Along the transect situated on the side of the Aletsch Glacier (Figure 6.4), no PODZOSOLS were found. At the lowest elevation (2580 m a.s.l.) ALOCRISOLS already occur. However, HT2 (2710 m a.s.l.) yielded a layer rich in conifer charcoal (*Larix decidua* and *Pinus cembra, Juniperus* sp.).

The interpretation of this discovery as the presence of a shepherd or hunter's camp fire dating back to the Subboreal (550-100 cal. BC, 2285±75BC uncal.), when human frequentation of the Alps was intense (Schär and Schweingruber, 1987; Burga, 1988; Tinner and Ammann, 2001), is supported by negligible findings of anthracomass close by in the site HT4, slightly above (HT3, 2740 m a.s.l.) and lower down (HT1, 2580 m a.s.l.). The majority of charcoal found in the HT2 layer is of juniper, a source of the easily gathered small branches needed for a camp fire. In particular, human presence in this period is confirmed in the Aletsch region by the presence of dwelling houses and necropoles at low elevation near Brig (Curdy *et al.*, 1999).

Soil data and soil charcoal evidence shows that, in this site, treeline was at a lower elevation compared to the other sites. Due to the close proximity of the glacier, the potential treeline at present is estimated to be ca. 100 m lower than at nearby Belalp. As the uppermost treeline at Belap was ca. 300 m higher in the past than today, up to 2570 m a.s.l., we argue that the topmost treeline along the upper part of the glacier could have reached 2500 m a.s.l. during the Holocene when taking into account the negative glacier effect. This means that forest extended up to 2300 m a.s.l. (at Märjelensee) along the glacier, but hardly any further up although, according to estimates of the variation in the length of Swiss glaciers, they were smaller during part of the Atlantic and the Subboreal than they are today (Hormes *et al.* , 2001; Tinner and Ammann, 2001). However, this does not exclude the presence of small, scattered conifers further up, especially *Juniperus,* in the tree species limit zone, thereby offering a possible source of fuel for the fire in HT2. Swards make up the present vegetation alongside the upper part of the glacier, with *Carex sempervirens* dominating at HT1, *C. curvula* at HT2 and HT4, and *Elyna myosuroides* at HT3.

Furka

The PODZOSOL at 2403 m a.s.l. (FK1, Figure 6.5) offers a measurable anthracomass (1.6 mg kg^{-1}). Present vegetation is a transitional subalpine-alpine sward dominated by matgrass (*Nardus stricta*). Higher up, at 2618 m a.s.l. (FK2) and 2785 m a.s.l. (FK3), the anthracomass is negligible, and podzolic activity absent. There, present vegetation consists of true alpine swards dominated by *Carex curvula.* Such a sward, in a flat area nearby at 2500 m a.s.l., was calculated, using DNA analysis and taking into account the annual growth rate, to be more than 2000 years old (Steinger *et al.* , 1996).

According to soils and soil charcoal, the upper treeline was, in the past, situated between 2400 and 2600 m a.s.l.. Present data cannot offer a more precise estimate. However, if we assume that the uppermost ancient treeline in this area was shifted in the same way as at Belalp, the treeline at Furka was at most 300 m higher than its present potential limit, i.e. it could have reached 2500 m a.s.l..

6.5.6 Treeline fluctuation

Human activity has lowered treeline limits in the Alps ever since the Neolithic age, some 4000-3000 yr BC. Present treeline is estimated to be 200-300 altitudinal meters lower than its potential upper limit, as shown by discoveries of branches and tree trunks in alpine bogs, or by toponymy (Mariétan, 1929; Tinner *et al.*, 1996; Burga, 1988; Wick and Tinner, 1997; Burga and Perret, 2001; Tinner and Ammann, 2001; Tinner and Theurillat, in press). According to the literature, treeline is not considered to have reached a much higher elevation during the warmest phases of the Holocene than its present potential limit. According to e.g. Burga (1988), Tinner *et al.* (1996), Burga and Perret (2001), the ancient treeline was only ca. 100 m higher. However, according to our results, treeline climbed significantly higher, ca. 300 m at Belalp, 200-250 m in Arpette, and ca. 300 m at Furka. The 50-100 m difference between Arpette and the two other sites may be explained by the southern, steep and rocky slope in Arpette which presently allows treeline to reach a higher elevation than it would climatically. Thus, geomorphology would act as a buffer.

Interestingly, our findings come close to a recent evaluation of the uppermost forest limit and the altitudinal extension of the treeline in the Valais based on pollen and macrofossiles analysis (Tinner and Ammann, 2001; Tinner and Theurillat, in press). There, (1) the uppermost forest limit is considered to have reached 120-180 m higher than at present, and (2) the transition zone up to the treeline was of the same amplitude as at present. If the same altitudinal lapse is applied in the present study area (present potential forest limit being ca. 2200 m in Belalp) the uppermost forest limit would then have reached 2320-2380 m a.s.l.. Taking into account a transition zone of 100-150 m, the uppermost treeline would have been at 2470-2530 m a.s.l. This is quite in accordance with our results, although pollen and macrorestes can be considered to be more conservative, giving an uppermost limit around 50 m lower than the one inferred from soil charcoal.

When comparing our results with the findings in the dry southern French Alps (Talon, 1997b), it comes out that the maximum altitudinal treeline fluctuation there during the Holocene was of the same order, although probably a little bit greater (Table 6.3). This could be explained by a dryer climate which allowed trees, especially *P. cembra*, to climb higher in this region. For the dry Northern French Alps (Vanoise), charcoal data show a 300 m altitudinal upward shift of *P. cembra* during the Holocene according to Carcaillet (2001), in correspondance with the amplitude of treeline fluctuation from AM data.

Charcoal radiocarbon dating at Belalp would support that the sinking of timberline between 3500 and 2500 BC in Belalp inferred from pollen and plant macrorest analysis (Tinner and Ammann, 2001; Tinner and Theurillat, in press) would result from human impact. Three of the dated charcoals are from the end of the Neolithic (BA-LE7, 3350-2500 cal. BC; BA-HO1, 2700-2100 cal. BC; BA-HO1, 2310-1880 cal. BC), and one from the the Bronze Age (BA-LE6, 1150-750 cal. BC). Both periods correspond to climatic optimum, when the Aletsch glacier was smaller than today (Furrer, 2001).

Table 6.3 Comparison of maximum treeline fluctuation in the central-northern and south-western Alps during the Holocene inferred from soil charcoal. Sites are ordered from north to south.

[a] present data; [b] Talon (1997b); [c] Theurillat, personal observations.

Site (latitude)	Elevation of present-day potential uppermost treeline (m a.s.l.)	Past uppermost treeline (m a.s.l.) [soil AM> 0.1 mg, conifer charcoal, and podzolized soil]	Maximum altitudinal treeline fluctuation (m)
Furka [a] (46°30’ N)	2200	> 2400 < 2620	> 200 < 420 assessed: 300
Aletsch [a] (46°30’ N)	2200	< 2580	< 380 assessed: 300
Belalp [a] (46°25’ N)	2300	> 2570 < 2665	> 270 < 365 assessed: 300
Arpette [a] (46° N)	2250 - 2300	> 2375 ≤ 2565	> 75 - 125 ≤ 265 - 315 assessed: 200-250
Queyras [b] (44°55’ N)	2550 [c]	> 2870	> 330
Ubaye [b] (44°40’ N)	2550-2600 [c]	> 2850	> 250 - 300
Haute-Tinée [b] (44°15’ N)	2600 [c]	> 2810	> 210

6.6 Conclusions

According to the present study, soil and soil charcoal analysis provide a reliable basis for the calculation of the limit reached by treeline at the subalpine-alpine ecocline in the past. It is here suggested that the uppermost limit was 300 m higher than at present (Table 6.3). The charcoal mass and soil types found along the five transects studied reveal an altitudinal zonation into three different belts (Figure 6.7).

(1) Up to ca. 2400 m a.s.l., the presence of charcoal is high (up to 19 mg kg^{-1}) and PODZOSOLS are well developed.

(2) Between 2400 and 2570 m a.s.l., a transition belt is characterized by lower anthracomass (0.11 and 1.57 mg kg^{-1}) and less developed PODZOSOLS.

(3) Finally, in the uppermost belt above 2550-2600 m a.s.l. charcoal is extremely rare or absent, and dominant soil types are ALOCRISOLS.

The limits given for the three belts are general. They would be tuned locally by specific factors, such as slope, aspect, physiography, hygric continentality or the proximity of a glacier.

On the basis of the higher mean charcoal mass and the occurrence of well developed TYPICAL PODZOSOL (Figure 6.7), the lower belt is attributed to the forested zone, the upper limit of which formed the highest timberline in the past. This zone was probably cleared by several fire events, attested by radiocarbon-dated charcoal and other evidence found at the timberline (Haas *et al.* , 1998).

The second belt formed a transitional zone, the subalpine-alpine ecocline, with its upper limit delineating the treeline. Finally, the upper belt corresponded to the zone of the limit of tree species, where small, scattered trees could still be found in favourable (steep, rocky) places in the alpine belt.

A corresponding subdivision occurred also in the Southern French Alps where the uppermost treeline was even more than 300 m higher than at present (Figure 6.8). The highest elevation of treeline was attained during the warmest periods of the Holocene where mean annual air temperature would be about

1.4-1.7 K higher than today (considering an air temperature decrease of 0.56 K per 100 m of increasing altitude).

The subalpine-alpine ecocline is likely to undergo an upwards altitudinal species shifting in the present alpine belt in response to forecasted future global warming and to new types of land use, such as the abandonment of the practice of pasturing and the development of recreational activities.

In the past, even during periods of more favourable thermic conditions, treeline limit was never more than 200-350 m higher than today's potential treeline in the European Alps. Such species shifting would take place under the least extreme scenario of expected global warming (IPCC, 2001); the effects of more severe global warming are unpredictable and are very likely to lead to the local and regional extinction of alpine species (e.g. Theurillat *et al.* , 1998; Theurillat and Guisan, 2001).

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CHAPTER 7: POLLEN AND MACROREST ANALYSIS

7.1. Introduction

The reconstruction of the history of the vegetation in this study is based on the combination of different palaeobotanical methods: in this chapter the contribution brought by pollen and plant macrorest analysis is discussed. The combination of pollen and plant macrofossil analysis has shown to be able to supply a reliable proxy of vegetation at the timberline ecotone. Although an extensive data set of pollen and macrorest results is available for comparison, nevertheless, the site here under investigation, presents some peculiarities. Indeed, the mire Lengi Egga, is one of the very few ever studied above present treeline, and the first in which a study on Holocene plant macrofossil was performed.

The analysis of plant macrorest and pollen was carried out by Dr. Willy Tinner, University of Bern (Institute of Plant Science, Section palaeoecology, Altenbergrain 21, Bern, Switzerland). The result of this study are fully discussed elsewhere (Tinner and Theurillat, in press), while here a summary of results is reported

7.2. Site Location and Methods

The peat bog Lengi Egga is situated at 2557 m a.s.l., in Belalp area, in close proximity of the study site BA-LE5. Lengi Egga is a mire subdivided by a perennial streamlet, the mean diameter is about 170 m, the basin is formed by late glacial moraine ramparts, and consists of siliceous scists (Figure 7.1).

A modified Livingston piston corer was used to take two cores with a diameter of 8 cm. The maximum depth reached was 191 cm. Plant macrorests and pollen extraction and identification were performed. Chronology was assessed by radiocarbon dated plant macrorests.

7.3. Results and discussion

7.3.1 Pollen analysis

The study of pollen (Figure 6.2) allows to identify four main phases: the oldest period (Younger Dryas) is characterised by the dominance of pollen of *Pinus sylvestris* t., *Artemisia*, and *Poaceae* (EP-1); at the beginning of the Holocene *Pinus sylvestris* t. is the dominant type (EP-2 and 3), then *Pinus cembra* augmented but still with low percentage (<15%) (EP 4-7); in the section EP-8-11, *Pinus cembra* pollen is substituted by *Picea* and *Alnus viridis*; the youngest local pollen assemblage zone is characterised by high abundance of herb pollen. During all the Holocene, marked medium-termed fluctuations of tree-pollen percentages are present.

The quantity of tree and shrub pollen suggests that in proximity of the peat bog, woody species were never dominant. A pollen based history of vegetation may not be reliable in open ecosystem such as the ecocline, because of the input of allochtonous pollen. Pollen influxes, however, allow to better distinguish between local and allocthonous input, moreover, the influxes can be compared with modern measurements at timberline (van der Knaap et al., 2001). Average influxes values at Langi Egga are very similar to those of pollen-traps situated above timberline.

7.3.2 Plant macrofossil analysis

At the basis of the core (Figure 7.3), before 9000 BC (9600 BP) moss fragments indicate the presence of pioneer vegetation (LE-1), between 9000 and 9500 BC (10000-9600 BP uncal.) macroscopic remains of Salix herbacea and Caryophyllaceae are present, and indicate the formation of closed vegetation (LE-2). After 9000 BC (9600 BP uncal.) the number of macrofossils increases sharply, and after 7500 BC the vegetation become more diverse (LE-3 and 4), reaching a maximum between 6200 and 5100 BC (LE-5). Between 7500 and 3000 BC (8500-4400 BP uncal., LE 3-8) herb and shrubs are abundant (e.g.: *Cirsium spinosissimum, Helianthemum, Leontodon*, *Potentilla, Potentilla aurea., Saxifraga stellaris, Silene exscapa., Vaccinium*, and *Juniperus nana*). The past 3000 years are characterised by regular findings of Salix herbacea leaves (LE 11-9). After 2300 BC the lake was transformed into a mire; *Carex* reaches high values, and single but regular findings of *Larix decidua* needles and Betula cfr. alba fruits occur. Charred needles of Picea and Larix were found in the zones L-9 and 10. Tree remains are of marginal importance compared to herbaceous taxa. The abundance of alpine species suggests that the peat was always above the treeline.

Figure 7.1 The peat bog Langi Egga is situated at 2557 m a.s.l..

Figure 7.2 Pollen-percentage digram (selected taxa) of Lengi Egga, Switzerland. Water plants and ferns are excluded from pollen sum. Concentration (conc.) and influx (infl.) values are given for Betula, Larix, and Pinus cembra. The numbers 1 to 5 in the summary diagram (trees, shrubs, herbs) indicate periods of major vegetational responses to climatic change. LPAZ= Local pollen assemblage zone. Cult. = cultural indicators.

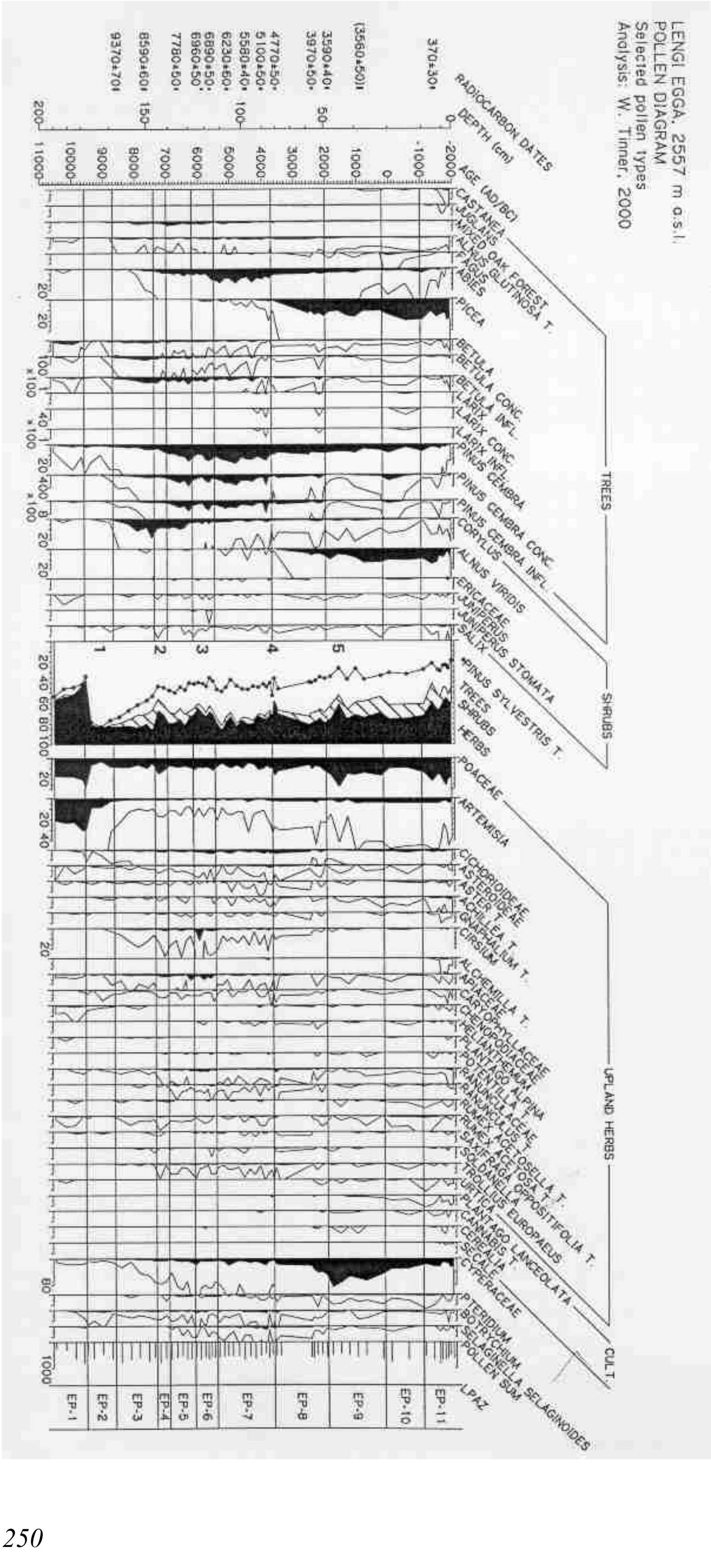
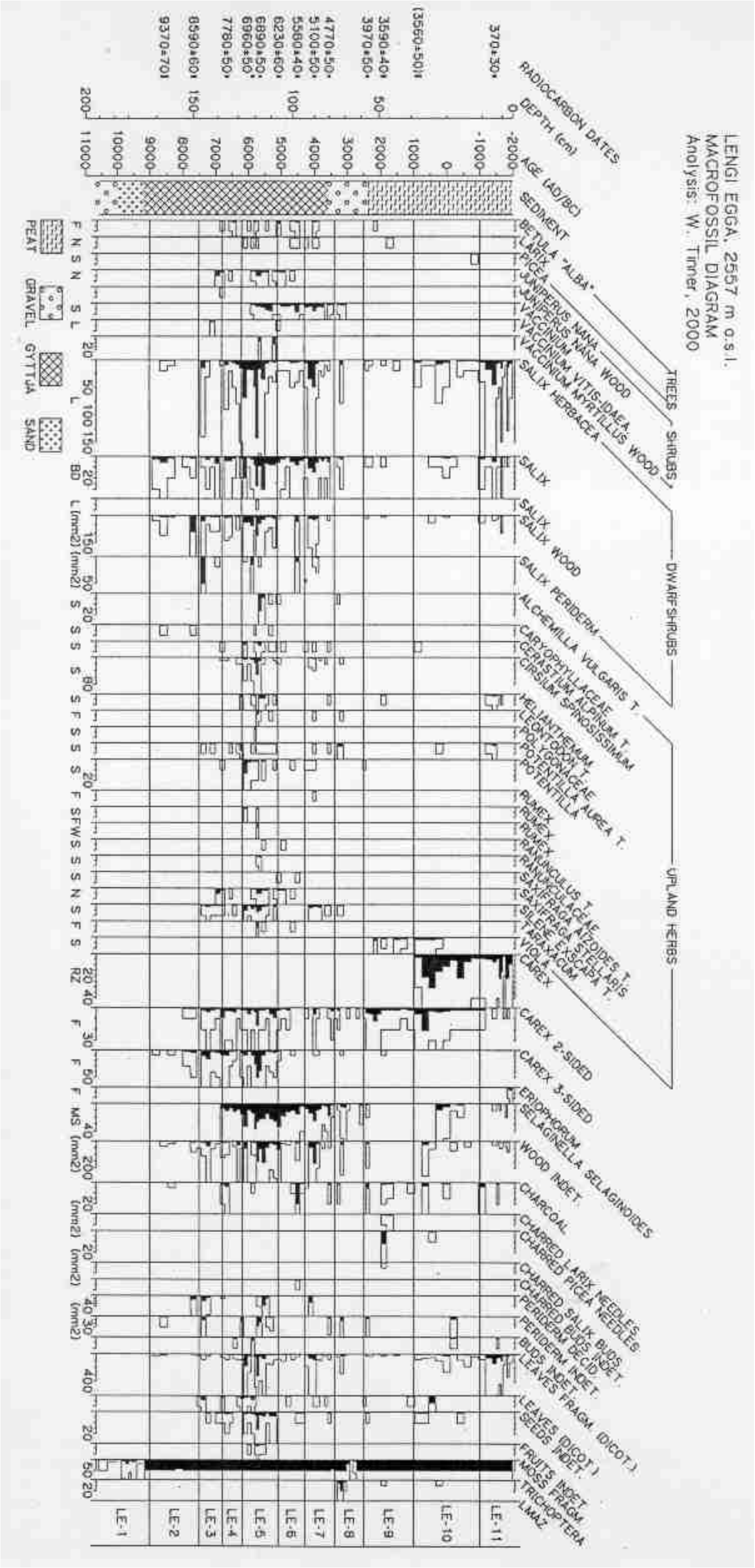


Figure 7.3 Plant-macrofossil concentrations at Lengi Egga (findings per 90 cm^3). LMAZ = local macrofossil-assemblage zones. Dicot. = dicotyledon. BD = buds, BS = budscales, F = fruits, L = leaves, MS = macrospores, Nedles, RZ = rhizoms, S = seeds.



7.3.3 History of vegetation at Lengi Egga

Macrofossil and pollen data (Figures 7.2-7.3)suggest that above the timberline ecocline, alpine meadows dominated all along the Holocene in the Lengi Egga area. Pollen percentages at Lengi Egga suggest that several important tree diebacks occurred during the Holocene. The strongest reduction of arboreal pollen (EP-11) is thought to be induced by human activities. However, the reduction of trees is synchronous with negative temperature excursion in the northern Alps and in the northern Atlantic, and it may also be related to Little Ice Age cooling. This climatic cooling did not affect the local alpine vegetation at Lengi Egga probably adapted to even harsher conditions, but is recorded by trees growing at lower altitude.

By comparison with other peat bogs in the central Swiss Alps, located below treeline (Gouillé Rion, 2343 m a.s.l.) and at the limit of treeline (Gouillé Loéré, 2503 m a.s.l.), it is suggested the hypothesis of a more or less stable Holocene upper forest boundary at most 100-150 m higher than today's treeline (Tinner and Theurillat, in press). The timberline migrated upwards of about 100 m (between Gouillé Loéré and Lengi Egga) between 9000 and 2500 BC (9600-4000 BP uncal.); then at about 2500 BC (400 BP uncal) the timberline is depressed of about 200 meters, probably both by human disturbance (Bronze Age in the area begins at 2300 BC *(3850 BP uncal.)* and harsher climatic conditions.

7.4 Conclusions

The results here briefly presented support the hypothesis that the mire Lengi Egga was always situate above treeline. For comparison with other studies on peat bog below the treeline in the Central Alps the maximum extension of the forest can be inferred to be about 100-150 m higher than present treeline.

7.5 Cited references

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CHAPTER 8: SYNTHESIS OF THE RESULTS AND CONCLUSIONS

8.1 Introduction

The problem of detecting the uppermost limit matched during the Holocene by treeline was here addressed by an innovative approach for subalpine-alpine ecosystems. Methodologies that have largely proved their validity for paleoecological reconstruction (such as soil study, pedoantrachology, pollen analysis, plant macrorests analysis and dendrochronology), were matched with new techniques linked to soil biogenic silica, never tested before in alpine soils.

Two sets of results were produced:

(1) a first set of findings groups methodological results linked to the study of biogenic silica in plants and soils.

(2) a second group of results concerns the palaeoecological evidences on which the reconstruction of the palaeotimberline position is based.

8.2 Methodological results

The study of plant biogenic silica in alpine ecosystems is still at its infancy, and several methodological issues still await further evaluations. To contribute to fill this gap, and with a view of applying this findings to treeline reconstruction, biogenic silica was extracted from above ground tissues of the reference collection of subalpine and alpine plants. Data on plant biogenic silica were then put in relations with biogenic silica in top soil layers, with the aim to investigate the genesis of soil phytolith assemblages.

8.2.1 Biogenic silica in subalpine-alpine plants

Among the 28 species tested, all but two species contained biogenic silica, and some of the dominant species were silica accumulators [e.g.: *Calamagrostis villosa* (5.9%), *Carex sempervirens* (2.29%), *Festuca scabriculmis* (2.41%), *Calluna vulgaris* (0.68%), *Larix decidua* (1.09%, needles; 0.54% wood), and *Picea abies* (0.85%, needles; 0.16% wood)].

The production of biogenic silica was then estimated at the level of the plant community. The comparison between the input of biogenic silica of different plant communities put in evidence the great relevance of grasslands in the biogeochemical cycle of silica. Mean annual silica production of subalpine grasslands (9.4 g m^2 y^{-1}) is about one order of magnitude higher than that of heaths (0.54 g m^2 y^{-1}), shrub formations (0.48 g m^2 y^{-1}), litterfall of conifer forests (1.6 g m^2 y^{-1}), and of the upper alpine grassland (1.2 g m^2 y^{-1}).

The interest of biogenic silica in palaeoecological studies is associated with its ubiquity in plant species and its availability in palaeoecological archives: the quantitative estimate of biogenic silica allowed to assess that biogenic silica analysis in subalpine-alpine soils is a valuable exercise.

8.2.2 Phytolith morphology

Silica deposited in plants is released in soils and sediments under the form of particulated silica (i.e. phytoliths).

An inventory of phytolith typologies from the plants of the reference collection was built and phytolith frequencies were measured. An atlas of distinctive typologies was prepared.

Monocotyledons yielded well silicified idiomorphic phytoliths, mainly of epidermal origin ("short cells" or "trapezoid" in grasses and "cones" in sedges). Phytoliths in *Ericaceae* species were mainly silicified epidermal jigsaw cells, stomata complexes and vessels; in conifers silica bodies were principally tranfusion tissues, and endodermal cells.

Multivariate descriptive statistical analysis showed that grasses and sedges are well differentiated from *Ericaceae* and conifers on the basis of the frequency of phytoliths. However, some of the species of conifers and *Ericaceae* cannot be unequivocally identified.

Phytoliths from the examined set of species showed to have the potential of distinguishing between grass *versus* woody species. However, a strictly morphological approach in phytolith studies showed some limitations because of the repetitive shapes of some silicified cells, that may be common to different tissues of the same plant, or to tissues of unrelated species.

8.2.3 Aluminium in plant biogenic silica

The morphological study of phytoliths bears some intrinsic limitations when applied to the study of alpine species. A useful complementary approach was shown to be the analysis of the chemical composition of the opal reticule of phytoliths. Phytolith composition was checked by means of X-ray microanalytical techniques (semiquantitative method) on plants from the reference collection. In the species examined, the occurrence of aluminium in the opal silica reticule was able to source woody species: indeed, biogenic silica from conifers and *Ericaceae* contained aluminium in up to 97% of the tested phytoliths, while, in general, grass and sedge phytoliths contained in only up to 10% of the cases or no aluminium at all.

This method opens a new venue in phytolith researches since, coupled with the morphological approach, enhances phytolith diagnostic taxonomical potential: indeed, this methodology can help in overtaking the deadlocks linked to redundant morphotypes, as well as in identifying phytoliths that have undergone taphonomical processes in soil. On the basis of the present results, it can be argued that aluminium should have far reaching application as marker of conifer biogenic silica, when vegetation shifts involving conifers versus herbaceous species are under investigation (e.g. in alpine, boreal and mediterranean ecosystems).

In addition, the screening of phytolith chemical composition of the most common species in the study area, allowed a better understanding of the expected life span of phytoliths in soil. *Ericaceae* and conifer phytoliths being aluminium rich, should be more resistant to dissolution processes in soil.

8.2.4 Modern analogs of soil phytolith assemblages

The study of modern analogs provided a basis for the interpretation of fossil phytoliths assemblages in soil. Biogenic silica deposited in soil undergo different sets of processes: deposition, translocation and dissolution act differently in the top horizons (holorganic and mineral-organic) and in the deeper horizons (mineral).

This study enlighted that in topmost holorganic horizons the deposition processes are dominant, while, already in the deeper mineral-organic horizon translocation and dissolution processes prevail: O horizons give a snapshot of plant stand composition, while A horizons are rather the result of time-integrated processes.

Biogenic silica records in topsoils reflects the input of biogenic silica from plant stand: biogenic silica content below the highly productive *Festuca scabriculmis* and *Carex sempervirens* subalpine grasslands was up to 16%, while, below the less productive *Carex curvula* turvs, biogenic silica was only up to 3.9%.

In general, in the low altitude sites the frequency of aluminium phytoliths in top horizons was higher. This is interpreted as the result of the input of scattered woody vegetation (ericoid shrubs and conifers) that are more frequent at lower elevation.

The content in silica, the frequency of Al phytoliths and the percentages of phytolith typologies (both measured and estimated) suggested that the formation of phytolith assemblages in alpine grassland is dominated by a mechanism of *in situ* inheritance, while the loss of biomass due to grazing and avalanches seems to play a secondary role in the redistribution of phytoliths.

The comparison between the modelled theoretical input of phytoliths and the measured frequencies evidenced the active role of the taphonomical processes already in the top soil: indeed, while the frequency of well silicified short cells showed to be predictable on the basis of plant stand productivity, in contrast, for more fragile or weakly silicified morphotypes, the theoretical input was a weak predictor.

As it was partially expected on the basis of reference collection data, modern phytolith assemblages showed a lack of resolution power in discriminating between alpine grassland types. Indeed, only grasses belonging to the same subfamily (Pooideae) and that yield short cells of only one type grow in alpine ecosystems.

In addition, sedges diagnostic phytoliths (cones) were poorly preserved in soil, for this reason the sensitivity of phytoliths analysis in distinguishing among subalpine and alpine grasslands is limited.

This work supplied a contribution to the understanding of fundamental issues about the processes ruling the formation of phytolith assemblages in soil: a better knowledge of phytolith signature given by present vegetation is the basis to improve the interpretation of fossil records.

8.3 Evidences for the reconstruction of the past uppermost treeline position

8.3.1 Soil zonation with altitude

In the present study, soils were analysed both as a source of palaeoecological information and as archives for palaeobotanical proxies (charcoals and biogenic silica); soils supply a virtually unlimited availability of sampling sites and a high spatial precision, that no other proxy can offer in alpine ecosystems.

A striking result was the close correlation between soil-type and altitude evidenced in the study area. In the altitudinal belt between 2300 m a.s.l. and 2500 m a.s.l. (at Furka and in Val d'Arpette), and 2550 m a.s.l. (at Belalp) soils were PODZSOLS (profiles A-E-B-C). Higher on, the podzolic activity in soil blurs in all the sites in a narrow altitudinal belt of only 50 meters, between 2500-2550 m.

The present vegetation of alpine meadows cannot lead to the fully developed PODZOSOL MEUBLES detected at and below ca. 2400 m. These soil types must be the result of the pedogenesis in presence of an ancient plant communities with high net primary production and acidic litter: i.e. conifer woodlands and heathlands.

Above 2550 m, soils are characterised by a sequence of horizons A-Sal-C (ALOCRISOLS), or are undeveloped mineral soils with an A-C profile (BRUNISOLS). Both types are consistent with long lasting occurrence of alpine meadows.

It is therefore argued that the upper limit of podzolic activity at 2500-2550 m a.s.l. marks an ancient vegetation border and it is interpreted as the past uppermost position of the palaeotreeline.

8.3.2 Biogenic silica in soil

Biogenic silica and aluminious biogenic silica showed to be suitable proxies to investigate dry terrestrial ecosystems along transitional gradients. In all the transects a low content of B.S. and a high content of Al-B.S. recorded in the deeper part of the soils were detected in soils up to 2500-2550 m a.s.l..

In contrast, in soils at higher elevation, B.S. was more accumulated and Al-B.S. was very low.

The transition between different signals for B.S. and Al-B.S., is located in correspondence of the limit of the podzolisation, and is thought to mark the ancient border between the alpine vegetation dominated by grassland (strong B.S. accumulator, and weak Al-B.S. producer) and the subalpine ericaceous heathlands or conifer woodland (low amount of B.S. and high Al-B.S.).

The record of aluminium rich phytoliths showed to be consistent with the other independent palaeocological evidences. This methodology proved, therefore, to be valuable in alpine ecosystems, although more assertive conclusions await larger data sets.

Although alpine soils are often highly dynamic systems that are subjected to active depositional processes and colluvial activity, the very good correspondence between soil discontinuities and phytolith profiles showed that subalpine-alpine soils are conservative media, and therefore, highly reliable archives of palaeoecological proxies.

Finally, the role of biogenic silica as a sink or as a pool in soils was put in relations with climatic fluctuations in the last part of the Holocene. It is hypothesised that in temperature limited ecosystems, such as the alpine, the fluctuations of the record of B.S. in soil deeper horizons may mirror climatic fluctuations during the last part of the Holocene. The alternating of accumulation-dominated vs. dissolution-dominated cycles was tentatively matched with Holocene colder and warmer phases, respectively.

8.3.3 Charcoals in soil

Soil charcoal analysis (pedoanthracology) supplied spatially-precise data in the study area to reconstruct the fluctuations of the treeline. The mass of charcoals in soil showed to vary with elevation. Three belts could be outlined:

1) in the sites up to ca. 2400 m a.s.l., the anthracomass had the highest values (up to 19 mg kg^{-1}), between 2400 and 2570 m a.s.l.,

2) a transition belt characterised by a lower anthracomass (0.11 and 1.57 mg kg^{-1}) was detected; in the uppermost belt,

3) above 2550-2600 m a.s.l., charcoals are extremely rare or even absent. The altitudinal range of these belts was adjusted locally by specific factors, such as slope, hygric continentality or the proximity of the glacier.

It is argued that the lower belt corresponded to the forested zone, its upper limit being the highest limit of timberline in the past. This zone was probably cleared, mainly during the Subboreal, by several fire events, as attested by radiocarbon-dated charcoals. Higher on, the second belt formed a transitional zone, the subalpine-alpine ecocline (or kampfzone), with its upper limit delineating the treeline. Finally, the upper belt corresponded to the limit of tree species, where small, scattered trees could still be found in favourable (steep, rocky) places in the alpine belt.

8.3.4 Pollen and plant macrorests analysis

Macrofossil and pollen data suggest that above the treeline, alpine meadows dominated all along the Holocene in the Lengi Egga area. Pollen percentages at Lengi Egga suggest that several important tree diebacks occurred during the Holocene. The strongest reduction of arboreal pollen is thought to be induced by human activities. However, the reduction of trees is synchronous with negative temperature excursion in the Northern Alps and in the Northern Atlantic, and it may also be related to Little Ice Age cooling. This climatic cooling did not affect the local alpine vegetation at Lengi Egga probably adapted to even harsher conditions, but is recorded by trees growing at lower altitude.

8.3.4 Treeline uppermost position

The palaeoecological evidences supplied by the different proxies show a good agreement in individuating the uppermost altitude reached by the treeline.

Each method focusses on some aspects, and yields some advantages and limitations: all the facets have to integrated to supply a reconstruction as complete as possible of the vegetation history in the study area.

On the basis of soil, charcoal and biogenic silica analysis an altitudinal zonation of vegetation into three different belts is suggested:

(1) Up to ca. 2400 m a.s.l., high antrachomass, high rate of Al-biogenic silica and fully developed podzsols mark the uppermost limit reached by the forested zone.

(2) Between 2500 and 2570 m a.s.l., a transition belt characterised by lower anthracomass and weakly podzolised soils, correspond to the kampfzone, with its upper limit delineating the treeline.

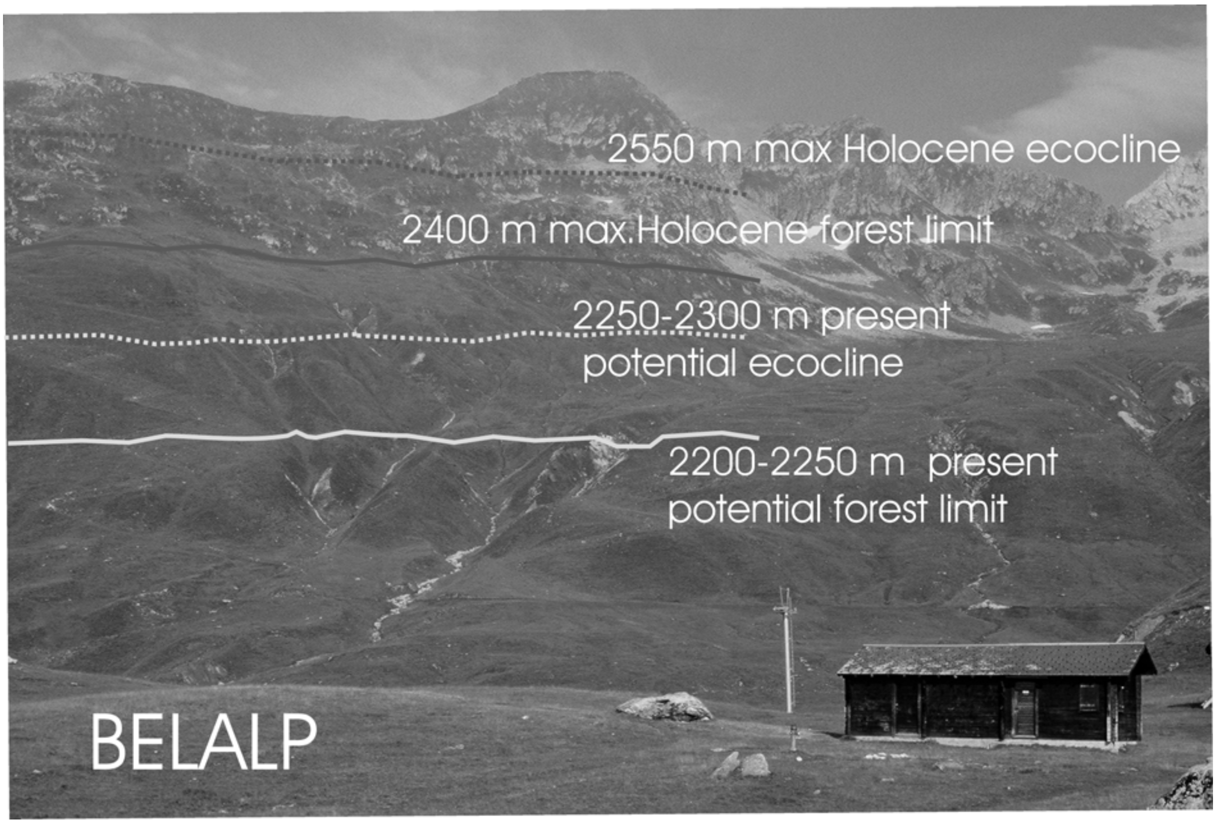
(3) In the uppermost belt, above 2550-2600 m a.s.l., charcoals are extremely rare or absent, the rate of Al-biogenic silica is low and the podzolic activity absent: this belt corresponds to the tree species limit zone, in which alpine meadows have always been dominant, but where small, scattered trees could still be found in favourable locations.

The altitudinal range of these belts was adjusted locally by specific factors, such as slope, hygric continentality or the proximity of the glacier.

The elevation of 2500-2550 m was attained by the treeline during the warmest periods of the Holocene, when mean annual temperature was about 1.4(1.8)°C higher than today: on the basis of the evidences here gathered, even during periods of more favourable thermic conditions, the treeline was never more than 200-350 m higher than today’s potential treeline.

The analysis of pollen fluxes and plant macrofossils at Langi Egga (2557 m a.s.l.) confirms the persistence of an alpine belt devoid of trees all along the Holocene. By comparison with other peat bogs in the Central Swiss Alps located below treeline (Gouillé Rion, 2343 m a.s.l.), and at the limit of treeline (Gouillé Loéré, 2503 m a.s.l.), it is suggested the hypothesis of a more or less stable Holocene upper forest boundary at most 100-150 m higher than today's treeline (Tinner and Theurillat, unpublished). The timberline migrated upwards of about 100 m (between Gouillé Loéré and Lengi Egga) between 9000 and 2500 BC (9600-4000 BP uncal.); then at about 2500 BC (400 BP uncal) the timberline is depressed of about 200 meters, probably both by human disturbance (Bronze Age in the area begins at 2300 BC (3850 BP uncal.) and harsher climatic conditions.

Dendrochronological evidences showed that in favourable sites in the alpine belts *Pinus cembra* can grow and develop up to the age of 100-200 years under the form of krumholtz. This indirect evidence strongly supports the hypothesis that, with temperature not so different from the present ones, and probably in more continental conditions, the treeline could have climbed as high as 200 m higher than present and, locally, even 300 meter.



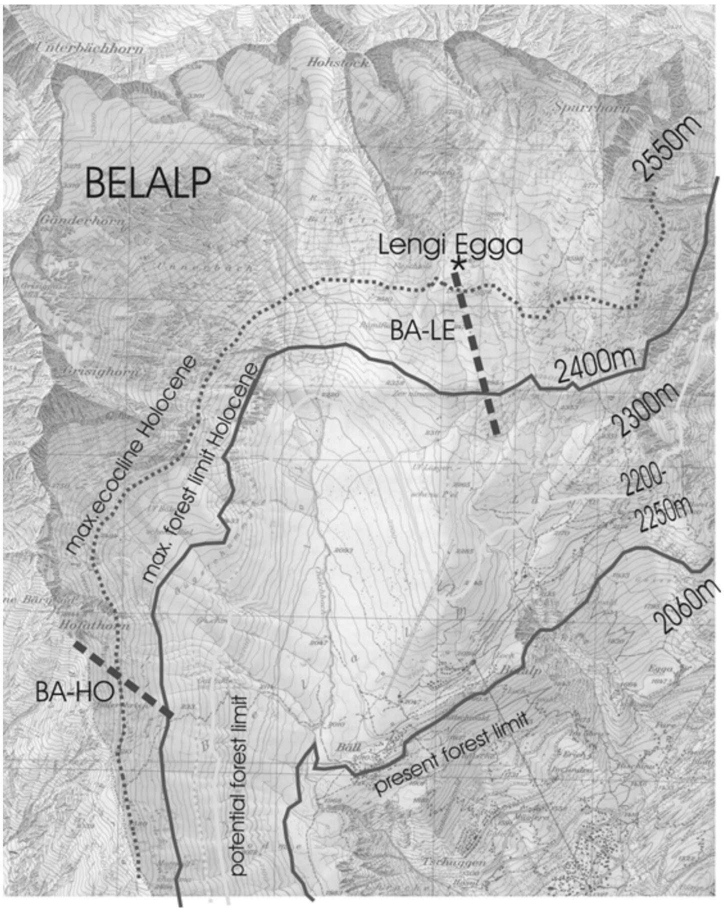


Figure 8.1 Graphic reconstruction of the position of the past uppermost limits of the subalpine-alpine ecocline (2550 m a.s.l.) and forest limit at Belalp (2400 m a.sl.). The transects BA-HO and BA-LE are indicated by dashed lines.

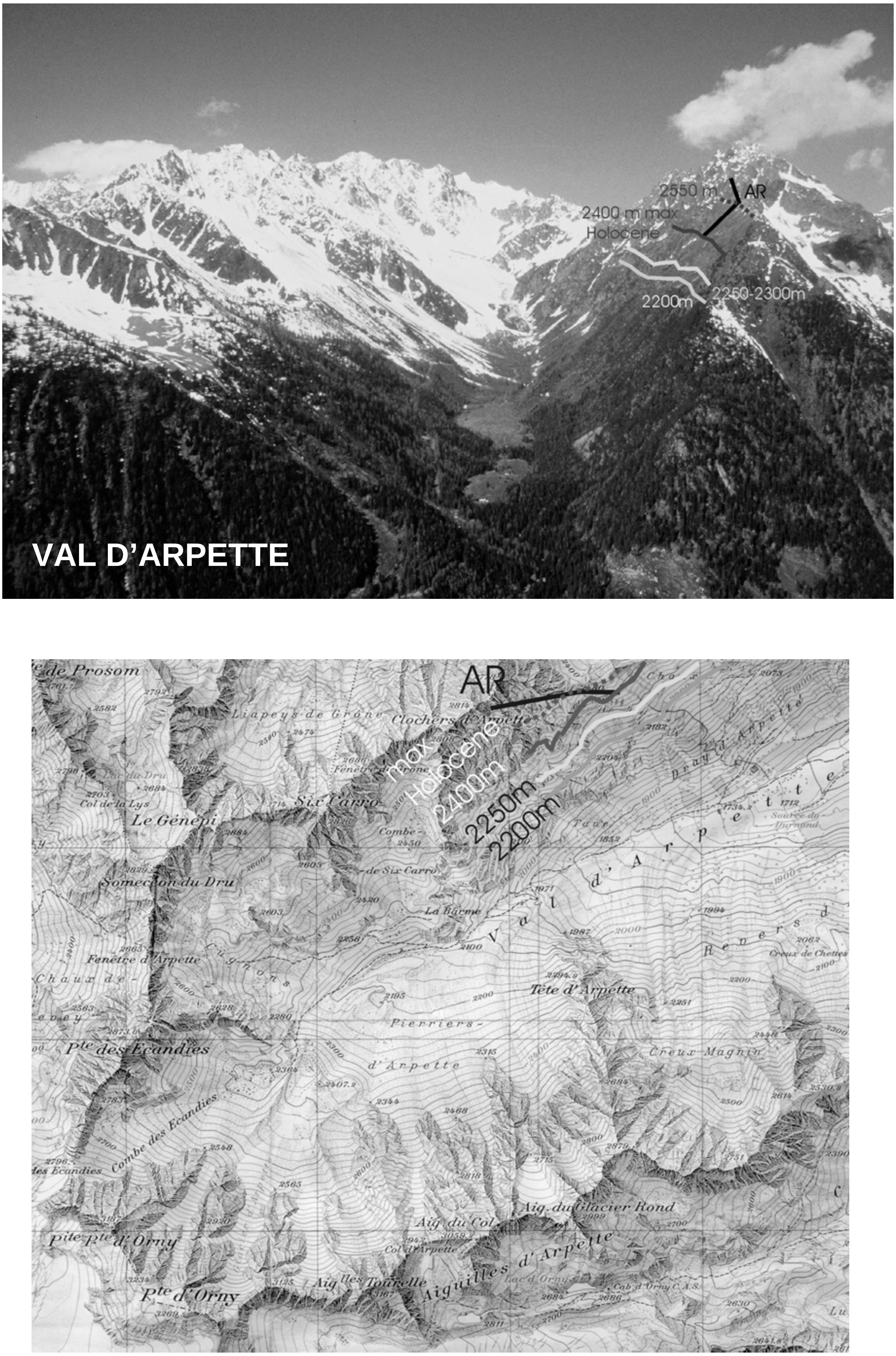


Figure 8.2 Graphic reconstruction of the position of the past uppermost limits of the subalpine-alpine ecocline (2550 ma.s.l.), and forest limit (2400 m a.s.l.) in Val d'Arpette. Present forest limit is at 2200 m a.s.l., present potential limit is at 2250 m a.s.l..

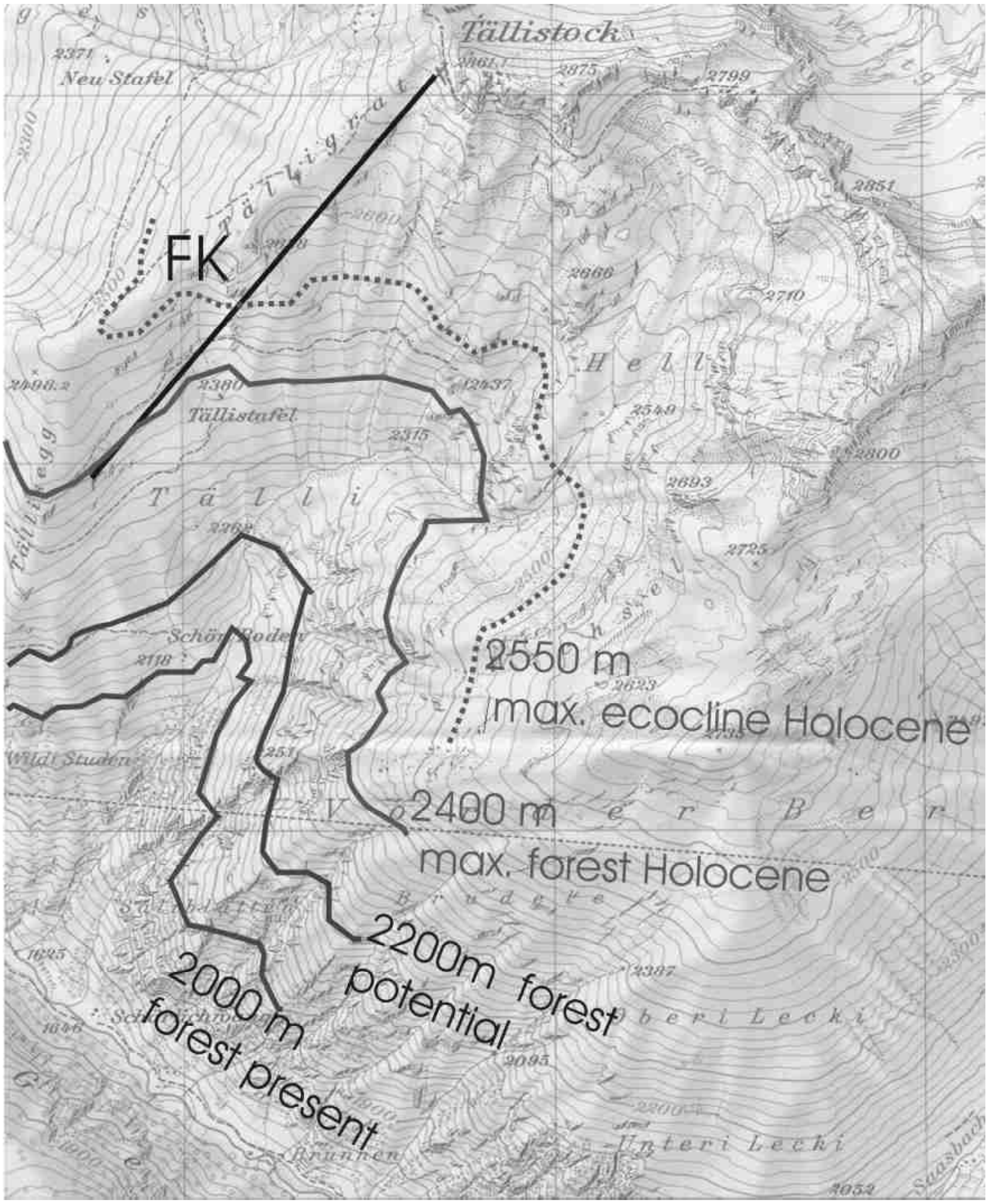


Figure 8.3 Graphic reconstruction of the position of the past uppermost limits of the subalpine-alpine ecocline, and forest limit At Furka Pass.

8.4 Summary of conclusions

The methodological investigations carried out on plant biogenic silica evidenced that annual biogenic silica input of subalpine grassland is of one order of magnitude higher than in alpine grasslands, heathlands and conifer forests; the inventory of phytolith typologies showed that phytoliths have the potential to distinguish between monocotyledons, and *Ericaceae* or conifers; a new methodology based on the presence of aluminium rich phytoliths was proposed to source woody species phytoliths. The study of modern analogs of phytolith assemblages showed that biogenic silica mass and frequency of monocotyledon phytoliths in topsoils are predictable on the basis of the input of the plant stand.

The palaeobotanical investigations carried out at the subalpine-alpine ecocline detected the presence of a palaeotreeline situated at about 2500-2550 m a.s.l. in the study area. Schematically three altitudinal belts were individuated:

1) up to ca. 2400 m a.s.l. = uppermost limit reached by the close forest (i.e. palaeo timberline)
2) between 2400 m and 2570 ma.s.l. = subalpine-alpine ecocline, at about 2600 m a.s.l. was located the uppermost limit of the paleo treeline
3) above 2550-2600 m a.s.l. = persistence of alpine belt dominated by herbaceous species, with single trees in fabourable spots.

According to the present reconstruction, the treeline was up to 300 meters higher than its present potential limit. Such elevation would lead to the hypothesis that temperature could be about 1.8C° higher than present if the other climatic factors were the same than present. However, if climate during middle Holocene was more continental, as seems the case, the temperature lapse might have been even smaller.

During Holocene phases of more favourable thermic conditions, with temperatures probably only 0.8-1.2 (1.8)C° higher than present, the treeline limit was at maximum 200-350 m higher than today's potential treeline; if the effects of the forecasted global warming would be more severe, the species upwards shift will be stronger and might very likely lead to the extinction of alpine species.

8.4 Suggestions for new researches

Several issues related to the methodology used for the reconstruction of the treeline position are worth of further investigations.

Biogenic silica content should be investigated in other relevant species and/or tissues to make the reference collection more complete; in particular, root tissues should be examined since nearly no data are available on plant below-ground organs.

Aluminium presence in biogenic silica should be checked on woody and herbaceous species from very different vegetation types to test the suitability of this technique to trace woody species also in different ecosystems.

In addition to the semi-quantitive detection of aluminium by means of microanalytical techniques, the quantitative evaluation of Al content in biogenic silica by means of mass spettroscopy might turn out to powerful for species diagnostic.

Furthermore, it would be relevant to investigate the chemistry of aluminious opal silica, to measure the stability of Si-Al links, and the affinity of phytolith surface for Al once in contact with soil solution.

The study of modern analogs of phytolith assemblages should be developed by including also heathland and woodland assemblages. This would allow a better comprehension of the mechanisms of deposition of biogenic silica in the main vegetation types at the alpine-subalpine ecocline.

Biogenic silica can be easily extracted from sediment from cores sampled from subalpine-alpine peat bogs (as it was tested by the author, unpublished results). For instance, in the samples from Langi-Egga cores, abundant phytoliths and diatoms were present. Changes in phytolith frequency and chemical composition could be paired with macrorest and pollen records: such a comparison will be of invaluable interest in phytolith studies. At the subalpine-alpine ecocline, such study should be performed on cores from peat bogs situated below and above the palaeotreeline: this would allow to compare the records from sites in which a vegetation shift woody/ herbaceous vegetation occurred, with sites in which the record of the herbaceous vegetation is continuous.

Moreover, the correlation between peaks of biogenic silica in lake cores and climatic fluctuations should be investigated: this may help to validate or discard the hypothesis of the alternating of accumulation-dominated and dissolution-dominated cycles formulated for alpine soils in Chapter 5.2.

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ANNEXE A

Description et nomenclature des sols de cinq sites des Alpes suisses.

Projet Paléoécocline de l'Université de Genève.

Gaëlle Vadi

Laboratoire d'Écologie végétale et de phytosociologie, Rue Émile Argand 11, 2007 Neuchâtel, Suisse

1. Introduction

Cette étude s'inscrit dans le cadre de la thèse menée par Adriana Carnelli à l'Université de Genève, recherche destinée à prouver l'éventuelle présence passée d'un couvert forestier à l'étage alpin. Les investigations étant basées sur la recherche et l'identification de vestiges tels que les phytolithes et les charbons, il était nécessaire d'assortir une description fine du contexte pédologique à chacun des échantillons.

Les cinq sites étudiés se situent en domaine alpin. Une premiere campagne des recherches pédologiques a etè effectuées durant l'été 1998. Deux sites constituent les terrains d'étude privilégiés de l'Université de Genève dans les Alpes valaisannes, soit le Val d'Arpette et Belalp. Une typologie pédologique a été réalisée par Marlyse Fierz-Gallandat (FIERZ & GOBAT, 1996) pour ces deux régions. Le troisième terrain étudié en 1998 se situe au Furka Pass, à la frontières des Alpes valaisannes et uranaises; aucune typologie n'y a été effectuée à notre connaissance. On a été appelés à compléter les données de la station de Belalp ainsi qu'à décrire des sols dans une station surplombant le glacier d'Aletsch durant l'été 1999. Les méthodes utilisées, tant sur le terrain qu'en laboratoire, ont été identiques. Les deux sites étudiés en 1999 se situent également en domaine alpin. Le site de Belalp avait déjà été visité en 1998. Nous y avons décrit trois sols supplémentaires (Belalp-Lengi Egga), se situant cette fois à l'est du village, mais présentant les mêmes conditions d'exposition. Le dernier site se situe sur le flanc est du glacier d'Aletsch, au-dessus des moraines.

2. Matériel et Méthodes

2.1. Descriptions et prélèvement

Les sols ont été décrits classiquement (BAIZE & JABIOL, 1995) durant l'été 1998, et 1999 à partir de fosses pédologiques. Les sols de Belalp et du Furka Pass, ainsi que le sol numéro 1 du val d'Arpette ont été décrits et échantillonnés par nos soins. Le sol AR2 a été récolté de façon systématique par Jean-Paul Teurillat. Nous avons tenté de « recréer » la séquence des horizons à l'aide des analyses chimiques et la description des échantillons reçus. AR3 a été sommairement décrit et récolté par Adriana Carnelli. Les sols de Belalp, ainsi que le sol numéro 1 d'Aletsch (HT1) ont été décrits et échantillonnés par nos soins. Le deuxième sol d'Aletsch (HT2) a été sommairement décrit et échantillonné de façon systématique par Adriana Carnelli. Nous avons tenté de "recréer" la séquence des horizons à l'aide des analyses chimiques et de la description des échantillons "frais" (à réception).

Les valeurs de pH qui figurent dans les descriptions des profils ont été obtenues à l'aide du pH-mètre de terrain Hellige.

Dans un second temps, nous avons analysé plusieurs paramètres, selon les méthodes détaillées ci-dessous, dans un certain nombre d'échantillons afin de préciser dans les cas douteux ou délicats la nature exacte des horizons et par conséquent le rattachement des sols aux références.

La nomenclature des horizons et des sols a été faite selon le Référentiel pédologique français (AFES, 1995).

2.2. Analyses chimiques

Le pH des différents horizons a été mesuré avec un pH-mètre à électrode de type Metrohm, dans des suspensions avec l'eau désionisée (pH H_2O) et le chlorure de potassium (pH KCl), selon le rapport volumétrique 1:2,5. Ces valeurs ont été déterminées pour tous les horizons décrits.

Le dosage de la teneur en carbone organique et du taux de saturation a été établi dans certains horizons seulement. En effet, ces deux analyses vont nous permettre de discriminer le type d'horizon dans les cas se situant à la limite de deux catégories ou ne présentant pas de caractéristiques claires lors de la description in situ.

Le carbone organique a été déterminé par oxydation d'une solution acide de bichromate de potassium puis dosage de l'excès de bichromate par titration avec le sel de Mohr, en présence d'acide diphénylaminosulfonique de baryum. On estime la teneur en matière organique en multipliant la valeur ainsi obtenue par un facteur standard de 1,72.

Enfin, la capacité d'échange cationique a été effectuée selon la méthode dite « au pH du sol », avec échange par agitation dans le chlorure de potassium et le chlorure d'ammonium. Cette méthode est particulièrement recommandée lorsque l'on traite avec des sols acides, ce qui est le cas ici. Les teneurs en Ca^{2+}, Mg^{2+}, Na^+ et Al^{3+} sont déterminées dans l'extrait KCl tandis que K^+ est dosé dans NH_4Cl. Ces mesures ont été effectués au GEA de l'Université de Neuchâtel. L'acidité d'échange (teneur en ions H^+) est évaluée par titration d'un aliquote de l'extrait KCl avec NaOH 0,01M.

3. Résultats

Les descriptions de chaque sol font l'objet de fiches détaillées présentées. Les résultats globaux des analyses sont reportés en tableaux 1A-1C.

3.1. Les analyses chimiques

3.1.1. Le pH

Le pH H_2O nous renseigne quand à l'acidité active du sol, soit les ions H+ présents dans la solution de sol. Le pH KCl quand à lui provoque par échange cationique la désorption des ions H+ fixés sur le complexe argilo-humique du sol. Il fournit ainsi l'indication de l'acidité d'échange du sol. La différence des deux valeurs est nommée acidité potentielle. Celle-ci dépend essentiellement de la saturation du complexe argilo-humique. Ainsi, dans des sols saturés en calcaire, l'acidité potentielle est très faible (0,2 à 0,5 unités). Inversement, dans des sols acides, l'acidité de réserve est élevée et l'on observe des différences allant jusqu'à 2 entre pH H_2O et pH KCl (SOLTNER, 1992; GOBAT & al., 1998)

L'ensemble des sols étudiés (tabl. 1A-1C) frappe d'emblée par l'importance de l'acidité. En effet, le pH H_2O ne dépasse guère la valeur de 5, tous sites confondus. L'acidité d'échange du sol est élevée puisque le pH mesuré dans le chlorure de potassium oscille entre 2.93 et 4.30. Enfin, on note une forte acidité potentielle (ΔpH) qui se situe en général aux environs d'une unité et atteint des maxima de 2.16 à Belalp et 2.63 au Furka Pass. A cet égard, il semble que les roches présentes à Belalp et à la Furka soit particulièrement acides puisque c'est dans des horizons C que l'on atteint ces ΔpH particulièrement élevés. A Arpette, les valeurs obtenues signalent une roche-mère un peu moins acide.

Ce sont en général les niveaux supérieurs qui présentent les pH les plus faibles: 4,3 environ pour les horizons organo-minéraux (A ou AE) de BA-LE; 4,9 pour les horizons A d'Aletsch. Dans la profondeur, le pH augmente, atteignant jusqu'à 5,7 dans HT-1. Les pH mesurés dans le KCl (tabl. 1A-1C) confirment l'importance de l'acidité avec des valeurs situées entre 3,2 et 4,3.

L'acidité potentielle (tabl. 1A-1C) voisine avec la valeur de 1 dans les sols de Belalp-Lengi Egga et le premier sol d'Aletsch. Dans HT-2 par contre, l'acidité potentielle est beaucoup plus élevée puisqu'elle ne descend jamais sous la valeur de 1 et grimpe jusqu'à 1.77.

Si nous comparons les résultats, nous remarquons que les valeurs obtenues pour BA-LE5, BA-LE6 et BA-LE7 sont plus faibles que celles de BA-HO1 à BA-HO4 en ce qui concerne les pH H_2O et KCl. Par contre, les ΔpH présentent des gammes comparables. Ces différences de pH ne traduisent pas à notre avis un changement fondamental de pédogenèse entre les deux sites d'étude. Il s'agit plutôt de l'expression de l'influence des facteurs abiotiques et notamment climatologiques qui agissent directement sur le sol par le biais du régime hydrique et des températures et indirectement par leurs effets sur la croissance des plantes (apports de sécrétions racinaires et de litière, prélèvement de cations). La meilleure preuve en est le fait que les deux pH varient de la même façon et que l'acidité potentielle de ces sols demeure comparable à celle des sols décrits l'an dernier à Belalp.

Les sols d'Aletsch présentent quand à eux des valeurs de pH qui les rapprochent des sols du Furka Pass, avec des valeurs de pH H_2O un peu plus élevées qu'à Belalp (session 99) mais des ΔpH bien plus grands. Nous pensons qu'il pourrait s'agir de similitudes au niveau de la roche-mère des deux sites mais nous ne pouvons préciser cette hypothèse puisque nous ne disposons pas de données géologiques précises.

3.1.2. Teneur en carbone organique

Le carbone dans le sol est présent sous forme minérale (dans les carbonates par exemple) ou sous forme organique (litières végétales, humus, exsudats racinaire, etc…). Il est possible de déterminer la nature des couches pédologiques selon les proportions relatives de ces deux formes. Ainsi, les horizons organo-minéraux (A) contiennent une forte part de carbone organique tandis que des horizons plus profonds, à dominance minérale, en contiennent de faibles proportions. En outre, la mesure du carbone organique peut être à l'aide d'un simple indice étendue à l'estimation du taux de matière organique contenu dans l'échantillon.

L'évaluation de la teneur en carbone organique a été poursuivie dans les trois sols d'Arpette, mais pour des raisons qui diffèrent d'un cas à l'autre.

Pour Arpette-1, il s'agissait essentiellement de déterminer la nature véritable de l'horizon BPs2. En effet, la couleur foncée de celui-ci pourrait indiquer un niveau organique de type A ou un niveau d'accumulation de composés humifères (BPh) qui auraient été enfouis à la suite d'une phase de colluvionnement et seraient réintégrés dans le nouveau sol ainsi constitué. Au vu des résultats, nous abandonnons cette hypothèse puisqu'il est manifeste que le taux de carbone organique diminue fortement dans cet horizon par rapport aux précédents. En outre, le taux de matière organique (3 %) n'y est en rien comparable aux valeurs habituelles d'un horizon A (10 à 20 %) et est inférieur à la mesure effectuée dans les horizons BPh (5 %) et BPsBPh (6 %) du même profil.

Dans le cas du deuxième sol d'Arpette, le but essentiel résidait dans la caractérisation fine des diverses couches. Ainsi, la teneur relativement élevée de la strate 2-5 cm confirme la présence d'un horizon organo-minéral de type A. La teneur en matière organique diminue dans l'horizon suivant (5-10 cm). En accord avec le taux de saturation de celui-ci (cf § 3.1.3.) nous avons considéré cette couche comme un horizon structural aluminique (Sal). Enfin, nous avons procédé à l'analyse de la couche 30-40 cm ainsi que des poches noires qui y ont été décrites. Ces dernières sont effectivement enrichies en carbone organique par rapport à la matrice dans laquelle elles se situent. Il s'agit vraisemblablement de matériel déposé en profondeur sous l'effet du colluvionnement. Nous pensons qu'il s'agit d'un ancien horizon BPh, le taux de matière organique (4 %) étant trop faible pour un horizon organo-minéral A. Il semblerait donc qu'une activité podzolique ait existé à un moment donné dans ce site, dont on ne retrouve ici qu'une relique enfouie.

Enfin, pour le troisième sol d'Arpette, nous avions choisi de déterminer la teneur en carbone organique des horizons supérieurs (2-6/7 et 6/7-16 cm) afin de préciser l'attribution que nous pressentions du côté des RANKOSOLS. Cependant, ayant reçu une photographie du profil, il s'est avéré que notre hypothèse était erronée et que nous nous trouvions plutôt en présence d'un BRUNISOL (cf § 3.2.1.).

3.1.2. Teneur en carbone organique

Le carbone dans le sol est présent sous forme minérale (dans les carbonates par exemple) ou sous forme organique (litières végétales, humus, exsudats racinaire, etc…). Il est possible de déterminer la nature des couches pédologiques selon les proportions relatives de ces deux formes. Ainsi, les horizons organo-minéraux (A) contiennent une forte part de carbone organique tandis que des horizons plus profonds, à dominance minérale, en contiennent de faibles proportions. En outre, la mesure du carbone organique peut être, à l'aide d'un simple indice, étendue à l'estimation du taux de matière organique contenue dans l'échantillon.

Nous avons mesuré le taux de carbone organique dans les horizons BP de BA-6 (tabl. 2) afin de définir plus précisément le fonctionnement du sol. Il existait en effet un doute quand au premier horizon BP dont la couleur peu tranchée ne permettait pas une attribution sans équivoque à un niveau de précipitation de composés humiques (BPh). La couche suivante, quant à elle, présentait la coloration caractéristique des précipitations de fer (BPs, brun-orangé). Cette dernière nous a par conséquent servi de niveau de référence dans l'analyse. Les résultats démontrent que nous avons bel et bien une accumulation de matière organique dans la première couche BP, avec une teneur en carbone organique deux fois plus élevée que celle de BPs. Le qualificatif humifère (h) peut donc être attribué à cet horizon. Ce sol présente par ailleurs des teneurs en matière organique comparables aux horizons de même nature analysés durant la saison 1999, ce qui confirme notre hypothèse.

Dans le second sol d'Aletsch (HT-2), les mesures de matière organique ont été appliquées aux échantillons sis entre 2 et 30 centimètres afin de discriminer les différents horizons. En effet, la simple description des échantillons reçus et la détermination du pH n'étaient pas toujours suffisants pour définir avec sûreté une limite. Au vu des résultats (tabl. 2), 2 limites apparaissent manifestement à 10 et à 15 cm ainsi qu'une troisième, plus discrète, à 20 cm.

Les deux premières discontinuités, complétées des données morphologiques recueillies sur le terrain et à l'arrivée des échantillons, nous permettent de définir un horizon organo-minéral riche en matière organique (> 10 %) de 2 à 10 cm puis un horizon à caractère organique indéniable mais moins prononcé entre 10 et 15 cm. Les niveaux suivants présentent tous une teneur en matière organique inférieure à 5 %, ce qui exclut pour eux le caractère organique. Nous reviendrons plus en détails sur la nomenclature des horizons de HT-2 dans le § 3.2.2.

Nous notons également que le sol d'Aletsch présente des teneurs en carbone organique supérieures à celles que nous avons mesurées dans des horizons comparables au Val d'Arpette.

3.1.3. Taux de saturation

Nous avons choisi de déterminer le taux de saturation de certains horizons de manière à élucider s'ils étaient des horizons structuraux aluminiques, Sal. En effet, la double structuration de ces horizons, polyédrique subanguleuse et microgrumeleuse (AFES, 1995), n'apparaissait pas toujours de façon évidente sur le terrain, en raison de son développement insuffisant ou à cause de l'extrême sécheresse de certains profils. Nous avons donc eu recours aux critères analytiques proposés par le Référentiel pédologique (AFES, 1995), soit:

- 2 à 8 mé/100 g d'Al^{3+} extraits par KCl 1N;
- Al^{3+} représente 20 à 50 % de la capacité d'échange cationique (T);
- un rapport Al^{3+}/somme des bases échangeables (S) supérieur à 2;
- un taux de saturation (V) très faible, le plus souvent inférieur à 20 %.

Les résultats obtenus indiquent que l'ensemble des ces horizons présente une géochimie dominée par l'aluminium (AFES, 1995), caractère spécifique des ALOCRISOLS.

La forte acidité des profils d'Aletsch (les cations Al^{3+} contribuent à acidifier le sol), ainsi que l'observation d'une discrète structuration double dans le niveau 10-15 cm de HT-2 nous ont menés à vérifier l'importance de l'aluminium au sein du complexe d'échange de trois horizons (Sal de HT-1, 10 - 15 et 15 - 20 cm de HT-2).

Les résultats (tabl.3) prouvent que deux des horizons sont effectivement des horizons structuraux aluminiques. Il s'agit de l'échantillon de HT-1 ainsi que de la portion 10 – 15 cm de HT-2. Par contre, l'échantillon 15 – 20 cm de HT-2 ne remplit que deux des critères énumérés ci-dessus. Nous ne le considérerons donc pas comme un horizon aluminique mais comme un niveau de transition entre ASal et S2, horizon structural proprement dit (voir § 3.2.2.).

3.2. Description des sols

3.2.1. Val d'Arpette

AR1:PODZOSOL OCRIQUE colluvial, à dysmoder

Ce profil assez complexe présente une succession de couches nombreuses et peu épaisses, dont l'imbrication augmente au fur et à mesure que l'on descend dans le profil. Cependant, les caractères morphologiques (présence simultanée des horizons d'accumulation BPh et BPs; transition graduelle entre A et BP, dépôt d'acides organiques à la surface des pierres de l'horizon BPs2) et analytiques (pH faible, teneur en matière organique des horizons d'accumulation) permettent d'attribuer à ce sol la référence PODZOSOL OCRIQUE. Il est cependant manifeste que des phénomènes de colluvionnement sont intervenus lors de sa genèse, comme l'atteste la présence de « poches » dans les horizons C2 et ABPh. Ce colluvionnement est plus faible que ce que nous avons observé dans le sol numéro 2. L'humus est de type dysmoder, avec un horizon OH bien formé au dessus d'un A de juxtaposition.

AR2: ALOCRISOL TYPIQUE colluvial, brun, podzolisé

Les limites entre les horizons ont été fixées par comparaison des données morphologiques (obtenues *in situ* par Jean-Paul Teurillat et sur les échantillons frais par nos soins) et analytiques. Les limites ont été basées sur des discontinuités flagrantes d'un ou plusieurs paramètres tels que: couleur, squelette, pH, structure et texture. La comparaison ultérieure avec une photographie du profil nous a permis de confirmer notre choix dans la plupart des cas.

La présence, analytiquement prouvée, d'un horizon Sal nous conduit à attribuer ce sol à la référence ALOCRISOL TYPIQUE. La succession épaisse d'horizons C parsemés de poches de matériel plus organique constitue la preuve manifeste d'une forte activité colluviale. Ces poches présentent une teneur en carbone organique comparable à celles de l'horizon BPh du PODZOSOL OCRIQUE (AR1), mais inférieure à celle d'un horizon A typique. En outre, à l'instar de ce que nous avons décrit dans le PODZOSOL OCRIQUE, des poches noires apparaissent à la périphérie des blocs. Nous attribuons donc le qualificatif « podzolisé » au profil AR2, tout en étant conscient du fait qu'une vérification en amont serait nécessaire pour étayer l'occurrence de la podzolisation sur le site.

La description de la partie supérieure du solum n'était pas suffisamment détaillée pour nous permettre de déterminer la forme d'humus.

AR3: BRUNISOL OLIGOSATURE leptique, à mull

Ce sol présente une faible différenciation. Dans une première approche, alors que nous ne disposions que d'une description succincte et des échantillons, nous l'avions nommé RANKOSOL haplique, alpin. Cependant, ayant reçu une photographie du profil, il est apparu que le squelette de celui-ci ne correspondait pas à ce que l'on observe habituellement dans les RANKOSOLS. Reconsidérant nos données sous l'angle d'une évolution pédologique plus poussée, nous sommes parvenus à l'identification d'un horizon SC microstructuré, sis entre 6 et 16 centimètres de profondeur. Notre diagnostique s'oriente alors en direction des BRUNISOLS.

La phase analytique a malheureusement été établie sur la base de la première interprétation de ce solum. Ainsi, nous avions soumis les horizons A et SC au dosage du carbone organique afin de discriminer la nature du RANKOSOL présupposé. Dans le cadre de la nouvelle proposition nomenclaturale, nous serions appelés à déterminer le taux de saturation de l'horizon SC afin de préciser la référence. Néanmoins, la coloration de l'horizon SC, un brun tirant plutôt sur le gris, se démarque de la teinte plus brune-rousse caractéristique de l'horizon Sal de l'ALOCRISOL TYPIQUE (AR2). De plus, la strate située entre 6 et 7 cm présente une structuration pédologique généralisée, même si celle-ci est faiblement développée (micropolyèdres). Ces caractères étayent l'attribution de ce sol à la catégorie des BRUNISOLS. En outre, il existe une assez bonne corrélation entre les valeurs du taux de saturation V et le pH mesuré dans les divers horizons. Ainsi, un sol brunifié présentant une valeur de 4.57 pour le pH H_2O de son horizon A est un BRUNISOLS OLIGOSATURE (GOBAT & HAVLICEK, 1996). Le qualificatif « leptique » indique que la profondeur cumulée des horizons A et S ne dépasse pas la valeur de 40 cm.

Enfin, la description de la couche supérieure n'était pas suffisante pour pouvoir nommer la forme d'humus. Cependant, l'examen de la photographie ne révèle pas de trace d'un horizon holorganique de type OH mais il se pourrait qu'un discret horizon OF se soit tout de même développé. Nous pensons être en présence d'une forme de mull sans qu'il ne nous soit possible de préciser plus avant cette dénomination.

3.2.2. Belalp-Hofathorn

BA-HO1: PODZOSOL MEUBLE à eumoder

Nous sommes en présence d'une séquence de type E/BPs avec une transition progressive de la zone éluviale (E) à la zone illuviale (BPs). Le sol est donc clairement un PODZOSOL MEUBLE. L'humus est de type eumoder, avec des niveaux OF clairement établis et un horizon OH peu développé.

La proportion de cailloux augmente vers le bas du profil, de même que leur taille et leur degré d'altération. Les valeurs de pH se situent aux environs de 5 dans l'eau et entre 3 et 4 dans le KCl. L'acidité potentielle (ΔpH) est élevée sur l'ensemble du profil (>1), et plus particulièrement dans la zone d'illuviation.

BE-HO2: PODZOSOL OCRIQUE à hémimoder

Il est relativement difficile de placer des limites dans ce sol, en raison d'une faible différentiation au niveau des couleurs et d'une homogénéité générale. Cependant, la présence des horizons d'accumulation BP ainsi que la relative décoloration des horizons supérieurs sont suffisamment avérés pour qu'il soit attribué à la référence PODZOSOL OCRIQUE. L'humus est un hémimoder, avec deux horizons OF mais pas d'horizon OH, sur un A de juxtaposition.

Les valeurs de pH se situent toutes sous la valeur de 5 et sont inférieures à celles du PODZOSOL MEUBLE (Belalp-1). Il en va de même pour les valeurs de pH dans le KCl. L'acidité potentielle est toujours élevée (>1), avec des valeurs comparables à celles du PODZOSOL MEUBLE (BA-HO1).

BA-HO3: ALOCRISOL TYPIQUE brun, à hémimoder

Les deux parties décrites peuvent être attribuées à la référence des ALOCRISOLS TYPIQUES, en raison de l'apparition d'horizons structuraux caractéristiques (Sal), dont la présence est avéré par les analyses (pH et taux de saturation). Les humus sont dans chaque cas de type hémimoder quoique les débris végétaux n'y apparaissent pas de façon évidente et qu'ils contiennent une forte proportion de boulettes fécales.

Les valeurs de pH dans l'eau se situent entre 4.5 et 5.2. Elles sont tout à fait comparables à celles que l'on trouve dans les autres sols décrits à Belalp. Les résultats obtenus dans le KCl sont légèrement plus faibles dans la partie gauche que dans la partie droite du profil. Nous y voyons le reflet de ce qui nous avait poussé, sur le terrain, à décrire séparément les deux parties de la fosse, soit une évolution légèrement plus poussée à gauche qu'à droite.

BA-HO4: ALOCRISOL TYPIQUE brun, podzolisé, à eumoder

Ce sol présente les caractéristiques évidentes de l'ALOCRISOL TYPIQUE, avec un niveau Sal clairement mis en évidence par sa double structure et une géochimie nettement dominée pas l'aluminium en SalC. La tendance à l'éluviation détectée dans l'horizon A(E) est à l'origine du qualificatif « podzolisé » ajouté à la référence. En effet, ce phénomène, quoique discret, nous semble important à signaler, d'autant plus qu'il s'accompagne d'une augmentation de l'acidité (pH KCl diminue et ΔpH augmente). L'humus est de type eumoder, avec un niveau OF suivi d'une zone présentant des poches enrichies en boulettes fécales, trop discontinues pour former un véritable horizon OH.

Ce sol est étonnamment profond (50 cm) compte tenu de son altitude (2'830 m). Nous pensons qu'il s'agit d'un effet de la topographie. Nous nous trouvons en effet sur une forte pente (20°), juste sous la crête. Conséquence de cette accumulation de matière, ce sol présente moins de squelette que l'ALOCRISOL situé à 2600 m (Belalp-3). En profondeur, les langues de gneiss n'apparaissent que dans la partie droite de la fosse. Elles forment une zone de gros blocs gris peu altérés (R), friables en surface mais plus cohérents que les pierres grises trouvées sur la gauche du profil (C). La répartition des racines dans le profil est plus homogène à droite qu'à gauche, avec toutefois une concentration plus élevée en SalC. On trouve des racines jusque dans les interstices des langues de gneiss décrites précédemment.

3.2.3. Furka Pass

FK1: PODZOSOL MEUBLE à mor

Ce sol est un PODZOSOL MEUBLE, bien caractérisé par la présence d'horizons d'éluviation (E) et d'illuviation (BP) aux colorations nettement distinctes. L'humus est un mor, avec un horizon OH de plus d'un centimètre d'épaisseur en transition nette sur un horizon AE de juxtaposition.

Les valeurs de pH sont faibles dans l'eau (pH < 5.0 sauf dans l'horizon C) ainsi que dans le KCl (pH < 4.0 sauf dans l'horizon C). L'acidité potentielle (ΔpH) est élevée (> 1) dans l'humus et dans la partie éluviale du profil. Elle a tendance à diminuer (<1) à partir de 17 centimètres environ, dans la zone d'illuviation. La valeur de l'horizon C nous permet d'évaluer l'acidité potentielle de la roche-mère. Celle-ci se situe aux alentours de 1, signalant une roche acide, probablement riche en aluminium.

FK2: ALOCRISOL TYPIQUE brun, à mésomull, de gneiss altéré

Nous sommes en présence d'un ALOCRISOL TYPIQUE, caractérisé tant par sa morphologie (structure et couleur de l'horizon Sal1) que par sa géochimie (taux de saturation de l'horizon Sal2 et pH du profil). Les traces d'un horizon OLv ou OF relevées lors de la description nous enjoignent à penser que nous sommes en présence d'un mésomull et non d'un mull véritable.

Dans ce sol, moins évolué que le PODZOSOL MEUBLE (FK1), la roche est présente à 30 cm déjà mais elle est très peu cohérente et se délite facilement en plaques, ce qui nous a permis de creuser jusqu'à une profondeur de 50 centimètres.

Les valeurs de pH sont faibles, avec une légère augmentation dans les horizons profonds, en raison de la proximité de la roche-mère. L'acidité potentielle est élevée, en particulier dans l'horizon Sal1 où les dérivés minéraux de l'aluminium dominent. La valeur obtenue dans l'horizon C concorde avec celle que nous trouvions dans le même type d'horizon dans le PODZOSOL MEUBLE (FK1).

FK3: ALOCRISOL TYPIQUE brun, à eumull, de gneiss altéré

Nous sommes en présence d'un autre ALOCRISOL TYPIQUE. Quoiqu'il ne présente pas de façon évidente la double structuration des horizons Sal, ses caractéristiques analytiques ne laissent pas planer de doute quand à la nature des processus géochimiques qui s'y déroulent. L'humus est de type eumull; il est presque inexistant.

Cette fosse profonde (85 cm) présente 2 aspects successifs:

- 0-30 cm: sol proprement dit.
- 30-85 cm (et probablement plus): roche en place, totalement altérée et dans laquelle on trouve encore des racines.

Entre 35 et 40 cm, ainsi qu'à environ 50 cm, on observe de gros blocs de roche plus stables, avec probablement une forte teneur en quartz (allure plus "cristalline" et roche plus ou moins transparente). Le reste de la roche corrodée est formé de grandes plaques de gneiss avec une forte teneur en mica (brille beaucoup). On y reconnaît la structure de la roche mais celle-ci s'effrite dans la main sitôt qu'on la touche. Il s'agit d'un phénomène assez étonnant car l'aspect est celui d'une roche saine alors qu'elle est totalement corrodée.

Les valeurs de pH dans l'eau sont relativement faibles pour la partie « sol » proprement dite (0 à 28 cm). Elles augmentent dans l'altérite. Le pH KCl suit à peu près la même évolution, à l'exception d'une chute brutale dans l'horizon C3. C'est dans cette zone également que l'on obtient une valeur énorme pour l'acidité potentielle (> 2.5). Ces brusques changements confirment la discrimination des niveaux C2 et C3. Nous nous trouvons en présence d'une roche très acide constituée de minéraux à forte teneur en aluminium, ce qui a conditionné l'ensemble de la pédogenèse pour aboutir à la formation d'un ALOCRISOL.

3.2.4. Belalp-Langi Egga

BA-LE 5: PODZOSOL MEUBLE peu évolué, à dysmoder et hémimoder discontinus

Les PODZOSOLS MEUBLES présentent en général une séquence diagnostique E/BP que nous ne retrouvons pas ici. Cependant, d'autres critères morphologiques excluent l'attribution à la référence des PODZOSOLS OCRIQUES: les transitions entre les couches sont nettes à partir de 8 cm, les couleurs sont bien marquées et l'on observe la présence d'un horizon BPh bien développé. En outre, la comparaison de ce sol avec le PODZOSOL OCRIQUE décrit à la même altitude (BA-2), nous pousse à considérer BA-5 comme plus évolué en direction du véritable PODZOSOL MEUBLE. Nous attribuons donc le qualificatif «peu évolué» à ce solum, de façon à mettre en évidence le fait qu'il ne s'agisse pas d'un PODZOSOL MEUBLE véritablement typique.

L'humus est peu épais mais présente deux morphologies différentes, réparties en fonction de la présence de tourradons de graminées. Nous observons en effet un dysmoder sous les touffes et un hémimoder entre ces mêmes touffes. La litière des graminées restant préférentiellement liée au touradon, elle est difficilement accessible pour les décomposeurs, ce qui augmente son temps de décomposition et conduit à des accumulations de matière organique humifiée dans les horizons OF, OH et OHA.

BA-LE 6: PODZOSOL MEUBLE à hémimoder

Ce solum présente un horizon éluvial qui, quoique encore teinté de matière organique (nuance brune), est plus développé que dans le sol précédent. La détermination des niveaux d'accumulation podzolique s'est faite sur une base morphologique qui a été vérifiée par l'analyse des teneurs en carbone organique (tabl. 2). Ainsi, trois horizons BP sont distingués: BPh, enrichi en matière organique; BPs avec une teinte orangée caractéristique et peu de squelette (5 à 10 %); BPsC qui représente une zone de transition avec encore des traces de précipitation du fer (taches rouilles) et déjà un squelette très présent (30 %).

L'horizon OH est présent en mélange avec OF mais de manière continue, sis sur un horizon organo-minéral (A) de juxtaposition. Nous sommes en présence d'une forme de transition entre un hémimoder (absence d'horizon OH) et un eumoder (horizon OH individualisé). La faible épaisseur de l'horizon OFOH nous rapproche cependant plus de la première forme que de la seconde.

BE-LA 7: PODZOSOL MEUBLE à dysmull, superposé aux résidus d'une ancienne pédogenèse

Ce sol est indiscutablement un PODZOSOL MEUBLE, avec une zone éluviale morphologiquement (horizon Eh gris légèrement teinté de brun, tirant sur le blanc) et analytiquement (pH bas avec discontinuité entre A/Eh et BPh) bien marquée.

L'humus est un mull puisque l'horizon A est grumeleux. Il est de type hybride entre le dysmull et l'amphimull. En effet, si nous observons un horizon OH, celui-ci n'est pas très développé (horizon mixte OFOH très peu épais) (dysmull) mais continu (amphimull). A l'instar du sol précédent, la faible épaisseur de l'horizon mixte nous incite à favoriser la forme d'humus la plus active, à savoir le dysmull. Les mulls sont caractéristiques d'une bonne activité biologique, ralentie ici en raison des conditions climatiques, d'où un fonctionnement moins performant et l'apparition de la couche OFOH.

Nous observons une discontinuité à la base du solum. En effet, la présence de nombreuses taches de couleurs très variables (noir, brun, ocre, rouille) dans l'horizon IIC nous amène à penser qu'il s'agit en fait de résidus d'une ancienne pédogenèse qui auraient été mal décapés et sur lesquels un dépôt aurait permis l'établissement du sol actuel. Les discontinuités au niveau du squelette confirment notre hypothèse. Si la couche BPsC présente quelques cailloux très altérés, IIC n'a pas de squelette tandis que la roche sous jacente est compacte et seulement légèrement altérée. Les résidus de IIC représentent apparemment le mélange d'horizons organique (poche noire à droite du profil), riche en sesquioxydes (zone ocre-rouille), voire même engorgé puisqu'il nous semble avoir aperçu des taches gris-bleuté lors du rafraîchissement du profil, dans une pellicule argileuse qui recouvrait la poche noire. La présence ici d'un sol influencé par l'eau n'est pas à exclure tout à fait puisque nous nous trouvons en surplomb d'une zone marécageuse, avec un ru apparent au bas de la pente. Ne connaissant pas l'évolution géomorphologique de ce site, nous ne pouvons aller plus loin dans les raisons de la disparition du sol précédent et l'établissement de celui-ci (décapage glaciaire, glissement de terrain, accident géologique ?). De plus, l'imbrication des résidus et leur diversité ne nous permettent ni de savoir ce qui s'est produit, ni d'attribuer un nom au précédent sol.

3.2.5. Aletsch (Hindererhinertüre)

HT 1: ALOCRISOL TYPIQUE brun, à eumoder sporadique

L'horizon Sal de cet ALOCRISOL ne présente pas la double structure caractéristique des horizons aluminiques, mais il répond aux critères analytiques (tabl. 3) mentionnés par le Référentiel pédologique (AFES, 1998).

L'humus est de type eumoder sous les touffes de graminées, là où la transformation des litières est lente et peu efficace. Lorsque OH disparaît, la végétation repose directement sur un horizon A microgrumeleux, ce qui dénote d'une activité biologique efficace mais ralentie.

HT 2: ALOCRISOL TYPIQUE sur BRUNISOL OLIGOSATURE tronqué

La séquence des horizons de ce solum a été reconstituée après un échantillonnage systématique (tous les 5 centimètres) et subjectif (récolte séparée des discontinuités telles que les poches de couleur différente).

Une limite assez nette se marque entre 15 et 20 centimètres, avec une remontée du pH H_2O (passage de 4.9 à 5.2) et une nette diminution du taux de matière organique (passsage d'une moyenne de 5 % à moins de 2 %). La transition semble se faire entre les 15 premiers centimètres et le bas du profil sur une épaisseur de 5 centimètres, au sein d'un horizon de transition (S1) qui présente des valeurs intermédiaires de pH (5.0 dans l'eau) et de matière organique (2.34 %). Le caractère mixte de cette couche (15 à 20 cm) peut-être remarqué également au niveau de la dynamique de l'aluminium. En effet, cet horizon présente un critère d'horizon structural aluminique (taux de saturation, $V < 20$ %) mais se trouve à la limite des tolérances ($Al^{3+} / S = 2$, pH = 5.0) ou ne correspond pas aux autres critères ($Al^{3+} < 2$ méq/100g, Al^{3+} ne représente que 15 % de la capacité d'échange cationique (T), la structure de l'horizon est polyédrique instable).

Nous proposons donc une détermination hybride pour ce sol. La partie supérieure (0 à 15 cm) dénote d'un ALOCRISOL TYPIQUE avec une double stucturation discrète entre 10 et 15 centimètres, zone qui correspond également analytiquement (tabl. 3) à un horizon aluminique riche en matière organique (ASal). La partie inférieure (dès 20 cm), avec son horizon brun à structure polyédrique (S2), se rapproche plutôt d'un sol brun dont les pH H_2O sont relativement faibles (< 5,5), soit un BRUNISOL OLIGOSATURE. L'horizon S1 (15 à 20 cm) représente le niveau de transition entre les deux parties du solum.

Ce profil présente également deux singularités, à savoir deux poches noires étagées entre 12 et 18 centimètres, soit dans ou à proximité de la couche de transition S1. La première, assez discrète et en mélange avec des zones brunes, contient une grande quantité de charbons de 1 à 3 mm de long. La seconde, plus homogène et très organique, contient des charbons en plus faible quantité mais encore plus gros (jusqu'à 10 mm) et présente une structure vague à tendance grumeleuse.

Au vu des différents éléments énoncés, nous formulons l'hypothèse suivante quand à la formation de ce sol:

Il y a eu une époque où le solum était un BRUNISOL. Sa végétation sera plus aisément déterminée par l'analyse détaillée des charbons mais nous constatons que les gros spécimens présentent une structure qui rappelle celle du bois, d'où la présomption d'une végétation de type arbustif ou buissonnant. A un moment donné, cette végétation a brûlé et les cendres et charbons se sont déposés sur les horizons organo-minéraux A, dont la structure était probablement grumeleuse (comme l'atteste la poche dénommée b dans la fiche descriptive de l'annexe 1). La couverture végétale ayant été détruite, le sol est devenu plus sensible à l'érosion. Des phénomènes climatiques tels que de violents orages ou la fonte de neiges abondantes ont entraîné des glissements de terrain (solifluxion) et le BRUNISOL originel à été partiellement décapé (pas d'horizon A enfoui dans le profil à part la relique de la poche b) puis recouvert par un nouveau matériel (épaisseur d'environ 15 à 20 cm, avec une zone mélangée aux restes de l'ancienne pédogenèse à la base du dépôt) dont l'évolution pédologique s'est faite en fonction de conditions climatiques nouvelles ayant mené à l'établissement d'une végétation de type pelouse (végétation actuelle). Ainsi, le sol actuel (ALOCRISOL) est de nature plus acide que le BRUNISOL, ce qui conduit à la libération des ions Al^{3+} dont activité devient prépondérante au sein du solum.

4. Discussion

4.1. Val d'Arpette

La séquence des sols observés à Arpette correspond à la typologie établie par FIERZ & GOBAT (1996), à savoir la décroissance de la podzolisation avec l'altitude (fig. 1). Ces auteurs situent le maximum de la podzolisation dans la tranche d'altitude de 1'850 à 2'200 mètres. L'activité podzolique ralentit avec l'augmentation de l'altitude, en raison principalement d'une végétation moins acidifiante (les pessières, pinèdes ou landes à Rhododendron sont remplacées par des pelouses) et d'un enneigement plus court au printemps (FIERZ & GOBAT, 1996).

Les sols étudiés dans le présent contexte se situent au-dessus de la limite des investigations menées par FIERZ & GOBAT (1996). Cependant, ils ont été choisis pour leur position topographique particulière, soit dans des croupes permettant des accumulations de matériel pédologique. Ainsi, les effets de l'altitude sont atténués par la profondeur accrue des profils. Nous retrouvons ainsi la séquence qu'observaient FIERZ & GOBAT (1996) à l'extrémité supérieure de leur transect (2'430 à 2'445 m) mais s'étendant dans notre cas de 2'470 à 2'720 m.

La décroissance des phénomènes podzoliques apparaît de façon évidente puisqu'au PODZOSOL OCRIQUE, dans lequel en profondeur des dépôts d'acides organiques à la surface des blocs témoignent d'une podzolisation assez intense (FIERZ & GOBAT, 1996), succède un ALOCRISOL TYPIQUE parsemé de poches brunes enrichies en matière organique. Le BRUNISOL OLIGOSATURE, par contre, ne présente apparemment plus aucun signe de podzolisation.

Malgré les situation privilégiées dans lesquelles ces sols ont été mis à jour, l'activité colluviale, élément primordial de la pédogenèse à Arpette, est manifeste. Elle se note par l'imbrication des horizons et la présence au sein de ceux-ci de poches de matériaux divers. Dans l'ALOCRISOL TYPIQUE, la succession impressionnante des horizons C témoigne de l'intensité pouvant être atteinte par ce phénomène. Le BRUNISOL OLIGOSATURE est plus homogène et semble moins touché par l'activité colluviale que les sols précédents. Ceci peut être dû à son épaisseur plus faible ou à une position proche de la crête.

4.2. Belalp-Hofathorn

Selon la typologie établie par FIERZ & GOBAT (1996) sur le transect de Belalp (fig.1), les sols les moins podzolisés se situent aux extrémités altitudinales de celui-ci. Nos propres investigations permettent de rajouter une section au transect, en position terminale. La tendance à la diminution de l'activité podzolique est ainsi confirmée puisque des ALOCRISOLS succèdent aux PODZOSOLS. Nos sols s'arrangent logiquement du point de vue de l'évolution pédologique: PODZOSOL MEUBLE à 2'370 m, dans la zone définie comme siège privilégié de la podzolisation, puis PODZOSOL OCRIQUE à 2'550 m et enfin ALOCRISOLS TYPIQUES bruns à 2'684 et 2'830 m.

Les facteurs qui influencent ensuite la pédogenèse ne sont ni le matériel parental (ces sols étant tous issus d'orthogneiss très acide et probablement riche en aluminium) ni la végétation (tous sont recouverts par des pelouses acidophiles). Leur évolution pédologique dépendra avant tout de la profondeur des solums et de l'activité biologique (épisolum humifère). En effet, c'est le sol le plus profond (BA-HO1) qui présente le degré d'évolution le plus avancé (PODZOSOL MEUBLE). En outre, nous avons déjà signalé ci-dessus que l'ALOCRISOL le plus profond (BA-HO4) présentait des traces d'éluviation que nous ne retrouvons pas dans son corollaire moins épais (BA-HO3). Les humus décrits à Belalp sont tous des formes de moder. Ce type d'épisolum humifère indique une faible insolubilisation des composés organiques solubles, ce qui constitue l'un des déclencheurs de la podzolisation (AFES, 1995). Les formes décrites sont des hémimoders ou des eumoders. Si elles présentent le même mode de fonctionnement biologique, l'hémimoder est cependant moins évolué que l'eumoder dans lequel, même s'il est parfois discontinu, un véritable horizon OH commence à se former. En effet, la forme plus évoluée de l'eumoder est présente dans BA-HO4 (ALOCRISOL TYPIQUE podzolisé) tandis qu'on trouve un hémimoder dans l'ALOCRISOL TYPIQUE qui ne porte pas de traces de podzolisation (Belalp-3).

Belalp représente une station d'étude privilégiée des Alpes cristallines en ce qui concerne les sols (FIERZ & GOBAT, 1996). En effet, ceux-ci ne sont pas perturbés par des phénomènes externes tels que le colluvionnement (élément important de la pédogenèse à Arpette) et présentent des fonctionnement classiques traduits par une morphologie nette.

4.3. Furka Pass

L'altitude joue indubitablement un rôle dans la distribution des sols étudiés au Furka Pass (fig.1). En effet, aux altitudes élevées correspondent les sols les moins évolués (ALOCRISOLS TYPIQUES). La pédogenèse est ensuite influencée par la profondeur des profils, directement inféodée à la topographie. Ainsi, dans le sol situé en bas de pente (FK1) le dépôt de matériel fin qui recouvre la roche est plus épais (> 40 cm) que dans le sol situé sur replat (FK2: 30 cm) ou en pente (FK3: 28 cm).

Les valeurs de pH enregistrées dans les horizons les plus minéraux signalent une roche acide et riche en aluminium. Celle-ci conditionne le développement des sols. Ainsi, les sols rencontrés s'apparentent aux ALOCRISOLS ou aux PODZOSOLS, deux références dont la genèse est fortement dominée par les effets de l'acidité. La dégradation poussée de la roche dans les ALOCRISOLS de cette station est un phénomène intéressant. Dans le PODZOSOL MEUBLE, la roche apparaît sous forme de plaques cohérentes recouvertes d'une fine pellicule d'altération. Dans l'ALOCRISOL situé à 2'646 m. (FK2), la roche se délite facilement selon les plans de clivage en plaquettes cassantes. Enfin, dans la station la plus élevée (FK3), le gneiss est entièrement démembré, quoiqu'il présente un aspect de roche saine. Selon toute vraisemblance, l'état de dégradation de la roche est dépendant lui-aussi de l'altitude, ainsi que de l'épaisseur de la terre fine qui la recouvre.

L'activité biologique est également placée sous l'influence altitudinale. L'ALOCRISOL TYPIQUE à eumull (Furka-3), situé sous une crête, en situation non protégée par rapport à la placette FK-2, présente une productivité végétale moindre (pelouse rase, peu de litière). L'extension des racines jusqu'à une profondeur élevée (jusqu'à 70-80 cm pour FK-3) en témoigne. Les plantes sont en effet contraintes d'exploiter des volumes énormes de terre afin de récolter les éléments nutritifs nécessaires au maintien de leur minime production. Lorsque les conditions écologiques se font moins drastiques (accumulation de terre fine plus importante, protection par rapport aux vents, etc…), on ne trouve plus de traces de racines dans le substrat (FK1 où les racines n'exploitent pas l'horizon C).

L'absence de typologie sur le site ne nous permet pas de déterminer si les sols étudiés sont représentatifs des tranches altitudinales étudiées. Néanmoins, leur succession pédogénétique « logique » ainsi que leur cohérence par rapport à la végétation tend à corroborer cette assertion.

4.4. Belalp-Lengi Egga

Les sols décrits à Belalp au cours de l'été 1999 se placent de façon cohérente dans la succession altitudinal décrite sur la base des données de BA-HO et de FIERZ & GOBAT (1996). Les deux PODZOSOLS MEUBLES typiques se situent dans ou au voisinage de la zone présentant un maximum d'activité podzolique (2'000 à 2'400 m), tandis que le PODZOSOL MEUBLE peu évolué (BA-5) se trouve dans une tranche attribuée à des solums moins podzolisés, à savoir les PODZOSOLS OCRIQUES.

Le léger décalage altitudinal constaté est vraisemblblement dû à une exposition un peu différente (E-SE ou S tandis que les sols BA-1 à 4 étaient plutôt exposés à l'E, voire E-NE) ainsi qu'à une topographie plus douce.

4.5. Aletsch

Les sols de la station située au-dessus du glacier d'Aletsch sont beaucoup moins évolués que leurs corrolaires altitudinaux des autres sites (fig. 1).

En effet, à 2'403 m déjà (HT-1), nous nous trouvons en présence d'un ALOCRISOL TYPIQUE. A cette altitude, nous trouvons à Belalp (BA-LE6) de même qu'au Furka Pass (Furka-1) DES PODZOSOLS MEUBLES, tandis qu'au Val d'Arpette nous nous situons dans le domaine des PODZOSOLS OCRIQUES.

Le sol sis à 2'618 m (HT-2) se situe quand à lui dans une zone altitudinale ocupée dans tous les sites par des ALOCRISOLS TYPIQUES. Cependant, il montre que par le passé, son comportement était celui d'un BRUNISOL OLIGOSATURE, soit un sol encore moins évolué, que nous n'avons décrit qu'à Arpette, à une altitude de 2'720 m.

Il est probable que des conditions climatiques particulières régissent la station d'Aletsch. En effet, la présence voisine du glacier doit générer un microclimat à température annuelle moyenne inférieure à celle des trois autres sites. Il serait intéressant à ce niveau de connaître la pluviométrie de l'endroit ainsi que de savoir si la neige parvient à s'accumuler fortement ou non. De plus, l'activité érosive de même que les mouvements de terrain sont favorisés par les fortes pentes.

Preuve en est donnée par l'étude du solum HT-2. Nous avons pu mettre en évidence (§ 3.2.2.) le dépôt d'un nouveau matériel sur un ancien sol décapé (ALOCRISOL TYPIQUE <u>sur</u> BRUNISOL OLIGOSATURE). Détail d'autant plus intéressant dans le cadre de la présente étude, la présence de charbons en forte concentration dans le sol laisse à penser qu'autrefois se tenait ici sinon une forêt du moins une végétation buissonnante.

5. Conclusion

Le facteur qui domine l'étagement des sols étudiés, sur l'ensemble des sites, est indubitablement l'altitude. Une frontière se dessine en effet communément aux trois stations (fig.1) aux environs de 2'500 m avec une forte podzolisation en-dessous (PODZOSOLS MEUBLES et OCRIQUES) et une podzolisation atténuée (ALOCRISOLS) voire absente (BRUNISOL) au-delà de cette limite.

L'épaisseur de matériel fin déposé sur la roche est le second paramètre déterminant de la répartition des sols. Ce caractère explique les raisons du décalage de nos séquences pédogénétiques par rapport à celles signalées par FIERZ & GOBAT (1996), principalement à Arpette. En effet, les sites d'étude retenus dans le présent contexte sont disposés topographiquement dans des zones d'accumulation (replats, croupes, ruptures de pente), modifiant de fait les conditions initiales de genèse.

Enfin, les séquences verticales d'horizons ne subissent pas de phénomènes de réarrangements périodiques à Belalp, ni au Furka Pass. A contrario, les solums du Val d'Arpette sont soumis à des phases de colluvionnement dont l'intensité diffère d'un site à l'autre, manifestement en relation avec les dispositions topographiques des diverses placettes.

La répartition conforme des sols sur les trois sites étudiés devrait constituer une base suffisante à la comparaisons ultérieures des données récoltées. Il s'agira toutefois de ne pas considérer le Val d'Arpette comme modèle puisqu'il représente la station la moins stable pédologiquement.

L'important rôle de l'altitude dans la zonation des sols est confirmé mais il sera nécessaire également de tenir compte de facteurs climatiques, en particulier l'exposition et l'abondance des neiges. La limite de la podzolisation est confirmée. En effet, à une exception près (HT-1), la figure 1 montre nettement un clivage entre les PODZOLS et le groupe des ALOCRISOLS/BRUNISOLS. Ainsi, dans le contexte de l'étude (sols sous pelouses acidophiles dans des stations choisies pour leurs particularités géomorphologiques, et notamment leur potentiel caractère de sites d'accumulation), nous posons une limite aux environs de 2'550 m entre une zone de forte (PODZOSOLS MEUBLES) à moyenne (PODZOSOLS OCRIQUES) podzolisation et un secteur à podzolisation faible (ALOCRISOLS) voire nulle (BRUNISOLS).

Nous réitérons nos remarques quand à la base de comparaison des quatre sites. Il s'agira cependant de se montrer circonspect en ce qui concerne les stations du Val d'Arpette et du glacier d'Aletsch. En effet, ces deux stations présentent des phénomènes de mouvements de terrain qui peuvent mener à une perturbation de l'arrangement des sols (colluvionnement à Arpette, solifluxion à Aletsch). En outre, si l'on considère Belalp et le Furka Pass comme référence au niveau pédologique, on remarque que la succession des sols à Arpette, et plus manifestement à Aletsch, présente un décalage vers les altitudes inférieures des sols les moins podzolisés (fig. 1).

La relative instabilité des sols d'Arpette et d'Aletsch est cependant riche en informations concernant le passé. En effet, les brusques phénomènes d'enfouissement permettent de court-circuiter l'évolution naturelle des matières organiques et de préserver en profondeur des couches témoins d'événements anciens, à l'instar des poches à charbons décrites dans le profil HT-2.

6. Bibliographie

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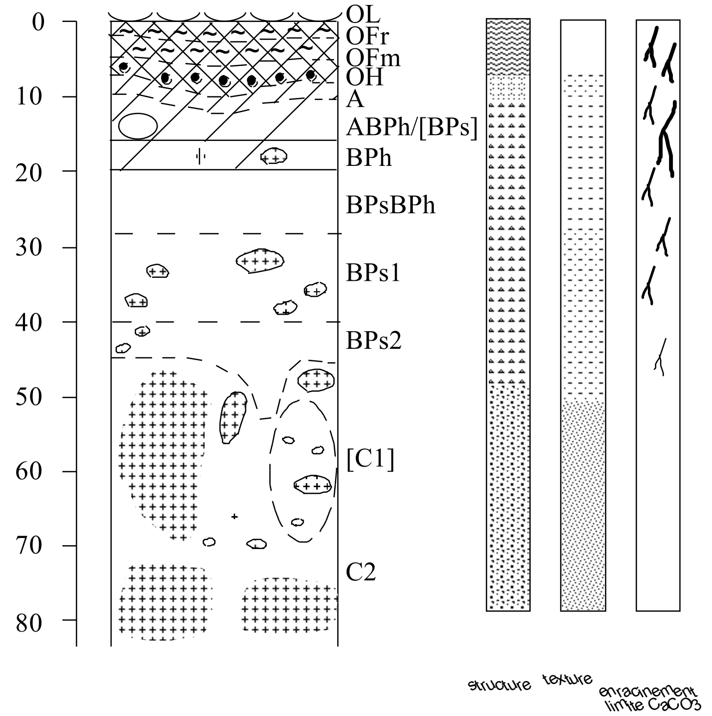
ARPETTE 1 (AR1)	PODZOSOL OCRIQUE colluvial, à dysmoder	
Date: 18.8.98	**Coordonnées:** 571.725/ 97.513	**CN n°:** 1345
Altitude: 2470 m	**Pente:** env. 100 %	**Exposition:** S
Géologie: moraine acide		
Végétation: pelouse acidophile à Festuca varia		
Topographie: petite croupe à fleur de pente		
Météo: nuageux + orage et pluie		



OL: +3 - 0 cm couleur: gris. Dense accumulation de feuilles et de gaines de graminées. A la base, passage progressif à une matrice plus décomposée et plus imbriquée. Limite horizontale, transition diffuse.

OFr: 0 - 3 cm couleur: brun-gris. Paquets de matière végétale avec grains de quartz et déjections holorganiques. Pas de mycélium apparent. Forte odeur de décomposition. Feuilles et restes de gaines encore identifiables. Limite ondulée, transition diffuse.

OFm: 3 - 5/6 cm couleur: brun-noir. Juxtaposition grains de quartz, boulettes fécales et fragments foliaires. Structure lâche donnée par racines (5/5, fines et moyennes). Présence de microfaune. Couche sporadiquement amincie. Limite ondulée, transition diffuse.

OH: 5/6 - 7/10 cm couleur: noir. Forte présence de boulettes fécales (>70 %). Débris végétaux inidentifiables. Structure lâche fournie par racines (5/5, fines) en réseau. Squelette (<5%): graviers angulaires de quartz (ø 1 mm) et plaquettes de mica. Limite ondulée, transition diffuse.

A: 7/10 - 10/12 cm couleur: brun-noir. Structure microgrumeleuse puis particulaire, cohérence surtout assurée par les racines. Texture limono-sableuse. Porosité moyenne à forte. Racines 3/5, fines et moyennes. Squelette (5%): graviers ø 1 à 4 mm. Limite ondulée, transition diffuse.

ABPh: 10/12 - 16 cm couleur: brun-roux-chocolat. Structure vaguement micropolyédrique, ess. particulaire, très peu d'aggrégation, superposition de grains de quartz et de terre fine. Texture limoneuse à limono-sableuse. Porosité moyenne. Racines 2/5 fines. Squelette (5%): graviers ø 1 à 10 mm. Limite horizontale, transition nette.

[BPs]: 12 - 16 cm poche plus jaunâtre à gauche dans ABPh. Structure micropolyédrique puis particulaire. Texture limoneuse à limono-sableuse. Porosité moyenne à forte. Racines 3/5, fines, moyennes et une grosse. Squelette (5%): graviers ø 1 à 6 mm. Limite ondulée, transition ± nette.

BPh: 16 - 20 cm couleur: brun-jaune. Niveau principal d'enracinement. Structure polyédrique puis particulaire. Texture limoneuse. Porosité moyenne. Racines 5/5, fines et moyennes. Squelette (10%): graviers ø 1 à 100 mm. Limite horizontale, transition nette.

BPsBPh: 20 - 28 cm couleur: brun-roux avec poches à tendance jaune-orangé. Structure polyédrique puis particulaire. Texture limoneuse (traces de sables). Porosité moyenne. Racines 4/5, fines et moyennes. Squelette (5%): graviers ø 1 à 10 mm. Limite horizontale, transition diffuse.

BPs1: 28 - 40 cm couleur brun-marron avec une pointe de rouge. Structure micropolyédrique puis particulaire. Texture limono-sableuse. Porosité moyenne à forte. Racines 4/5, fines et moyennes. Squelette (30-40%): ø 1 à 500 mm. Limite horizontale, transition diffuse.

BPs2: 40 - 45/53 cm couleur: brun foncé, presque noir. Frange au-dessus et entre les grosses pierres, dépôt d'acides organiques à la surface des blocs. Structure polyédrique puis micropolyédrique. Texture sablo-limoneuse. Porosité forte. Racines 3/5, fines et moyennes. Squelette (30%): ø 2 à 20 mm et jusqu'à 50 mm. Limite ondulée, transition diffuse. pH 4.

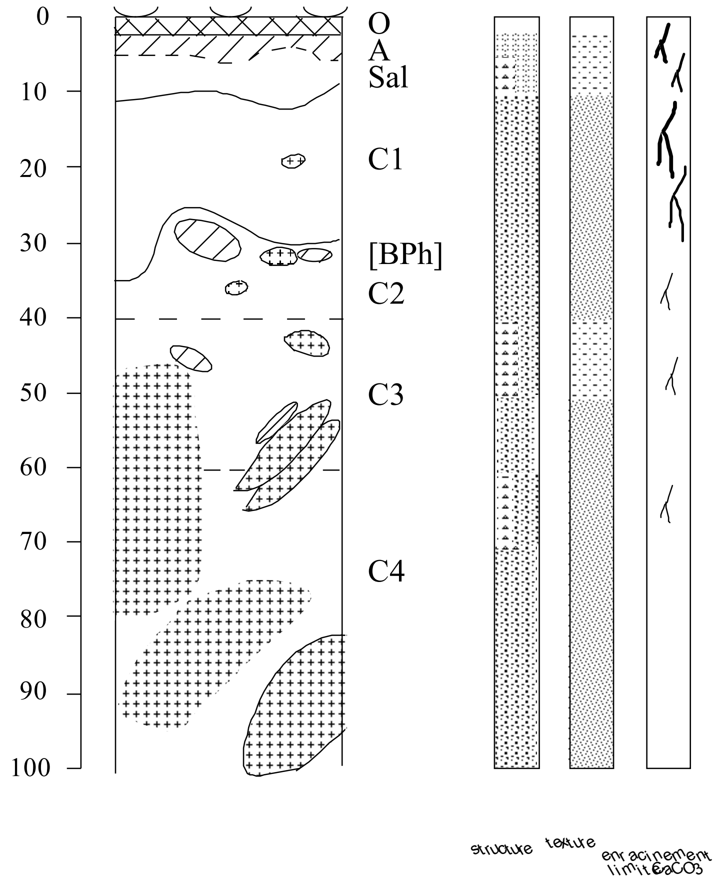
[C1]: 50 - 70 cm poche meuble plus jaune dans C2. Structure particulaire. Texture sableuse. Porosité forte. Racines 1/5, fines. Squelette (50%): ø 1 à 5 mm, 10 à 15 mm et 10 cm. Cailloux plutôt aplatis, altérés en surface (brunis). pH 4,5.

C2: 45/53 - 80 cm couleur: brun. Structure particulaire. Texture sableuse. Porosité forte. Racines 1/5, fines. Squelette (80%): graviers ø 10-15 mm puis 20-30mm et gros blocs jusqu'à ø 40 cm. Cailloux plutôt aplatis, altérés en surface (brunis).

Résultats des analyses

Horizon	pH H_2O	pH KCl	Corg (%)
OFr et OFm	4.54	3.30	n.d.
OH	4.47	3.42	n.d.
A	4.50	3.42	n.d.
ABPh	4.73	3.66	n.d.
BPh	4.99	3.94	3.02
BPsBPh	5.12	4.08	3.36
BPs1	5.18	4.13	2.67
BPs2	5.35	4.18	1.85
[C1]	5.14	4.30	n.d.
C2	5.27	4.27	n.d.

ARPETTE 2 (AR2)	ALOCRISOL TYPIQUE colluvial, brun, podzolisé	
Date: 6.9.98	**Coordonnées:** 571.125/ 97.713	**CN n°:** 1345
Altitude: 2565 m	**Pente:** ? °	**Exposition:** ?
Géologie: moraine acide		
Végétation: pelouse acidophile à Festuca varia (Festucetum variae)		
Topographie: ?		
Météo: ?		



O: 0 - 2(3) cm couleur: gris-brun.

A: 2 - 5 cm couleur: brun foncé. Horizon sec, très aéré. Pas de structure apparente mais aspect "floconneux" et grumeaux peu stables autour des racines, puis particulaire. Texture sablo-limoneuse. Porosité forte (horizon très sec). Racines 5/5, fines et moyennes. Squelette (< 5%): quelques graviers, ø 1 à 10-12 mm. pH 4.

Sal: 5 - 10 cm couleur: brun-roux foncé. Horizon sec mais plus frais que le précédent. Structure polyédrique puis microgrumeleuse autour des racines, pour le reste, essentiellement particulaire mais toujours très aérée. Texture limono-sableuse. Porosité forte (à moyenne). Racines 5/5, essentiellement fines. Squelette (<5%): graviers non altérés anguleux, ø 1 à 10-15 mm. pH 4,5.

C1: 10 - 30 cm couleur: brun-jaune (horizon très clair par rapport aux précédents). Toucher humide. Structure particulaire. Texture sableuse avec traces d'argiles, en particulier dans les 10 cm inférieurs. Porosité moyenne. Racines 4/5, essentiellement moyennes et quelques fines (10-20 cm) puis 2/5, fines (20-30 cm). Squelette (25%): graviers peu altérés (10-20 cm) puis à altération de surface (20-30 cm), anguleux, ø 4 à 20-25 mm; passablement de cailloutis et quelques petits blocs. pH 4,5.

C2: 30 - 40 cm couleur: brun-jaune. Horizon humide. Structure particulaire. Texture sableuse (présence ponctuelle d'argiles en périphérie des cailloux). Porosité moyenne. Racines 2 à 3/5, moyennes et fines. Squelette (50-60%): présence de gros grains de quartz d'un diamètre visible nettement; cailloux avec gangue d'altération, anguleux, ø 2 à 30 mm; blocs et beaucoup de cailloutis. pH 4,5 - 5.

[BPh]: 30 - 40 cm poche brun foncé incluse dans C2. Toucher un peu moins humide. Structure particulaire. Texture sableuse avec matière organique (gras et collant). Porosité moyenne à forte. Racines 1 à 2/5, fines. Squelette (50-60%): présence de grains de quartz; graviers ø 1mm; cailloux altérés en surface et à l'intérieur (cassants), anguleux, ø 8 à 20 mm; blocs et beaucoup de cailloutis. pH 4,5.

C3: 40 - 60 cm couleur: gris-brun. Présence de poches avec matériel brun-noir. Horizon humide. Structure polyédrique (gros polyèdres ø 50-60 mm, puis micropolyèdres) puis particulaire dans les 10 premiers centimètres puis particulaire, présence de grains de quartz et de mica ensuite. Texture sablo-limoneuse (40-50 cm) puis sableuse (50-60 cm). Porosité moyenne. Racines 1/5, fines. Squelette (50-60%): graviers ø 1 mm; cailloux anguleux ø 10 - 20 mm à gangue d'altération enrichie en argiles; blocs et beaucoup de cailloutis. pH 4,5 - 5.

C4: 60 - >100 cm couleur: gris-brun. Présence de poches avec matériel brun-noir. Horizon humide. Structure avec quelques gros polyèdres (ø 20 mm) se scindant en polyèdres plus petits (ø 10 mm} puis particulaire. Texture sableuse, avec traces d'argiles dans la partie inférieure à 70 cm. Porosité forte. Racines 0,5/5, fines, présentes jusqu'à 80 cm. Squelette (80-90 %): graviers ø 1 à 5 mm; cailloux anguleux à gangue d'altération, ø 10 à 50 mm, quelques uns sont cassants (60-70 cm), d'autres s'effritent entre les doigts (> 70 cm); blocs et un peu de cailloutis. pH 5.

Remarque:
Les valeurs fournies pour les racines sont des valeurs relatives établies par comparaison des échantillons reçus.

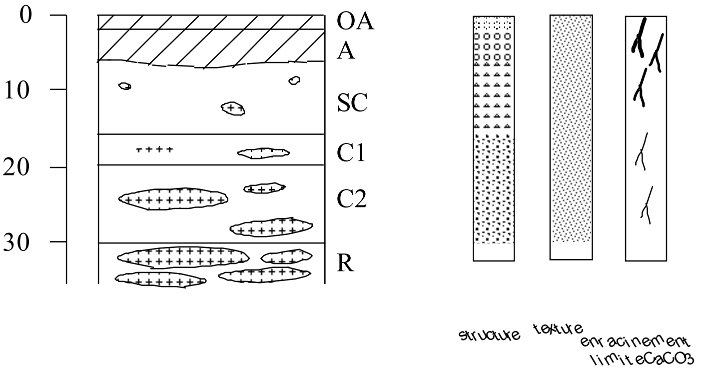
Résultats des analyses

Profondeur	Horizon	pH H_2O	pH KCl	Corg (%)
2-5 cm	A	4.74	3.36	5.17
5-10 cm	Sal	5.02	3.86	3.75
10-20 cm	C1	5.2	4	n.d.
20-30 cm	C1	5.18	4.08	n.d.
30-40 cm	C2	5.34	4.18	0.92
[30-40 cm]	[BPh]	5.3	4.09	2.42
40-50 cm	C3	5.36	4.24	n.d.
50-60 cm	C3	5.33	4.22	n.d.
60-70 cm	C4	4.97	4.16	n.d.
> 70 cm	C4	5	4.28	n.d.

Profondeur	Horizon	Mg^{2+}	Na^+	Ca^{2+}	K^+	Al^{3+}	H^+
		milliéquivalents / 100g					
5-10 cm	Sal	0.14	0.17	0.04	0.21	4.95	5.35

Profondeur	Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
5-10 cm	Sal	0.55	10.30	10.86	5	46

ARPETTE 3 (AR3)	BRUNISOL OLIGOSATURE leptique	
Date: 17.8.98	**Coordonnées:** 570.568/ 97.813	**CN n°:** 1345
Altitude: 2720 m	**Pente:** 32 °	**Exposition:** 235°N
Géologie: moraine acide		
Végétation: pelouse acidophile à Festuca rubra		
Topographie: ?		
Météo: ?		



OA: 0 - 2 cm. Couche contenant beaucoup de racines. Structure microgrumeleuse, feutrée à cause des racines (5/5, fines), juxtaposition organique-minéral.

A: 2 - 6/7 cm couleur: brun foncé. Structure ± grumeleuse autour des racines puis particulaire. Texture sableuse. Racines 3/5, moyennes et fines. Squelette (5%): graviers gris et allongés, peu altérés, ø 1 à 10 mm.

SC: 6/7 - 16 cm couleur: brun. Structure micropolyédrique puis particulaire. Texture sableuse. Racines 4/5, moyennes et fines. Squelette (40%) petits cailloux altérés et graviers peu altérés, ø 1 à 30 mm.

C1: 16 - 20 cm couleur: brun-jaune. Structure particulaire. Texture sableuse. Racines 2/5, fines. Squelette (40%): forte présence de cailloux gris et allongés, ø 1mm, 15-20 mm et 3-4 cm, ± cassés, avec une pellicule brune d'altération en surface.

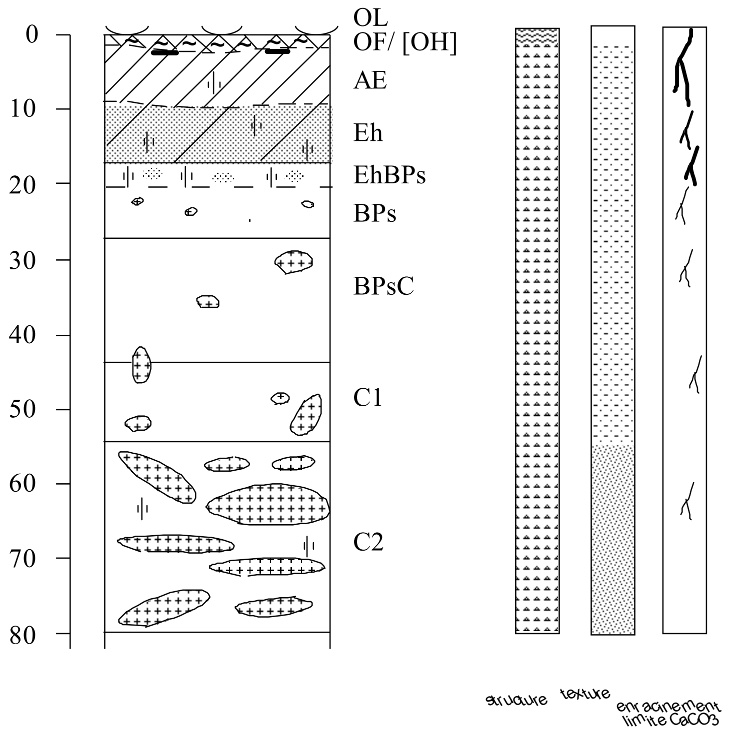
C2: 20 - 30 cm couleur: gris-brun clair. Structure particulaire. Texture sableuse. Racines 1/5, moyennes et fines, disposées en poches. Squelette (80%): cailloux allongés et altérés (bruns en surface), ø 1mm, 10-20 mm et jusqu'à 50-60 mm.

R: à 30 cm, roche en place (non échantillonné).

Résultats des analyses

Horizon	pH H_2O	pH KCl	Corg (%)
OA	5.17	3.95	n.d.
A	4.57	3.49	4.93
SC	4.79	3.71	3.92
C1	4.68	3.73	n.d.
C2	5.13	4.09	n.d.

BELALP 1 (BA-HO1)	PODZOSOL MEUBLE à eumoder	
Date: 11.7.98	**Coordonnées:** 639.325/135.400	**CN n°:** 1269
Altitude: 2370 m	**Pente:** 18°	**Exposition:** E-SE
Géologie: gneiss		
Végétation: pelouse acidophile à Festuca varia		
Topographie: petite croupe		
Météo: nuageux-brumeux puis grand soleil		



OL: +0,5 - 0 cm. Feuilles de graminées. Très peu de matériel.

OF: 0 - 2/3 cm. Séparation en deux sous-couches par la taille des racines (plus grosses en OF1 et plus fines en OF2). Dans chaque cas, limite ondulée (selon la microtopographie) et transition diffuse. pH 5 pour l'ensemble de la couche. Cette zone est essentiellement constituée d'une dense trame de racines et contient une forte proportion de boulettes fécales. On n'y trouve pas réellement de débris de feuilles ou de fragments de matériel végétal en cours de décomposition.

OF1: 0 - 1 cm. Racines 5/5, grosses, moyennes et fines.

OF2: 1 - 2/3 cm. Racine s 4,5/5, moyennes et fines.

[OH]: quelques mm, sporadique. couleur: noir. Couche très mince plaquée sous OF, avec une plus forte teneur en matière organique fine et en boulettes fécales, en mélange avec des grains de quartz. Racines 5/5, fines, pH 4,5.

AE: 2/3 - 9 cm couleur: brun-gris avec quelques taches de rouille. Horizon assez compact. Structure polyédrique puis particulaire. Texture limono-sableuse, porosité faible à moyenne. Racines 4/5, moyennes et fines. Squelette (quasi inexistant): quelques graviers très altérés ø 1 à 5 mm. pH 4. Limite ondulée, transition diffuse.

Eh: 9 - 17 cm couleur: gris légèrement brun avec taches d'oxydation du fer. Horizon assez compact. Structure polyédrique puis particulaire. Texture sablo-limoneuse. Porosité faible. Racines 2/5, fines. Squelette (qqs %): graviers très altérés ø 1 à 10 mm et un caillou ø 4 cm lors du prélèvement. pH 4. Limite horizontale, transition nette.

EhBPs: 17 - 20 cm couleur: alternances de plages grises et ocre foncé (rouille). Structure polyédrique puis particulaire (quasi pas d'agrégats, écailles polyédriques se décomposant au toucher). Texture limono-sableuse voire sableuse. Porosité faible. Racines 3/5, fines, moyennes et grosses. Squelette (10%): graviers ø 5 à 15 mm, très altérés, en surface et à l'intérieur. pH 4, Limite horizontale, transition progressive.

BPs: 20 - 27 cm couleur: rouille. Structure micropolyédrique puis particulaire (struct. évent. microgrenue: sorte de petits flocons qui se désagrègent sous le doigt). Texture sablo-limoneuse. Porosité moyenne. Racines 2/5, fines. Squelette (20%): graviers ø 0,5 à 15 mm, petits et plats, très altérés, cassants ou se délitant en feuillets. pH 4. Limite horizontale, transition nette.

BPsC: 27 - 44 cm couleur: rouille. Structure polyédrique puis particulaire (polyèdres petits et grands (ø1 - env. 10 mm) traversés par de fines racines et se démembrant facilement sous le doigt). Texture sablo-limoneuse. Porosité faible. Racines 2/5, moyennes et fines. Squelette (30-40%): cailloux ø 1 à 600 mm, cristallins, altérés en surface. pH 4. Limite horizontale, transition nette.

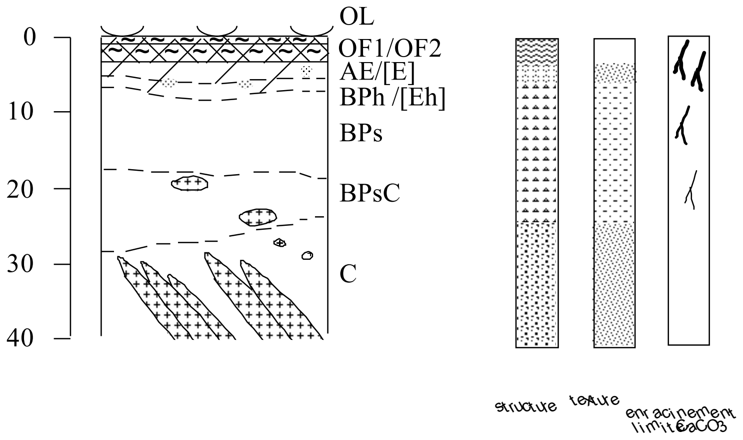
C1: 44 - 54 cm couleur: rouille. Structure polyédrique puis particulaire (polyèdres jusqu'à 10-15 mm avec racines fines et graviers, se démembrent au toucher). Texture sablo-limoneuse. Porosité moyenne. Racines 2/5, fines. Squelette (60%): ø 1mm à 20 cm, cristallins, altérés en surface. pH 4. Limite horizontale, transition nette.

C2: 54 - 80 cm couleur: rouille plus gris. Structure micropolyédrique. Cet horizon contient une majorité de cailloux et de graviers qui donnent la structure avec les quelques racines: aspect de graviers se désagrégeant au toucher. Texture sableuse avec, là où les cailloux s'effritent, des traces d'argiles. Porosité forte. Racines 1/5, fines. Squelette (90%): ø 1mm à 20 cm, cailloux plats, 5 cm, se délitant en feuillets et cailloux plus gros altérés seulement en surface. pH 4 - 4,5.

Résultats des analyses

Horizon	pH H_2O	pH KCl
OF	5.29	4.10
AE	4.70	3.36
Eh	4.72	3.41
EhBPs	5.00	3.75
BPs	5.02	3.79
BPsC	5.14	3.88
C1	5.23	4.07
C2	5.28	4.12

BELALP 2 (BA-HO2)	PODZOSOL OCRIQUE à hémimoder	
Date: 11.7.98	**Coordonnées:** 639.050/134.750	**CN n°:** 1269
Altitude: 2550 m	**Pente:** 3°	**Exposition:** -
Géologie: gneiss		
Végétation: pelouse acidophile à Carex curvula		
Topographie: replat		
Météo: grand soleil		



OL: +1 - 0 cm couleur: brun clair. Feuilles et gaines de graminées, mousses et lichens. Pas très présent.

OF1: 0 - 1 cm couleur: brun plus foncé. Zone avec dense feutrage de racines (5/5) de toutes tailles. Très peu de matière organique fine (max 10%). Débris non reconnaissables et brindilles. pH 4 (OF1 et OF2!). Limite horizontale, transition nette.

OF2: 1 - 3 cm couleur: brun-noir. Feutrage racinaire moins dense, racines (5/5) plus fines. Proportion de matière organique fine plus forte (env. 30 %), sans structure, juxtaposée à des grains de quartz. pH 4 (OF1 et OF2!). Limite horizontale, transition nette.

AE: 3 - 6/7 cm couleur brun-gris clair. Structure microgrumeleuse puis particulaire, juxtaposition matière organique, grains de quartz et mica uniquement maintenue par les racines. Texture sableuse + matière organique. Porosité forte (horizon très sec, probablement très drainant). Racines 4/5, moyennes et fines. Squelette (5-10%): graviers ø 5mm. pH 4. Limite ondulée, transition diffuse.

[E]: 4-6 cm couleur: gris clair. Poche sur la droite du profil résultant de l'altération en place d'un caillou; mica, serpentinite et quartz visibles. Structure particulaire. Texture sableuse. Porosité forte. Racines 5/5 moyennes et fines. Squelette (70%): ø 1 à 8 mm.

[Eh]: épaisseur env. 1 cm,. couleur: gris-brun. Poches sporadiques et très discrètes, directement sous AE. Structure polyédrique puis particulaire. Texture sableuse. Porosité forte. Racines 3/5, fines (rôle agrégateur). Pas de squelette.

BPh: 6/7 - 7/8 cm couleur: brun chocolat. Couche mince et ± discontinue, apparaît à gauche sous AE et à droite dans une zone où AE disparaît presque. Structure polyédrique puis particulaire. Texture sablo-limoneuse. Porosité moyenne (couche plus humide). Racines 2/5, fines. Squelette (5-10%): graviers ø 1 à 5 mm. pH 4. Limite ondulée, transition diffuse.

BPs: 7/8 - 17 cm couleur: brun ocre. Zone assez compacte par rapport aux suivantes, de plus en plus aérées. Structure polyédrique puis particulaire (polyèdres 5-10 mm se cassant sous les doigts mais un peu moins facilement que les précédents). Texture limono-sableuse. Porosité moyenne. Racines 2/5, fines et en disposition par poches. Squelette (5%): graviers ø 1 à 3-4- mm délités en feuillets ou en morceaux. pH 4. Limite ondulée, transition diffuse.

BPsC: 17 - 24/27 cm couleur: brun ocre, tire plus sur le jaune que le précédent. Structure polyédrique puis particulaire (polyèdres de 8-10 mm encore plus stables, grains de quartz et écailles de mica toujours visibles). Texture limono-sableuse. Porosité moyenne. Racines 1/5, fines. Squelette (20%): graviers ø 5 mm et 3-5 cm altérés, se délitant en feuillets. pH 4. Limite ondulée, transition diffuse.

C: 24/27 - 40 cm couleur: brun roux. Changement d'aspect assez net avec beaucoup plus de cailloux et des blocs placés quasi verticalement, très altérés, se cassant sous l'ongle. La structure de l'horizon se fait en fonction de cette roche. La terre fine contenue entre les feuillets est ± polyédrique mais devient particulaire dès qu'on la touche. Texture sableuse. Porosité moyenne. Racines 0,5/5, fines. Squelette (70%): ø 2 mm à plusieurs dizaines de cm, les éléments de la roche en place sont disposés comme des tranches de pain appliquées les unes contre les autres. pH 4,5.

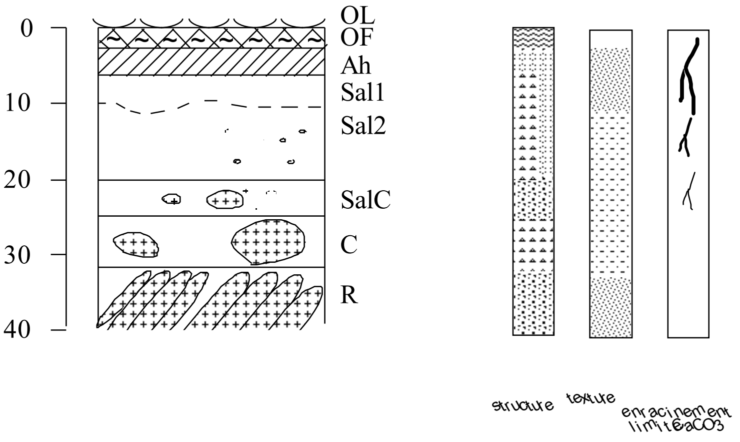
Résultats des analyses

Horizon	pH H_2O	pH KCl
OFr et OFm	4.77	3.67
AE	4.43	3.25
[Eh]	4.41	3.21
BPh	4.47	3.13
BPs	4.65	3.47
BPsC	4.80	3.34
C	4.82	3.11

BELALP 3 (BA-HO3)	ALOCRISOL TYPIQUE brun, à hémimoder	
Date: 12.7.98	**Coordonnées:** 638.825/135.450	**CN n°:** 1269
Altitude: 2684 m	**Pente:** 10-15°	**Exposition:** E
Géologie: gneiss		
Végétation: pelouse acidophile à Carex curvula		
Topographie: rupture de pente		
Météo: soleil et vent avec passages nuageux		

Ce profil a été décrit en deux fois, la partie gauche contenant moins de squelette nous ayant paru très différente en première approche. Il semblerait cependant que les caractéristiques générales des parties gauche et centre-droite du profil soient assez comparables et s'apparentent à la même référence.

a) Description de la partie gauche, plus compacte:



OL: +1 - 0 cm. Feuilles, tiges et gaines de graminées et d'alchémille.

OF: 0 - 3 cm. Structure feutrée donnée par le dense chevelu racinaire + matière organique non structurée en elle-même. Pas de résidus végétaux identifiables. Forte proportion de boulettes fécales. Racines 5/5, moyennes et fines. pH 5. Limite horizontale, transition nette.

Ah: 3 - 6 cm couleur: brun noir. Structure toujours très feutrée avec juxtaposition de microgrumeaux (bruns), de boulettes fécales (noires) et de grains de quartz. Texture sableuse + matière organique. Racines 5/5, toutes tailles. pH 4,5. Limite horizontale, transition ± nette.

Sal1: 6- 10/11 cm couleur: brun chocolat. Structure polyédrique puis microgrumeleuse (les morceaux viennent sous forme de polyèdres qui se désagrègent en microgrumeaux discrets). Texture sableuse + matière organique. Porosité forte à moyenne. Racines 4/5, moyennes et fines. Squelette (0%). pH 4. Limite ondulée, transition diffuse.

Sal2: 10/11 - 20 cm couleur: dominance brune, tire sur le roux. Structure en microagrégats avec parfois des faces (dominance), parfois des allures de grumeaux, puis particulaire. Texture sablo-limoneuse. Porosité moyenne. Racines 3/5, moyennes et fines (donnent la cohésion). Squelette (env. 10 %): graviers ø 1 mm à 3-4 cm. pH 4. Limite horizontale, transition nette.

SalC: 20 - 25 cm couleur: brun roux. Structure particulaire. Texture sablo-limoneuse. Porosité moyenne à forte. Racines 2/5, fines. Squelette (20%): 1 gros caillou se délitant sous la lame + résidus de l'altération. pH 4. Limite horizontale, transition nette.

C: 25 - 32 cm couleur: brun-gris. Structure polyédrique puis particulaire (polyèdres 2-8mm). Texture sablo-limoneuse à limono-sableuse. Porosité moyenne. Racines 1/5, fines. Squelette (env. 50 %): graviers ø 1 à 10-15 mm et gros blocs en place. pH 4. Limite horizontale, transition ± nette.

R: 32 et plus (fosse jusqu'à 40 cm) couleur: brun-gris. Dominance de la roche (squelette env. 90 %): roche en place cohérente mais pas mal altérée en surface et quelques graviers (ø 1 à 15 mm) totalement mangés qui se cassent sous les doigts. Quasi absence de la terre fine que l'on trouve dans les interstices (structure particulaire, texture sableuse). Présence de racines 1/5, fines et moyennes. pH 4.

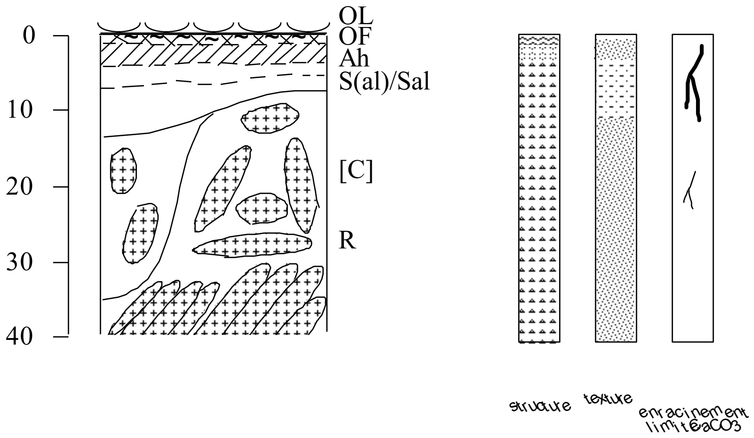
Résultats des analyses

Horizon	pH H_2O	pH KCl
OF	5.05	3.81
Ah	4.51	3.52
Sal1	4.62	3.56
Sal2	4.66	3.36
SalC	4.81	2.99
C	5.16	3.00

Horizon	Mg^{2+}	Na^+	Ca^{2+}	K^+	Al^{3+}	H^+
	milliéquivalents / 100g					
Sal2	0.16	0.12	0.02	0.21	7.45	8.44

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
Sal2	0.51	15.89	16.39	3	45

b) Description des parties centre et droite, plus lâches:



OL: idem
OF: 0 - 1 cm horizon très fin. Débris végétaux et quelques boulettes fécales. Structure dense données par la masse importante de radicelles. pH 5. Limite ondulée, transition diffuse.
Ah: 1 - 4 cm couleur: brun-noir. Structure microgrumeleuse puis particulaire avec juxtaposition de boulettes fécales et de matière minérale. Texture sableuse + matière organique. Porosité forte. Racines 5/5, moyennes et fines. Pas de squelette. pH 4. Limite ondulée, transition diffuse.
S(al): 4 - 7 cm couleur: brun chocolat. Structure polyédrique puis particulaire (polyèdres 8 mm à 2,5 cm maintenus par les racines puis se cassant en petits polyèdres avant de devenir particulaires). Texture limono-sableuse. Porosité moyenne. Racines 4/5, fines. Squelette (env. 5%): graviers ø 1 à 2 mm. pH 4. Limite ondulée, transition diffuse.
Sal: 7 - 8/13 cm couleur: brun roux. Structure polyédrique très lâche puis particulaire (polyèdres ø 5mm). Texture sablo-limoneuse. Porosité moyenne. Racines 4/5, fines, donnent une structure à l'ensemble mais l'horizon reste moins cohérent et moins compact que les précédents. Squelette (env. 5%): graviers ø 1 à 3-4 mm. pH 4. Limite ondulée, transition nette.
C: 13 - 35 cm couleur: brune au voisinage des racines, grisée vers les cailloux. Partie très lâche avec roches ± grosses mais totalement altérées, n'existe que dans la partie centrale. Structure: microagrégats et microgranules autour des racines puis particulaire. Texture sableuse. Porosité forte. Racines 2/5, fines.

Squelette (80%): graviers ø 1 mm à 3 cm, très altérés et blocs entiers altérés mais moins fortement que dans la partie gauche. pH 4,5. Limite ondulée, transition nette.

R: 8 - 35 cm couleur: brun clair. Roche en place avec gradient d'altération de haut en bas de l'horizon, très grise (par rapport à C où la roche est brunie = cortex d'altération). Présence d'un peu de terre fine ainsi que de racines entre les pans de roche. Structure polyédrique puis particulaire. Texture essentiellement sableuse. porosité forte (horizon très sec). Racines 1/5, grosses et fines. Squelette (95%): grains de quartz et de mica, graviers plats ø 5 mm, essentiellement des gros blocs. pH 5.

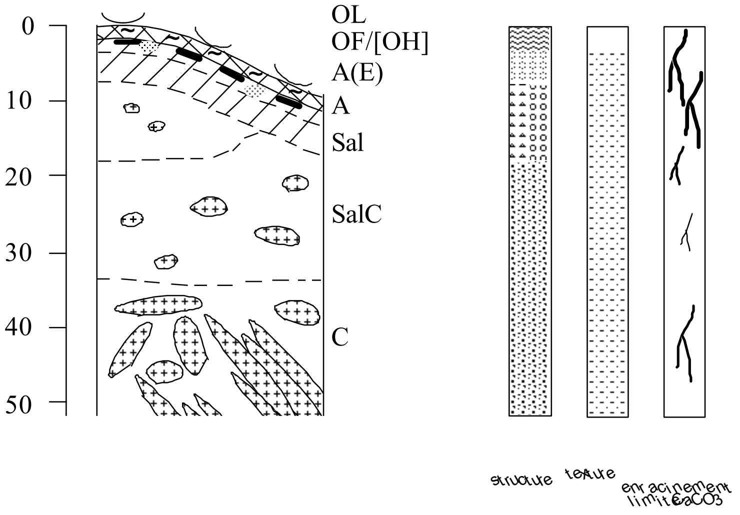
Résultats des analyses

Horizon	pH H_2O	pH KCl
OF	5.22	4.21
Ah	4.60	3.63
S(al)	4.52	3.44
Sal	4.73	3.14
C	5.07	3.11
R	5.13	3.35

Horizon	Mg^{2+}	Na^+	Ca^{2+}	K^+	Al^{3+}	H^+
	milliéquivalents / 100g					
Sal2	0.41	0.15	0.06	0.25	9.53	10.41

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
Sal2	0.87	19.94	20.80	4	46

BELALP 4 (BA-HO4)	ALOCRISOL TYPIQUE brun, podzolisé, à eumoder	
Date: 12.7.98	**Coordonnées:** 638.650/135.900	**CN n°:** 1269
Altitude: 2830 m	**Pente:** 20°	**Exposition:** E-NE
Géologie: gneiss		
Végétation: pelouse acidophile à Carex curvula		
Topographie: pente sous la crête		
Météo: soleil et vent		



OL: +0,5 - 0 cm. Feuilles de graminées. Quasi inexistant.

OF: 0 - 3 cm à gauche, 10 - 12 cm à droite. Gaines et rhizomes de graminées, résidus de feuilles fragmentées et dense réseau racinaire. Pas mal de microfaune (acariens). pH 4,5. Limite ondulée, transition nette.

[OH]: quelques mm à la base de OF, couleur: noir. Fin plaquage avec beaucoup de boulette fécales. Toujours beaucoup de racines, la plupart très fines. Horizon sporadique, sous forme de ligne enrichie en déjections holorganiques.

A(E): 3 - 4 cm à gauche, 13 - 15 cm à droite couleur: brun gris, devient blanchâtre en séchant. Structure microgrumeleuse très instable maintenue principalement par les racines puis particulaire (grumeaux les plus stables 5 mm, les plus petits se désagrègent facilement). Texture sablo-limoneuse. Porosité forte à moyenne (horizon très sec). Racines 4/5 voire 5/5, fines et moyennes. Squelette inexistant. pH 4. Limite ondulée, transition diffuse.

A: 4 - 7 cm à gauche, 15 - 19 cm à droite couleur: brun gris, légèrement plus brun que A(E). Structure microgrumeleuse (ø 1 - 3 mm) puis particulaire. Texture sablo-limoneuse voire limono-sableuse. Porosité moyenne. Racines 3/5, fines. Pas de squelette. pH 4. Limite ondulée, transition diffuse.

Sal: 7 - 18 cm, seulement à gauche couleur: brun roux. Structure mixte, polyédrique et grumeleuse puis particulaire (polyèdres ø 2 à 10-12 mm, agrégats collés sur les racines). Texture limono-sableuse. Porosité moyenne. Racines 3/5, moyennes et fines. Squelette (10-20%): graviers plats ø 3-4 mm, très altérés et cailloux jusqu'à 1 cm de long, gris, altérés légèrement en surface. pH 4. Limite ondulée, transition diffuse.

SalC: 18 - 34 cm à gauche, 19 - 35 à droite couleur: brun roux. Structure micropolyédrique (ø 1 à 5 mm) mais essentiellement particulaire, assez compacte, peu perturbée par les racines. Texture sablo-limoneuse. Porosité moyenne. Racines 2/5, fines (à gauche, une grande racine en transit vertical). Squelette (20-30%): graviers ø < 5 mm très altérés et ø 8 à 10 mm altérés et cassants, cailloux 3-4 à 10 cm peu altérés en surface. pH 4+ à gauche, 4 à droite. Limite ondulée, transition diffuse.

C: 34/35 - 50 cm couleur: brun ocre. Horizon contenant une forte proportion de blocs minéraux, avec de la terre fine entre les roches, là où cheminent les racines. Structure en microagrégats (de l'ordre du mm avec de légères faces) mais essentiellement particulaire. Texture limono-sableuse à sablo-limoneuse. Porosité moyenne à faible. Racines 3 à 4/5, grosses et couvertes de radicelles, moyennes et fines (la limite supérieure de l'horizon est marquée par l'émergeance de grosses racines au-dessus d'une pierre plate). Squelette (80-90%): gros feuillets brunis et cassants (biscuits mous) dans le haut de l'horizon, plus solides, gris et brillants, altérés en surface seulement vers le bas; cailloux plats 4- 10 cm et graviers de toutes tailles jusqu'aux grains de quartz et de mica. pH 5.

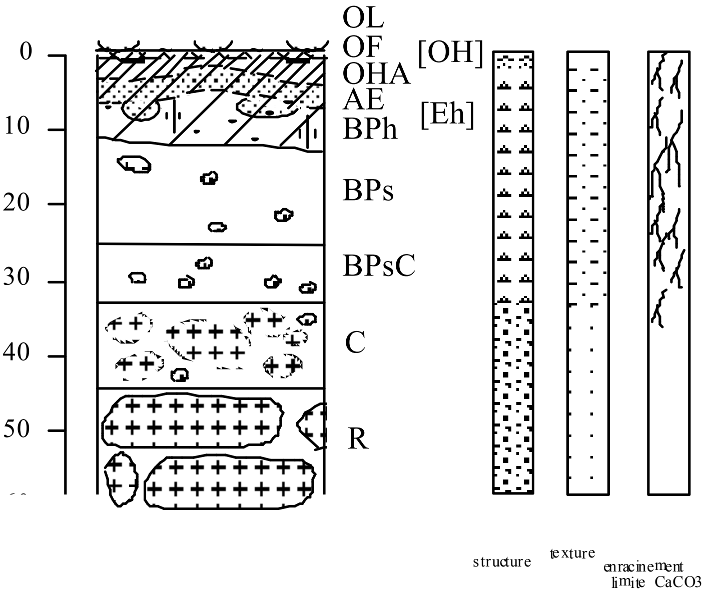
Résultats des analyses

Horizon	pH H_2O	pH KCl
OF et [OH]	5.10	4.30
A(E)	4.56	3.06
A	4.39	3.15
Sal	4.30	3.12
SalC	4.53	3.29
C	4.89	3.55

Horizon	Mg^{2+}	Na^{+}	Ca^{2+}	K^{+}	Al^{3+}	H^{+}
	milliéquivalents / 100g					
SalC	0.11	0.19	0.03	0.18	7.38	8.39

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
SalC	0.50	15.77	16.27	3	45

BELALP 5 (BA-LE5)	PODZOSOL MEUBLE peu évolué, à dysmoder et hémimoder discontinus	
Date: 3.8.99	**Coordonnées:** 641.113/138.113	**CN n°:** 1269
Altitude: 2550 m	**Pente:** 12°	**Exposition:** ESE (148° N)
Géologie: gneiss		
Végétation: Nardetum avec Carex curvula		
Topographie: légère pente en bordure de replat		
Météo: variable, couvert		



OL: quelques mm. Rares feuilles de graminées. Peu épais.

OF: quelques mm. Couleur: brun, légèrement roux, couche de transition OL - OH. Présence de débris végétaux (feuilles de graminées) et de matière organique non figurée (à la limite des 30 %).

[OH]: 0 - 1.5 cm. Cette couche n'est présente que sous les touffes de graminées. Couleur: noir. Présence de matière organique non figurée en forte proportion, sous forme de boulettes fécales. Toucher gras-soyeux (matière organique et limons). Beaucoup de racines fines. pH 4.5.

OHA: 0/1.5 - 2/3.5 cm. Couleur: brun noir. Structure microgrumeleuse (grumeaux de 4 - 5 mm, très lâches ou 2 - 3 mm un peu plus compacts). Texture limono-sableuse, avec de la matière organique (petites boulettes fécales juxtaposées à des grains de quartz et des sables). Porosité moyenne à faible. Racines 3/5, fines. Squelette inexistant. Limite ondulée, transition diffuse. pH 4+.

AE: 2/3.5 - 5/6 cm. Couleur: gris noir. Structure polyédrique (polyèdres de 2 - 5 mm, moyennement stables, bcp de grains de sable et de quartz). Texture sablo-limoneuse. Porosité forte. Racines 2/5, moyennes et fines. Squelette (<5%): graviers ø 2 - 5 mm. Limite ondulée, transition progressive. pH 4.5.

[Eh]: 5 - 8.5 cm. Couleur: gris brun, poches nettement plus claires que AE. Structure polyédrique (polyèdres ø 3 mm très peu stables + quelques gros de 10 mm moyennement stables). Texture sableuse avec traces de limons. Porosité forte. Racines 2/5, moyennes. Squelette (5-10%): graviers gris et blancs, ø 1 - 2 mm. Limite ondulée, transition nette. pH 4+.

BPh: 6/8.5 - 11 cm. Couleur: noir roux avec taches de fer oxydé, présence d'un liseré quasi noir sous la poche de Eh de gauche. Structure polyédrique (polyèdres moyennement stables de grande taille (5 mm) se cassant en polyèdres de ø 2 - 3 mm, un peu moins stables). Texture sablo-limoneuse avec de la matière organique, toucher assez doux et frais. Porosité forte à moyenne. Racines 3/5, moyennes et fines.

Squelette (<5%): quelques graviers. Limite quasi horizontale, transition progressive mais pas floue. pH 4.

BPs: 11 - 25 cm. Couleur: roux. Structure polyédrique (polyèdres peu stables, ø 5 - 6 mm, se cassant en plus petits polyèdres). Texture limono-sableuse. Porosité moyenne à faible. Racines 3/5, moyennes et fines. Squelette (20%): un caillou ø 6 cm; graviers ø 1 cm pour les plus gros, quelques mm pour les plus petits, tous faiblement altérés en surface. Limite subhorizontale, transition nette. pH 4.

BPsC: 25 - 33 cm. Couleur: ocre roux. Structure vaguement polyédrique (quelques polyèdres peu stables, ø 3 mm), puis particulaire. Texture sablo-limoneuse. Porosité moyenne à forte. Racines 2/5, fines et moyennes. Squelette (15-20%) : les éléments sont plutôt petits; gneiss très altérés ø 2 cm; cailloux 10-15 mm peu altérés; graviers 2 - 10 mm peu altérés. Limite horizontale, transition nette (squelette). pH 4.

C: 33 - 45 cm. Couleur: brun grisâtre. Structure particulaire. Texture sableuse. Porosité forte. Racines 1/5, fines. Squelette (80-90%): présence d'un important cortex d'altération autour des cailloux, aspect minéral mais s'effrite sous la lame du couteau; pas de gneiss, plutôt des granites arrondis (tachetés blanc, noir et rouille), les plus résistants présentent également des quartzites non altérées ø 5 - 6 mm; beaucoup de graviers ø 5 - 10 mm (résidus d'altération). Limite horizontale, transition nette. pH 4.

R: dès 45 cm. Couleur: sable. Roche ± en place recouverte d'une fine pellicule d'altération. Structure particulaire. Texture sableuse fine. Porosité faible. Pas de racines. Squelette (90-100%).

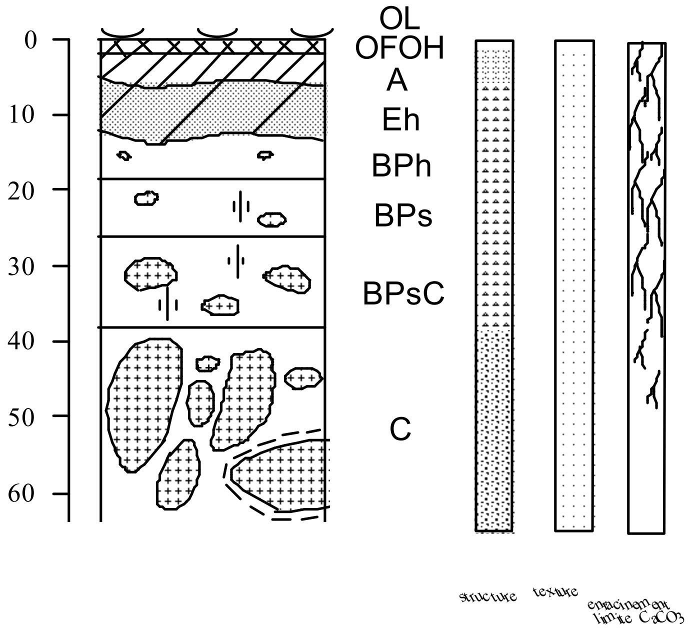
Remarques:

– L'enracinement est assez homogène sur les premiers horizons, il n'y a pas véritablement de couche préférentielle.
– Faune: carabes, papillons, mouches. La microfaune n'est pas visible.

Résultats des analyses

Horizon	pH H_2O	pH KCl
OHA	n.d.	n.d.
AE	4.3	3.2
[Eh]	4.4	3.3
BPh	4.6	3.7
BPs	5.0	4.0
BPsC	5.1	4.0
C	5.2	4.1

BELALP 6 (BA-LE6)	PODZOSOL MEUBLE à hémimoder	
Date: 3.8.99	**Coordonnées:** 641.325/137.563	**CN n°:** 1269
Altitude: 2415 m	**Pente:** 12 °	**Exposition:** S (189° N)
Géologie: gneiss		
Végétation: pelouse à *Carex sempervirens* et *Nardus stricta*		
Topographie: replat		
Météo: couvert		



OL : quelques mm. Touffes de graminées.
OFOH: 0 – 1 cm. Couleur : brun-noir. Horizon formé de résidus de feuilles, de racines et de matière organique.
A : 1 - 5 cm. Couleur: brun. Horizon de juxtaposition. Structure grumeleuse instable (grumeaux de ø 5 mm maximum). Texture sableuse avec traces de limons. Porosité forte. Racines 5/5, dense feutrage de racines fines, quelques moyennes. Squelette inexistant. Limite légèrement ondulée, transition nette. pH 4+.
Eh : 5 - 11 cm. Couleur: gris brun. Structure polyédrique (polyèdres de 5 mm, moyennement stables), puis particulaire. Texture sableuse. Porosité forte. Racines 3/5, moyennes. Squelette inexistant. Limite ondulée, transition nette. pH 4+.
BPh : 11 - 18 cm. Couleur: brun légèrement roux. Structure polyédrique (polyèdres ø 7 mm, peu stables). Texture sableuse. Porosité forte. Racines 4/5, moyennes et fines. Squelette (5 %): quelques cailloux ø 3 cm ; essentiellement des graviers jusqu'à 10 mm. Limite horizontale, transition nette (couleur, structure, squelette). pH 4.
BPs : 18 - 26 cm. Couleur: brun orangé. Structure polyédrique (polyèdres ø 7-8 mm, moyennement stables, se cassant en petits polyèdres peu stables). Cet horizon a une structure très lâche par rapport au précédent, ceci étant dû essentiellement au dense chevelu racinaire. Texture sableuse (plus grossière que BP1). Porosité forte. Racines 5/5, moyennes. Squelette (5 à 10 %): cailloux jusqu'à 5 cm ; graviers jusqu'à 15 mm ; les éléments du squelette présentent une légère pellicule d'altération. Limite horizontale, transition nette (couleur, racines, squelette). pH 4-4+.
BPsC: 26 - 38 cm. Couleur: brun-gris. Structure polyédrique (polyèdres ø 4 mm, très instables), puis particulaire. Texture sableuse avec traces de limons. Porosité forte. Racines 4/5, moyennes. Squelette

(30%): graviers jusqu'à 15 mm quasiment pas altérés ; granites bariolés comme dans BA-5 avec altération. Limite horizontale, transition nette (cailloux). pH 4.5.

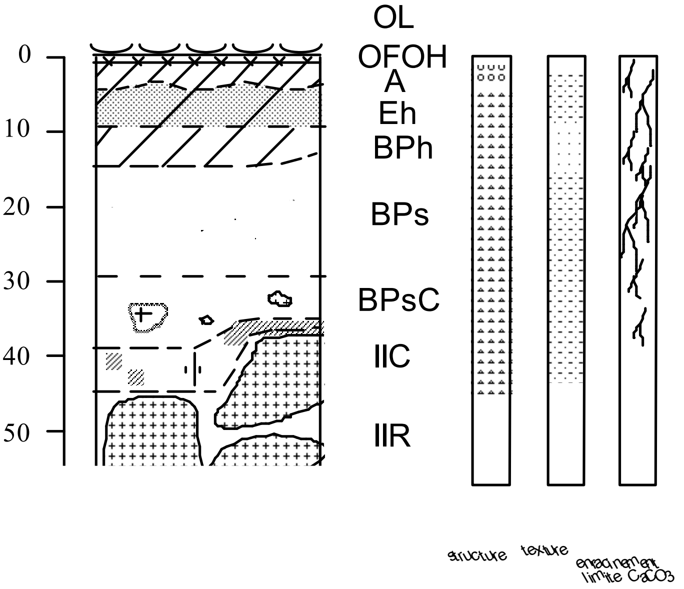
C : 38 - 62 cm. Couleur: jaune-gris. Structure particulaire. Texture sableuse. Porosité moyenne à faible. Racines 1/5, fines, insérées en bordure des cailloux. Squelette (90%): graviers 8-15 mm peu altérés ; plaquettes de gneiss de 5 cm très altérées ; blocs granitiques de 6-12 cm peu altérés. pH 4.5.
Le squelette, très important dans cet horizon, se présente sous forme de gneiss très altérés (surtout sur la gauche de la partie décrite) et de granites tricolores peu voire pas altérés.

Remarque:
– Un caillou tombé de BPh laisse apparaître une loge tapissée de radicelles

Résultats des analyses

Horizon	pH H_2O	pH KCl	Corg (%)
A	4.3	3.3	n.d.
Eh	4.5	3.3	n.d.
BPh	4.9	4.0	2.66
BPs	4.8	4.2	1.21
BPsC	5.2	4.3	n.d.
C	5.4	4.2	n.d.

BELALP 7 (BA-LE7)	PODZOSOL MEUBLE à dysmull , superposé aux résidus d'une ancienne pédogenèse	
Date: 4.8.99	**Coordonnées:** 641.300/137.188	**CN n°:** 1269
Altitude: 2305 m	**Pente:** 20 °	**Exposition:** S (171° N)
Géologie: gneiss		
Végétation: pelouse à *Carex sempervirens* et *Nardus stricta*		
Topographie: replat avant pente		
Météo: soleil		



OL : + 0.5 – 0 cm. Gaines et feuilles de graminées.

OFOH: 0 – 1 cm. Horizon formé de matériel foliaire fragmenté avec racines et boulettes de matière organique.

A : 1 – 2/3 cm. Couleur: brun. Structure grumeleuse (grumeaux de ø 2 - 12 mm, moyennement à peu stables). Texture limono-sableuse. Porosité moyenne. Racines 4/5, essentiellement fines, quelques moyennes. Squelette inexistant. Limite ondulée, transition floue et ± progressive (essentiellement structure et couleur). pH 4 à 4+.

Eh : 2/3 - 9 cm. Couleur: légèrement brun. Structure vaguement polyédrique (polyèdres jusqu'à 15 mm, peu stables, se cassant en polyèdres ø 2 mm), puis particulaire. Texture limono-sableuse à sablo-limoneuse. Porosité moyenne. Racines 3/5, essentiellement moyennes. Squelette (< 5%) : quelques graviers. Limite horizontale, transition progressive (≤ 1 cm). pH 4.

BPh : 9 – 13/15 cm. Couleur: brun chocolat. Structure polyédrique (polyèdres ø 12 - 15 mm, moyennement à peu stables, se cassent en plus petits polyèdres (ø 3 mm) puis particulaire ou directement particulaire). Texture sableuse avec traces de limons et présence de matière organique. Porosité moyenne à forte. Racines 2/5, fines. Squelette inexistant. Limite ondulée, transition floue (évolution progressive de la couleur). pH 4.

BPs : 13/15 - 29 cm. Couleur: brun légèrement roux. Structure polyédrique (polyèdres jusqu'à ø 25 - 30 mm, stables à moyennement stables, se cassant en petits polyèdres (ø 5 mm) peu stables puis particulaire). Texture sablo-limoneuse. Porosité faible à moyenne. Racines 2/5, moyennes. Squelette (5 %): graviers. Limite subhorizontale, transition diffuse (squelette). pH 4.

BPsC: 29 – 35/39 cm. Couleur: globalement brun mais avec beaucoup de traces en mosaïque (brun foncé, brun rouille, etc…). Structure polyédrique (polyèdres jusqu'à ø 30 - 40 mm, stables, se cassant en polyèdres ø 10 – 15 mm puis en polyèdres toujours plus petits). Les polyèdres sont assez compacts et donnent l'impression d'être très secs. Texture sablo-limoneuse. Porosité forte. Racines 1/5, fines. Squelette (10%): essentiellement des graviers et 1 ou 2 cailloux genre gneiss, ronds et totalement corrodés. Limite ondulée, transition diffuse (couleur, squelette). pH 4.

IIC : 35/39 – 40/45 cm. Couleur: en mosaïque, avec des taches passant du noir à l'ocre. Structure polyédrique (polyèdres jusqu'à ø 30 mm, avec plaquages noirs sur les faces et intérieur brun avec zones ocre-rouille, moyennement stables). Texture sableuse fine, avec traces de limons, d'argiles et de matière organique. Porosité faible à moyenne. Racines 1 à 2/5, fines. Squelette inexistant.

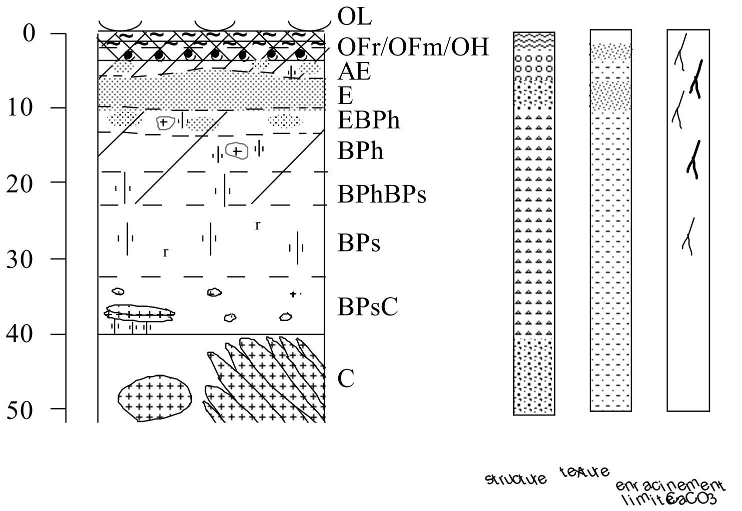
Cette couche assez compacte et bigarrée présente différents faciès. Sur la droite, on trouve une poche très noire qui contient beaucoup de matière organique (pH 4.5). A gauche de la fosse, il y a une poche plutôt ocre mais avec encore des poches de matière organique (pH 4.5 – 4.5+). Enfin, au centre, on trouve une poche qui présente des taches rédox (pH 4+ voire 4.5). Il s'agit probablement des traces d'un ancien sol qui serait resté entre et sur les blocs de l'horizon R avant un nouveau dépôt. Rappellons que ce profil se situe en haut d'une petite pente et surplombe une zone marécageuse très humide (cours d'eau longeant le bas de la pente).

IIR : dès 40/45 cm. Roche en place sous forme de blocs légèrement altérés en surface et plus fortement contre le haut du profil où quelques uns d'entre eux sont très attaqués. Ces roches diffèrent beaucoup de celles de BA-5 et BA-6. Elles sont plus grises et ressemblent plus à des gneiss avec des quartzites à l'intérieur.

Résultats des analyses

Horizon	pH H_2O	pH KCl
A	4.3	3.4
Eh	4.4	3.3
BPh	5.0	4.0
BPs	5.1	4.1
BPsC	5.2	4.1
IIC centre	5.1	4.2

FURKA PASS 1 (FK1)	PODZOSOL MEUBLE à mor	
Date: 25.8.98	**Coordonnées:**	**CN n°:**
Altitude: 2420 m	**Pente:** 12°	**Exposition:** 134°N
Géologie: gneiss		
Végétation: pelouse acidophile à Nardus stricta		
Topographie: replat en bas de pente		
Météo: couvert puis ensoleillé. Tempête la veille et gelée pendant la nuit.		



OL: +1 - 0 cm. Feuilles et gaines de graminées, mousses. Horizon peu important.

OFr: 0 - 1 cm. Feuilles mortes superposées, de plus en plus feutrées, avec de plus en plus de boulettes fécales. Limite horizontale, transition nette.

OFm: 1 - 1,5 cm. Couche fine avec débris quasi inidentifiables, forte proportion de boulettes fécales (20-30%). Racines 2/5, moyennes et fines. Limite horizontale, transition diffuse.

OH: 1,5 - 3 cm couleur: noir. Structure ± grumeleuse, essentiellement fournie par les racines. Beaucoup de boulettes fécales (> 70%). Texture sableuse + matière organique. Racines 2/5, fines. pH 4,5. Limite horizontale, transition nette.

AE: 3 - 4/6 cm couleur: brun-gris avec dominance grise, sur la droite quelques taches rouille à la limite inférieure. Structure microgrumeleuse à grumeleuse. Texture limono-sableuse. Porosité moyenne. Racines 3/5 à gauche, 2 voir 1/5 à droite, moyennes et fines. Pas de squelette. pH 4. Limite ondulée, transition progressive.

E: 4/6 - 10 cm couleur: gris. Structure vaguement polyédrique puis particulaire. Texture sableuse. Porosité forte. Racines 2/5 (plus nombreuses à gauche), moyennes et fines. Squelette (5-10%): graviers ø 3 à 4 mm et poches de graviers ø 8 à 15 mm (quartz et gneiss relativement altéré, avec taches d'oxydation sur la roche), présence de quelques cailloux plus gros et altérés à la base de l'horizon. pH 4. Limite ondulée, transition progressive.

EBPh: 10 - 13 cm couleur: gris foncé. Structure polyédrique (puis éventuellement particulaire). Texture sablo-limoneuse. Porosité forte à moyenne. Racines 1/5, moyennes. Squelette (10%): quelques cailloux (blancs laiteux avec taches d'oxydation dessus) plus gros (ø 3 à 4 cm) avec un fort cortex d'altération et graviers ø 5 à 10 mm. pH 4. Limite ondulée, transition progressive.

BPh: 13 - 17 cm couleur: noir dominant, quelques taches d'oxydation autour des cailloux. Structure polyédrique et grumeleuse (polyèdres ø 10-12 mm ou 5-6 mm dominants et quelques grumeaux de petite taille, ø 2-5 mm). Texture sablo-limoneuse + beaucoup de matière organique. Porosité moyenne. Racines 2/5, fines et moyennes. Squelette (10-15%): gneiss en lamelles se cassant à la lame ou dans la main pour les plus gros, traces d'oxydation du fer sur et dans les cailloux ainsi qu'autour d'eux (pellicule d'altération). pH 4. Limite ± horizontale, transition progressive.

BPhBPs: 17 - 22 cm couleur: brun-noir avec mosaïque de poches ocres, rousses et noires. Structure polyédrique. Texture sablo-limoneuse à limono-sableuse. Porosité moyenne. Racines 2 à 3/5, moyennes et fines. Squelette (20%): nombreux graviers de toutes tailles jusqu'à ø 15mm, tous altérés (se désagrègent ou cassent dans la main); cailloux ø 3 à 4 cm, très altérés. pH 4. Limite horizontale, transition progressive.

BPs: 22 - 32 cm couleur: brun-ocre avec nombreuses traces d'oxydation et de discrètes taches verdâtres (pluie?). Structure micropolyédrique à particulaire (quelques rares faces, structure peu évidente essentiellement due aux cailloux). Texture sablo-limoneuse (proportion de sables accrue par rapport au précédent). Porosité moyenne à forte. Racines 1/5, fines. Squelette (40 %): toutes les tailles de ø 2 à 3 mm (dominants, maximum d'altération) à 20-30 mm (altération moyenne) puis 4 à 5 cm (minimum d'altération. Il y a beaucoup de cailloux dans cet horizon, ce qui le rend difficile à creuser). La plupart de ces cailloux semble cohérente mais ils s'effritent entre les doigts en une pâte très rouge mêlée de sables et de micas. pH 4. Limite horizontale, transition diffuse.

BPsC: 32 - 40 cm couleur: ocre-gris. Horizon ± induré. Structure polyédrique puis particulaire (un peu mieux développée qu'en BPs, la structure semble toujours donnée par les cailloux désagrégés). Texture limono-sableuse (éventuellement traces d'argiles dues à l'altération). Porosité moyenne. Racines 1/5, fines. Squelette (50%): tailles relativement plus petites qu'au-dessus quoique le squelette soit proportionnellement plus important; forte présence de graviers ø 5 à 6 mm moins altérés qu'avant; cailloux ø 15 à 20 mm un peu moins cassants qu'auparavant. Trouvé un nodule de fer. pH 4 - 4,5. Limite ± horizontale, transition nette. Sur la gauche, cet horizon se termine sur une superposition de plaques de gneiss complètement détériorées, suivies par une barre de taches d'oxydation à 38 cm.

C: 40 - 50 cm couleur: gris-brun. Horizon contenant une forte proportion de roche et de graviers et très peu de terre fine. Structure particulaire. Texture limono-sableuse (probablement traces d'argiles mais pas évident car horizon détrempé), présence de grains de quartz et d'écailles de mica. Porosité moyenne. Pas de racines. Squelette (90%): tous ø, de quelques mm à 10-15 mm, moins altérés voire pas; cailloux ø 5-6 cm et grosses roches en place (40 cm de long) avec faible altération en surface (pellicule dans laquelle la suspicion d'argiles s'accroît).

Résultats des analyses

Horizon	pH H_2O	pH KCl
OL et OF	4.81	3.39
OH	4.40	3.23
AE	4.31	3.08
E	4.50	2.93
EBPh	4.63	3.31
BPh	4.66	3.62
BPhBPs	4.73	3.83
BPs	4.84	3.87
BPsC	4.46	3.89
C	5.25	4.06

FURKA PASS 2 (FK2)

ALOCRISOL TYPIQUE
brun, à mésomull, de gneiss altéré

Date: 25.8.98

Coordonnées:

CN n°:

Altitude: 2646 m

Pente: 2°

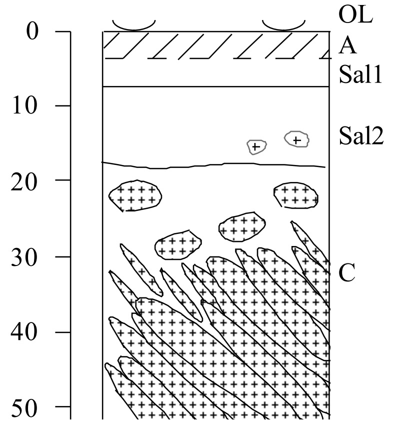
Exposition: 231°N

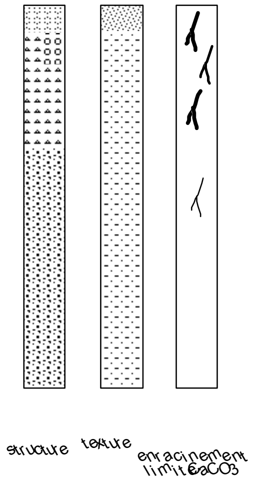
Géologie: gneiss

Végétation: pelouse acidophile à Carex curvula

Topographie: replat

Météo: soleil et léger vent. Tempête la veille et gelée pendant la nuit.





OL: +0,5 - 0 cm. Quasiment absent. Quelques rares feuilles mortes, lichens et gaines minuscules. L'humus est quasi inexistant. On n'observe vaguement des traces qui pourraient être assimilées à un horizon OF ou à un horizon OLv.

A: 0 - 3 cm couleur: brun-noirâtre. Structure feutrée essentiellement due aux racines qui forment un lacis très dense, présence de microgrumeaux entre les racines. Il semble y avoir juxtaposition de boulettes fécales ± noires, de particules organo-minérales brunes et de grains de quartz et de mica. Texture sableuse + matière organique. Porosité forte (horizon extrêmement sec). Racines 5/5, moyennes et surtout fines. Squelette (0%): vague présence de graviers ø 1mm. pH 4. Limite horizontale, transition diffuse (racines).

Sal1: 3 - 7 cm couleur: brun chocolat. Structure en polyèdres qui se "cassent" en grumeaux. Texture limono-sableuse. Porosité moyenne à faible. Racines 3/5, essentiellement fines et quelques moyennes. Squelette (5%): graviers ø 3mm plats et altérés; morceau de quartz fumé de ø 15 mm, non altéré. pH 4. Limite horizontale, transition ± nette.

Sal2: 7 - 17 cm couleur: brun un peu plus roux. Structure pas évidente, le fort taux de racines permet de maintenir un semblant de structure en macropolyèdres mais pour l'essentiel micropolyèdres se cassant facilement. Texture limono-sableuse. Porosité moyenne à faible. Racines 4/5, moyennes et fines. Squelette (10%): graviers de l'ordre du mm; nombreux graviers ø 6-10 mm aplatis et cassants (gris=gneiss) ou brillants et plus dodus (quartz); quelques cailloux ø 3 à 4 cm ± aplatis et altérés en surface (couteau). pH 4+. Limite ± horizontale, transition nette.

C: 17 - 50 cm couleur: brun-gris-roux. Enorme horizon formé de la roche en place qui ne possède plus de cohésion véritable et se délite facilement. Présence de terre fine entre les différentes plaques jusqu'à 50 cm. Grande concentration de racines dans les interstices, avec la terre fine. Structure particulaire. Texture sablo-limoneuse. Porosité moyenne à forte. Racines 1 à 2/5, essentiellement moyennes et quelques fines. Squelette (90%): graviers de toutes tailles (jusqu'à l'écaille de mica), essentiellement aplatis; plaques de roche mates et brunies en surface (altération), quelques fois avec taches d'oxydation, ne se cassent pas transversalement mais se délitent selon leurs plans de clivages en plaques brillantes et grises contre l'intérieur (micas). pH 4,5.

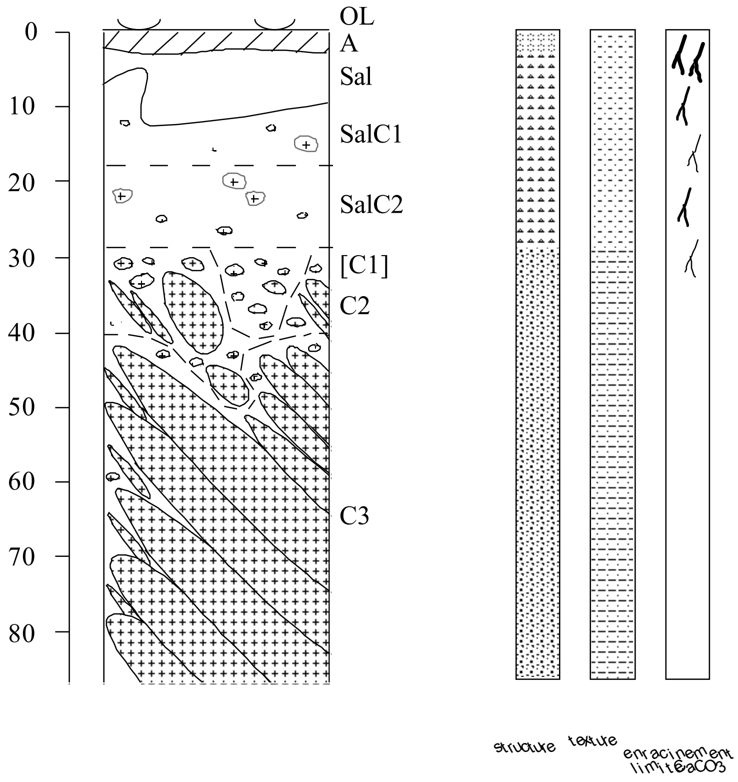
Résultats des analyses

Horizon	pH H_2O	pH KCl
A	4.47	3.32
Sal1	4.64	3.19
Sal2	5.02	3.96
C	5.11	4.17

Horizon	Mg^{2+}	Na^{+}	Ca^{2+}	K^{+}	Al^{3+}	H^{+}
	milliéquivalents / 100g					
Sal2	0.03	0.11	0.01	0.05	4.2	4.78

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
Sal2	0.21	8.98	9.18	2	46

FURKA PASS 3 (FK3)	ALOCRISOL TYPIQUE brun, à eumull, de gneiss altéré	
Date: 25.8.98	**Coordonnées:**	**CN n°:**
Altitude: 2795 m	**Pente:** 16°	**Exposition:** 243°N
Géologie: gneiss		
Végétation: pelouse acidophile à Carex curvula		
Topographie: pente		
Météo: soleil et léger vent. Tempête la veille et gelée pendant la nuit.		



OL: +0,5 - 0 cm. Quasiment inexistant. Quelques feuilles mortes, lichens.

A: 0 - 3 cm couleur: brun-gris. Structure essentiellement dominée par un dense lacis racinaire, avec microgrumeaux (en particulier autour des racines) puis particulaire. Divers éléments sont juxtaposés (mais cela reste moins net que dans le sol n° 2): terre fine brune, quelques rares boulettes fécales noires, grains de quartz et écailles de mica. Texture sablo-limoneuse avec une discrète présence de matière organique. Porosité forte (horizon relativement sec). Racines 5/5, essentiellement fines et quelques moyennes (ø 3mm). Squelette (0%): présence rare de graviers ø 2-3 mm. pH 4. Limite ± ondulée, transition nette.

Sal: 3 - 4/11 cm couleur: brun chocolat. Structure polyédrique (gros polyèdres ø 15 - 20 mm et polyèdres plus petits ø 5 mm) puis particulaire. Texture limono-sableuse. Porosité moyenne. Racines 2/5, essentiellement moyennes et quelques fines. Squelette (0%): quelques graviers anecdotiques (ø 1 mm). pH 4. Limite ondulée, transition nette.

SalC1: 4/11 - 17 cm couleur: brun tirant sur le jaune, voire le roux. Structure polyédrique (polyèdres ø 5-10 mm) puis particulaire. Présence de grains de quartz et d'écailles de mica. Texture sablo-limoneuse. Porosité moyenne. Racines 2/5, moyennes. Squelette (env. 20%): graviers ø 5 mm, 7-8 mm puis 10-15 mm, tous très altérés et cassants; cailloux ø 2-3 cm, très altérés. pH 4. Limite horizontale, transition graduelle.

SalC2: 17 - 27/28 cm couleur: brun tirant sur le jaune, voire le roux. Structure polyédrique (polyèdres ø 5-10 mm) puis particulaire. Présence de grains de quartz et d'écailles de mica. Texture sablo-limoneuse. Porosité moyenne. Racines 3/5, moyennes. Squelette (30%): essentiellement cailloux ø 2 à 4 cm. pH 4,5. Limite ± horizontale, transition diffuse.

[C1]: 27/28 - 40 cm à droite couleur: ocre-gris. Zone qui diffère de ce qu'il y a autour et en dessous. Il s'agit peut-être d'une transition ou d'une "coulée" de l'horizon précédent à la faveur du gros cailloux quartzeux. Structure particulaire. Texture sablo-limoneuse à limono-sableuse (peut-être même y a-t-il des traces d'argile d'altération). Porosité moyenne à faible. Racines 1/5, essentiellement moyennes et quelques fines. Squelette (50%): graviers de type gneiss, ø 1 mm à 20-30 mm, tous s'effritent avec un effort modéré. pH 5.

C2 et C3: 27/28 - 85 cm couleur générale: ocre-gris. Grande zone de roche totalement corrodée qui se "dilue" quasiment dans la main et y laisse beaucoup de paillettes de mica. Structure apparente de roche en plaques ± épaisses superposées, se démembrant sitôt qu'on les touche. Texture probablement mixte avec sables, limons et argiles libérées par la roche. Porosité moyenne à faible. Racines 0,5/5, quelques racines fines se glissant entre les plaques. Squelette (> 90%): gneiss intègre en apparence mais en réalité très corrodé; présence de deux cailloux de quartz ± impur altérés seulement en surface (pellicule brune) dans le tiers supérieur de l'horizon, d'où une distinction lors du prélèvement:
- C2: 27/28 - 40/50 cm: cailloux plus quartzeux. Limite ondulée, transition diffuse.
- C3: 40/50 - 85 cm: gneiss dominant

pH 4,5 pour l'ensemble des deux horizons.

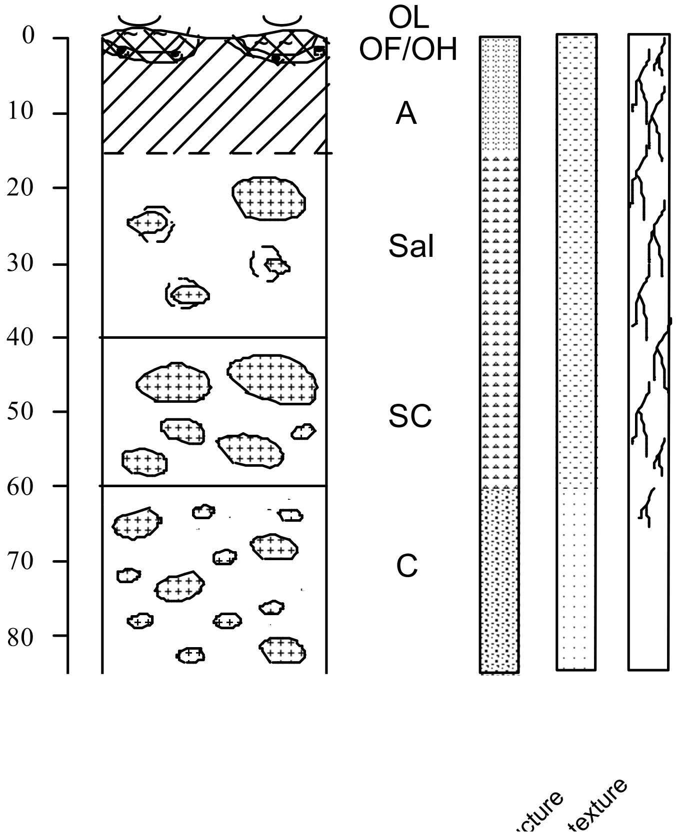
Résultats des analyses

Horizon	pH H_2O	pH KCl
A	4.60	3.40
Sal	4.79	3.32
SalC1	5.07	3.71
SalC2	5.27	4.03
[C1]	5.55	4.12
C2	5.66	4.05
C3	5.69	3.06

Horizon	Mg^{2+}	Na^+	Ca^{2+}	K^+	Al^{3+}	H^+
	milliéquivalents / 100g					
Sal	0.09	0.10	0.03	0.10	5.61	6.51
SalC1	0.04	0.11	0.01	0.07	2.36	2.96
SalC2	0.02	0.10	0.01	0.06	2.27	2.88

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
Sal	0.32	12.13	12.44	3	45
SalC1	0.24	5.32	5.56	4	43
SalC2	0.19	5.15	5.34	3	43

<table>
<tr><td>ALETSCH
Hindererhinertüre (HT1)</td><td colspan="2">ALOCRISOL TYPIQUE
brun, à eumoder sporadique</td></tr>
<tr><td>Date: 25.8.99</td><td>Coordonnées: 649.300/147.275</td><td>CN n°: 1249</td></tr>
<tr><td>Altitude: 2580 m</td><td>Pente: 12°</td><td>Exposition: SE (197° N)</td></tr>
<tr><td colspan="3">Géologie:</td></tr>
<tr><td colspan="3">Végétation: pelouse à <i>Nardus stricta</i></td></tr>
<tr><td colspan="3">Topographie: croupe avec terrassettes de solifluxion</td></tr>
<tr><td colspan="3">Météo: soleil</td></tr>
</table>



La présence d'humus est fortement liée aux touffes de graminées. Là où il est présent, il présente trois couches distinctes mais mal développées.

OL: +0.5 – 0 cm. Feuilles et gaines de fétuque. Horizon peu développé, apparaissant surtout sous les touradons.

OF: 0 – 0.5/2.5 cm. Horizon sporadique et très fibreux, lié également à la présence des touradons, composé de gaines très tassées et ± décomposées.

OH: 0.5/2.5 – 1/3 cm. Couleur : noir. Horizon sporadique, sans structure, résultant de la juxtaposition entre des granules de matière organique et des grains de quartz. Forte présence de racines fines (3/5).

A: 1/3 - 15 cm. Couleur: brun gris. Structure microgrumeleuse à grumeleuse (grumeaux de ø 2 - 5 mm, peu stables). Horizon présentant une juxtaposition des matières organique et minérale. Texture limono-sableuse à sablo-limoneuse. Porosité forte. Racines 5/5, fines, moyennes et grosses, niveau principal d'enracinement. Squelette (<5%): graviers ø max 5 mm. Limite horizontale, transition diffuse (structure et taux d'humidité). pH 4+.

Sal : 15 - 40 cm. Couleur: brun, tirant plus sur le jaune que l'horizon A. Structure polyédrique (polyèdres ø 10 - 12 mm et ø 5 – 6 mm, moyennement à faiblement stables, se cassent tous en polyèdres plus petits).

Texture limono-sableuse. Porosité moyenne à faible. Racines 4/5, grosses et moyennes. Squelette (40 %): pierres ø 10 cm ± allongées, siliceuses ; cailloux ø 3 – 5 cm, granites faiblement altérés en surface et allongés (quartzites ?) ; graviers jusqu'à ø 10 – 15 mm ; les pierres et les cailloux dominent. Limite horizontale, transition ± nette (squelette). pH 4.

SC: 40 - 60 cm. Couleur: brun tirant encore plus sur le jaune. Structure polyédrique (polyèdres ø 10 – 12 mm peu stables se cassant en polyèdres ø 6 – 8 mm et 4 – 5 mm peu stables), puis particulaire. Texture limono-sableuse. Porosité moyenne à faible. Racines 2/5, moyennes. Squelette (80 – 90 %): blocs 15 – 20 cm, cailloux 3 – 10 cm et graviers peu présents ; dominants : cailloux et blocs, type granite arrondis pour les cailloux, allongés pour les blocs. Limite horizontale, transition ± nette. pH 4.

C: 60 - 85 cm et plus. Couleur: brun-jaune. Structure particulaire. Texture sableuse avec traces de limons. Porosité forte. Racines 0.5/5, fines. Squelette (90%): granulométrie beaucoup plus fine que celle de l'horizon précédent ; quleques pierres ø 8 – 10 cm (peu nombreuses) ; cailloux ø 3 – 5 cm (dominants) ; graviers ø 3 – 10 mm (grand nombre. Les cailloux sont altérés en surface ou se cassent facilement. La proportion de squelette est comparable à celle de SC mais sa répartition est différente (taille des fragments plus inférieure). pH 4.

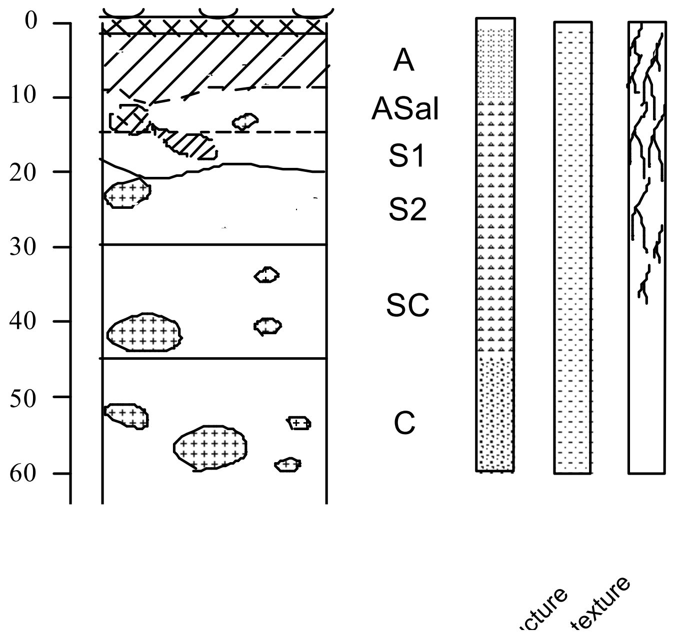
Résultats des analyses

Horizon	pH H_2O	PH KCl
A	4.7	3.7
Sal	5.1	4.0
SC	5.5	4.3
C	5.7	4.3

Horizon	Mg^{2+}	Na^{+}	Ca^{2+}	K^{+}	Al^{3+}	H^{+}
	milliéquivalents / 100g					
Sal	0.20	0.08	0.00	0.05	3.14	9.63

Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
Sal	0.32	12.78	13.10	2	24

ALETSCH Hindererhinertüre (HT2)	ALOCRISOL TYPIQUE sur BRUNISOL OLIGOSATURE tronqué	
Date: 25.8.99	**Coordonnées:**	**CN n°:** 1249
Altitude: 2710 m	**Pente:** nulle	**Exposition:**
Géologie:		
Végétation: pelouse à *Carex curvula*		
Topographie: larges croupes		
Météo: soleil		



Ce sol a fait l'objet d'une description de terrain réalisée par Adriana Carnelli qui a été complétée par la description des échantillons et l'analyse d'une photographie reçus par Gaëlle Vadi.

Humus: OL fragmentaire et poches ± épaisses sous les touffes de graminées.

A: 2 - 10 cm. Couleur: brun marron. Structure microgrumeleuse. Texture sablo-limoneuse. Racines 5/5, fines et moyennes, dense feutrage racinaire à ce niveau. Squelette (<5%): graviers et grains de quartz. Limite ondulée, transition diffuse.

ASal: 10 – 15 cm. Couleur: brun-rougeâtre. Structure polyédrique avec une sous-structure grumeleuse peu nette. Texture sablo-limoneuse. Racines 4/5, fines et moyennes. Squelette (5 – 10 %): cailloux ø 1 – 2 cm et beaucoup de graviers. Limite horizontale transition peu nette.

A cheval entre cet horizon et le suivant, présence de poches très noires qui ont été échantillonnées à part :

a) à 12 cm, sur la gauche du profil, zone présentant des alternances entre poches très noires (charbons) et taches brunes-noires. Macrostructure polyédrique, microstructure grumeleuse. Texture sablo-limoneuse à limono-sableuse. Racines 3-4/5, fines et moyennes. L'échantillon fourni présente un squelette de 5 – 10 %, formé de cailloux jusqu'à 1.5 cm de ø et de graviers de 8 – 15 mm ø. De nombreux charbons ont été observés dans l'échantillon ; ils mesurent 1 – 3 mm de long.
b) Poche noire en forme de larme sise entre 12 et 18 cm. Couleur : très noir. Structure vaguement grumeleuse. Texture sablo-limoneuse avec forte présence de matière organique. Présence de quelques racines. Squelette apparent < 5 %, formé de quelques graviers.

S1: 15 – 20 cm. Couleur: brun-noirâtre. Structure micropolyédrique peu stable, essentiellement autour des racines, puis particulaire. Texture sablo-limoneuse. Racines 3/5, moyennes et quelques fines. Squelette (10 – 20 %): pierres allongées de 25 – 30 cm de long et 3-5 voire 10 de large; cailloux ø 1 – 3 cm et beaucoup de graviers. Limite ondulée, transition ± nette (racines).

S2: 20 - 30 cm. Couleur: brun roussâtre. Structure polyédrique peu stable. Texture limono-sableuse. Racines 1/5, fines et moyennes. Squelette (~ 20 %): pierre ± arrondie ø approx. 6 cm, cailloux jusqu'à ø 4 cm et beaucoup de graviers ø 8 – 10 mm. Limite subhorizontale, transition ± nette (racines, structure).

SC: 30 – 45 cm. Couleur : transition brun-rouge à brun jaune. Strucure polyédrique peu stable à tendance particulaire. Texture sablo-limoneuse à limono-sableuse. Racines : traces, 1/5, fines. Squelette (~30 %) : pierres arrondies ø 10-15 cm, cailloux jusqu'à 5 cm ø, graviers 8 – 15 mm en grand nombre. Limite horizontale, transition ± nette (structure, texture).

C: 45 - 60 cm et plus. Couleur: brun-ocre à ocre-brun. Structure particulaire (traces de micropolèdres dans les 5 premiers cm de l'horizon, mais ils sont peu stables). Texture sablo-limoneuse. Racines 0/5. Squelette (~ 50 %): pierres 5 – 10 cm ; cailloux jusqu'à ø 3 cm (dominants) ; graviers 8 – 15 mm.

Résultats des analyses

Profondeur	Horizon	pH H_2O	pH KCl	Corg (%)
2 – 3 cm	A	4.9	3.8	7.73
5 – 10 cm	A	4.9	3.8	6.29
10 – 15 cm	ASal	4.9	3.6	4.00
15 – 20 cm	S1	5.0	3.6	2.34
20 – 25 cm	S2	5.2	3.8	1.75
25 – 30 cm	S2	5.3	3.9	1.55
30 – 35 cm	SC	5.4	4.1	n.d.
35 – 40 cm	SC	5.4	4.1	n.d.
40 – 45 cm	SC	5.4	3.9	n.d.
45 – 50 cm	C	5.4	3.9	n.d.
50 – 55 cm	C	5.4	3.9	n.d.
55 – 60 cm	C	5.6	3.8	n.d.
Poche noire (a)	-	5.1	3.7	n.d.

Profondeur	Horizon	Mg^{2+}	Na^+	Ca^{2+}	K^+	Al^{3+}	H^+
		milliéquivalents / 100g					
10 – 15 cm	ASal	1.03	0.14	0.06	0.13	3.55	10.36
15 – 20 cm	S1	0.58	0.07	0.03	0.10	1.57	8.09

Profondeur	Horizon	S (mé/100g)	A (mé/100g)	T (mé/100g)	V (%)	Al^{3+} dans T (%)
10 – 15 cm	ASal	1.35	13.91	15.26	9	23
15 – 20 cm	S1	0.78	9.66	10.44	7	15

Figure 1: Représentation synthétique de l'ensemble des sols en fonction de

On remarque une limite nette entre les sols marqués fortement par la

(PODZOSOLS) et les sols dans lesquels la podzolisation est très faible LOCRISOLS)

voire nulle (BRUNISOLS).

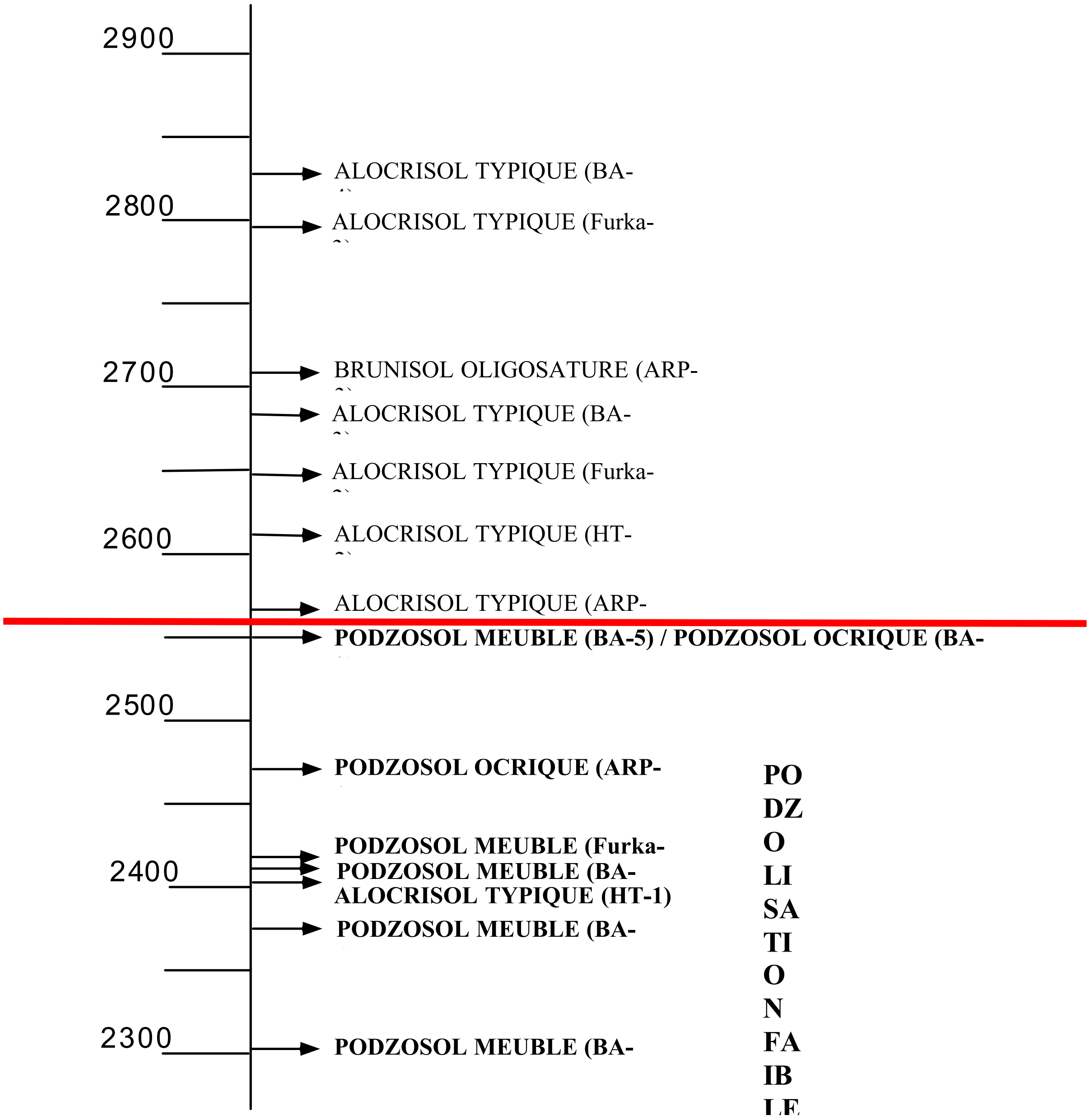


Tableau 1A: Valeurs de pH mesurées dans les différents sols.

Site	profil	horizon	pH H2O	pH KCl	pH
Arpette	1	OFr et OFm	4.54	3.30	1.24
		OH	4.47	3.42	1.05
		A	4.50	3.42	1.08
		ABPh	4.73	3.66	1.07
		BPh	4.99	3.94	1.05
		BPsBPh	5.12	4.08	1.04
		BPs1	5.18	4.13	1.05
		BPs2	5.35	4.18	1.17
		[C1]	5.14	4.30	0.84
		C2	5.27	4.27	1.00
	2*	2-5cm	4.74	3.36	1.38
		5-10cm	5.02	3.86	1.16
		10-20cm	5.20	4.00	1.20
		20-30cm	5.18	4.08	1.10
		30-40cm	5.34	4.18	1.16
		[30-40cm]	5.30	4.09	1.21
		40-50cm	5.36	4.24	1.12
		50-60 cm	5.33	4.22	1.11
		60-70 cm	4.97	4.16	0.81
		> 70 cm	5.00	4.28	0.72
	3	OA	5.17	3.95	1.22
		A	4.57	3.49	1.08
		SC	4.79	3.71	1.08
		C1	4.68	3.73	0.95
		C2	5.13	4.09	1.04

Tableau 1B Valeurs de pH mesurées dans les différents sols.

Site	profil	horizon	pH H2O	pH KCl	pH
Belalp	1	OF1 et OF2	5.29	4.10	1.19
		AE	4.70	3.36	1.34
		Eh	4.72	3.41	1.31
		EhBPs	5.00	3.75	1.25
		BPs	5.02	3.79	1.23
		BPsC	5.14	3.88	1.26
		C1	5.23	4.07	1.16
		C2	5.28	4.12	1.16
	2	OF1 et OF2	4.77	3.67	1.10
		AE	4.43	3.25	1.18
		[Eh]	4.41	3.21	1.20
		BPh	4.47	3.13	1.34
		BPs	4.65	3.47	1.18
		BPsC	4.80	3.34	1.46
		C	4.82	3.11	1.71
	3 partie gauche	OF	5.05	3.81	1.24
		Ah	4.51	3.52	0.99
		Sal1	4.62	3.56	1.06
		Sal2	4.66	3.36	1.30
		SalC	4.81	2.99	1.82
		C	5.16	3.00	2.16
	3 partie droite	OF	5.22	4.21	1.01
		Ah	4.60	3.63	0.97
		S(al)	4.52	3.44	1.08
		Sal	4.73	3.14	1.59
		C	5.07	3.11	1.96
		R	5.13	3.35	1.78
	4	OF et [OH]	5.10	4.30	0.80
		A(E)	4.56	3.06	1.50
		A	4.39	3.15	1.24
		Sal	4.30	3.12	1.18
		SalC	4.53	3.29	1.24
		C	4.89	3.55	1.34

Tableau 1C: Valeurs de pH mesurées dans les différents sols.

Site	profil	horizon	pH H2O	pH KCl	pH
Furka Pass	1	OL et OF	4.81	3.39	1.42
		OH	4.40	3.23	1.17
		AE	4.31	3.08	1.23
		E	4.50	2.93	1.57
		EBPh	4.63	3.31	1.32
		BPh	4.66	3.62	1.04
		BPhBPs	4.73	3.83	0.90
		BPs	4.84	3.87	0.97
		BPsC	4.46	3.89	0.57
		C	5.25	4.06	1.19
	2	A	4.47	3.32	1.15
		Sal1	4.64	3.19	1.45
		Sal2	5.02	3.96	1.06
		C	5.11	4.17	0.94
	3	A	4.60	3.40	1.20
		Sal	4.79	3.32	1.47
		SalC1	5.07	3.71	1.36
		SalC2	5.27	4.03	1.24
		[C1]	5.55	4.12	1.43
		C2	5.66	4.05	1.61
		C3	5.69	3.06	2.63

Tableau 2: Teneurs en carbone organique (Corg.) et en matière organique (M.O.).

Site	profil	horizon	Corg. (%)	M.O. (%)
Belalp	6	BPh	2.66	5
		BPs	1.21	2
Aletsch	2*	2 - 3 cm	7.73	13
		5 - 10 cm	6.29	11
		10 - 15 cm	4.00	7
		15 - 20 cm	2.34	4
		20 - 25 cm	1.75	3
		25 - 30 cm	1.55	3

ANNEXE B

Calculation of the estimated biogenic silica production in Chapter 4.1

To estimate the biogenic silica production of the plant communities listed in Tab.4.1.3, the different species that are present in the communities and their relative abundances, obtained averaging several vegetation surveys carried out in the sampling areas (Theurillat, Schüssel, unpublished), were taken into considerations.

For **swards** dominated by one species, the stands were considered as approximately monospecific and the silica input was assessed considering the biogenic silica production of the dominant species, its APP and the length of the vegetative season. This approximation introduced an overestimate of the silica production by some 20- 35%, since the presence in the swards of a small amount of forbs and low shrubs with a very low or negligible silica production is not considered. This calculation was applied to: *Carex curvula* cryophilous alpine sward; *Festuca scabriculmis* subsp. *luedii* thermophilous low alpine sward; *Carex sempervirens* mesophilous upper subalpine sward; *Nardus stricta* mesophilous subalpine sward, and to the *Calamagrostis villosa* understory mesophilous subalpine tall-herb community (Tab. 4.1.3).

For the plant communities constituted by **heaths** and **shrubs,** the calculations took into account the differential production of silica by herbaceous and woody tissues.

In the **subalpine** and **alpine heaths** in which several species are usually codominant (*i. d.*: *Vaccinium uliginosum* - *Empetrum nigrum* cryophilous upper subalpine dwarf shrub heath; *Rhododendron ferrugineum* - *Vaccinium myrtillus* mesophilous subalpine heath; *Arctostaphylos uva-ursi* - *Juniperus nana* thermophilous subalpine heath; *Arctostaphylos uva-ursi* - *Calluna vulgaris* meso-thermophilous subalpine heath), the average abundance (**A**) of each species was taken into account. This value is an average from vegetation surveys, expressed as percentage cover of each species in the community. The sum of the percentages of cover may exceed 100% as a consequence of the stratification in the canopy. The relative abundance of a species (**a**) is defined as: $\mathbf{a} = \mathbf{A}/\mathbf{A}_{\mathbf{tot}}$ (where $\mathbf{A}_{\mathbf{tot}}$ is the sum of the percentage covers).

In order to take into account the biomass of the species, the ratio between the biomass of herbaceous tissues (***h***) and woody tissues (***w***) for each community was taken from the literature (***h: w***) (Tab. A) and applied uniformly to every species in the community. The relative biogenic silica production for herbaceous tissues for a species (**H**), is therefore: $\mathbf{H} = \mathbf{a} \cdot \mathbf{p}h \cdot \mathbf{BS\%}_{\mathbf{corr}}$ (where $\mathbf{p}h = h/(h+w)$, and $\mathbf{BS\%}_{\mathbf{corr}}$ is the silica content in the herbaceous tissues of the species from Tab. 4.1.2).

In the same way the relative biogenic silica production for woody tissues for a species (**W**) is : $\mathbf{W= a\cdot p}\boldsymbol{w}\cdot \mathbf{BS\%_{corr}}$ (where $\mathbf{p}\boldsymbol{w}\mathbf{=}\ \boldsymbol{w/(h+w)}$ and $\mathbf{BS\%_{corr}}$ is the silica content in the woody tissues of the species from Tab 2). The total production of biogenic silica by in a certain community ($\mathbf{BS_{(H,W)}}$) was given by the addition of all the contributions from the herbaceous and woody tissue of the single species: $\mathbf{BS_{(H,W)}= H_{tot} + W_{tot}}$.

For the **shrub communities** dominated by one species (*i. d.* : *Salix helvetica* upper subalpine cryophilous shrubs; *Alnus viridis* mesophilous subalpine shrubs; *Loiseleuria procumbens* cryophilous low alpine dwarf shrub heath) the silica production is calculated in the same way, but the stands were considered monospecific.

For all the woody vegetations the herein estimates refer to the silica input into the soil due to the canopy. The possible presence in the understory of forbs and low shrubs can be neglected since their production of biogenic silica is very low. However, the neglect of the possible presence of grasses (e. g. *Calamagrostis villosa*) would lead to an underestimate of the silica input.

Finally, the predicted biogenic silica inputs displayed in Tab. 4.1.3 are calculated multiplying the length of the vegetative season, by the average APP of the community, by the production of silica in herbaceous and woody tissues in the community.

TABLE A.

PLANT COMMUNITIES AND LIST OF THE SPECIES	*h:w*	*A* (%)	a	ph	H	pw	W	BS$_{(H,W)}$
Vaccinium uliginosus- Empetrum nigrum **cryophilous upper subalpine dwarf shrub heath**								
Empetrum nigrum		50	0.36	0.8	0.046	0.2	0.0079	0.054
Vaccinium uliginosum		50	0.36	0.8	0.029	0.2	0.0058	0.0346
Vaccinium myrtillus		10	0.07	0.8	0.0022	0.2	0.0004	0.0027
Calluna vulgaris		10	0.07	0.8	0.038	0.2	0.0095	0.0476
Rhododendron ferrugineum		10	0.07	0.8	0.0022	0.2	0.00014	0.0024
Juniperus nana		10	0.07	0.8	0.0039	0.2	0.0021	0.0060
Total	4 : 1*a*	140	1.00	-	0.1214	-	0.0259	**0.147**
Rhododendron ferrugineum-Vaccinium myrtillus **mesophilous subalpine heath**								
Rhododendron ferrugineum		60	0.4	0.67	0.011	0.33	0.0013	0.012
Vaccinium myrtillus		40	0.27	0.67	0.0072	0.33	0.0027	0.0099
Juniperus nana		10	0.07	0.67	0.0033	0.33	0.0035	0.0067
Vaccinium vitis-idaea		10	0.07	0.67	0.0014	0.33	0.00069	0.0021
Vaccinium uliginosum		10	0.07	0.67	0.0047	0.33	0.0018	0.0065
Empetrum nigrum		10	0.07	0.67	0.0075	0.33	0.0025	0.010
Calluna vulgaris		10	0.07	0.67	0.0319	0.33	0.016	0.048
Total	2 : 1~	150	1.02	-	0.0667	-	0.028	**0.095**
Arctostaphylos uva-ursi, Juniperus nana **thermophilous subalpine heath**								
Arctostaphylos uva-ursi		90	0.75	0.67	0.015	0.33	0.052	0.067
Vaccinium vitis-idaea		10	0.08	0.67	0.0016	0.33	0.00079	0.0024
Juniperus nana		10	0.08	0.67	0.0037	0.33	0.004	0.0077
Calluna vulgaris		10	0.08	0.67	0.0364	0.33	0.018	0.0544
Total	2 : 1~	120	0.99	-	0.057	-	0.075	**0.131**
Arctostaphylos uva-ursi, Calluna vulgaris **thermophilous subalpine heath**								
Arctostaphylos u.-u.		60		0.8	0.012	0.2	0.021	0.033
Vaccinium v.-i.		10	0.08	0.8	0.00192	0.2	0.00048	0.0024
Juniperus n.		10	0.08	0.8	0.00448	0.2	0.0024	0.0069
Calluna v.		40	0.33	0.8	0.17952	0.2	0.04488	0.22
Total	4 : 1~	120	0.99	-	0.19792	-	0.06876	**0.267**
Salix helvetica **upper subalpine cryophilous shrubs**								
Salix herbacea	3 : 1~	100	1	0.75	0.04	0.25	0.1075	**0.137**
Alnus viridis **mesophilous subalpine shrubs**								
Alnus viridis	3 : 1*b*	100	1	0.75	0.097	0.25	0.01	**0.107**
Loiseleuria procumbens **cryophilous low alpine dwarf shrub heath**								
Loiseleuria procumbens	6 : 1*a*	100	1	0.86	0.2	0.14	0.0112	**0.218**

(a) from **Klug-Pümpel, B. 1978.** Phytomasse und Primärproduktion von unterschiedlich bewirtschafteten Almflächen im Gasteiner Tal. In: Cernusca A, *ed. Ökologische Analysen von Almflächen im Gasteiner Tal. Innsbruck: Universitätsverlag Wagner, 123-142*; *(b)* **Rehder, H. 1970.** Zur Ökologie insbesondere Stickstoffversorgung subalpiner und alpiner Pflanzengesellschaften im Naturschutzgebiet Schachen (Wettersteingebirge). *Dissertationes Botanicae* 6: 1-90.

(~) estimated values.

ANNEXE C

INVESTIGATING THE VEGETATION HISTORY AT THE ALPINE TREELINE IN THE CENTRAL ALPS: CONTRIBUTION FROM PHYTOLITHANALYSIS

A. L. CARNELLI[1], M. MADELLA[2] and J.-P. THEURILLAT[3]

[1] *Institut F. A. Forel, Université de Genève, 10 route de Suisse, CH-1290 Versoix, Switzerland;* [2] *The McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, U.K.;* [3] *Centre Alpien de Phytogéographie, Fondation J.-M. Aubert, CH-1938 Champex and Conservatoire et Jardin botaniques de la Ville de Genève, 1 ch. de l'Impératrice, CH-1292 Chambésy Switzerland*

[1] *Address for correspondence: carnelli@terre.unige.ch*

ABSTRACT

The altitudinal fluctuations of the treeline in the Alps during the Holocene have been investigated mainly through pollen and plant macrofossil analyses. The consensus today is that the forest reached 2400–2500m a.s.l. during the Atlantic climatic optimum (100 to 300m higher than present). This view is at present under discussion and new techniques are needed to resolve the debate. Alpine soils can act as archives of information suitable for the reconstruction of the vegetation history. The potential of soil phytoliths as tracers of alpine vegetation history in dry terrestrial environments is herein discussed. The biogenic silica content in the soil profile shows a minimum in the eluvial horizon and increases towards the bottom of the profile. The grass *short cells* concentration shows a peak in the upper part of the profile then decreases drastically at the base of the eluvial horizon. Polyhedral phytoliths are the most common morphotypes at the base of the soil profile. Their abundance can be explained by the dissolution of the more soluble opal of monocotyledons or it could be a genuine signature of arboreal species presence in the past. This second hypothesis is confirmed by means of EDX-analysis, which is shown to be a powerful tool to distinguish not-idiomorfic morphotypes.

INTRODUCTION

Above a certain altitude, in mountains all over the world, a striking vegetation boundary is present. The closed forested areas shift to a more open canopy zone (*kampfzone* or *krummholz zone*) and then into a treeless vegetation where only forbs and graminoids species grow. The altitude of this transition zone is variable depending on different regional and local factors. However, it is correlated to mean seasonal values of air temperature between 5.5 and 7.5 °C and to soil temperature of about 7 °C (KÖRNER, 1999). The correlation between temperature and altitudinal limit of the forest is valid at any latitude, and has been used as the basis for a functional explanation of the treelines. Plant species need a minimum temperature for the production of biosynthesised compounds sufficient for cellular growth and for the development and differentiation of new functional tissues. The production of new tissues is mainly reduced by the sink inhibition caused by low temperatures (KÖRNER, 1999). Trees experience growth limitations at a lower altitude then shrubs and forbs. Unlike many graminoids species or rosette forbs and dwarf shrubs, trees cannot benefit from radiant canopy warming during the day nor from stored warmth in the topsoil during the night. On a global scale, air and soil temperatures seem to be able to predict the altitude of the treeline at any latitude. However, other regional climatic and edafic factors have a local and direct influence on the treeline. In temperate regions, such as the Alps, trees growing at higher altitude suffer from frost damage, frost desiccation, mechanical damage due to avalanches or wind. The result is loss of biomass, and of limitation in seed production and developmental processes (TRANQUILLINI, 1979). These stress factors are not considered critical for established trees that can show a high phenotipic plasticity and can survive as krummholtz (stunted individuals). However, local factors are known to reduce the probability for re-growth of young trees and to prevent tree recruitment at higher altitude, therefore affecting the altitude of the treeline. The set of taxa occurring in a certain area will also influence the treeline altitude: ecophysiology and phenotypic plasticity play the major role in determining the altitudinal distribution of a species. The limiting factors for some widespread alpine species, for instance, were shown to be temperature requirements for bud burst and flowering (THEURILLAT and SCHÜSSEL, 2000). Other local or regional factors can influence the altitudinal range of the forest. For example, in the European Alps, the present distribution of the forest is higher in the areas with a more continental and/or arid climate (EGGENBERG, 1995).

The close relationship between treeline and climatic factors make palaeo-treelines a suitable proxy to reconstruct past climate changes (PAYETTE *et al.*, 1989). Interest in past vegetation shifts triggered by climate has risen in recent years since these data are needed for modelling future responses of vegetation cover. High mountain ecosystems are particularly vulnerable to climatic change. It is hypothesised that in the Central Alps an increase of 3.3 K would induce an altitudinal shift in the arboreal vegetation of 600m (THEURILLAT and GUISAN, 2000). The correlation between climate and treeline is nevertheless very complex, since the advance or retreat of a forest is not easily prompted by climatic change (LAVOIE and PAYETTE, 1996) (HÄTTENSCHWILER and KÖRNER, 1995). Forests respond relatively slowly to such changes because the established closed canopy produces a favourable self-sustaining microclimate, and also because of the ability of plant phenotypic plasticity to act as a buffer. For millennia, the European Alps have been subjected to human pressure (grazing, agriculture and forestry). The reconstruction of their vegetation history is paramount to the understanding of the degree of impact of past and present human activity, and can determine if the present vegetation is in equilibrium with the climatic and ecological factors. The present research discusses some preliminary data concerning the use of phytolith analysis in alpine soils to investigate the history of vegetation at the subalpine-alpine ecocline.

METHODS

Site location and modern vegetation

The Valais region of the Swiss Alps (Bel Alp-Aletsch glacier region) (FIG. 1) is the area of the present study. In this region, the *subalpine* vegetation belt – the highest belt where the forest can survive – is located approximately between 1600 and 2300m a.s.l. The vegetation is dominated by Boreal-type forests (*Picea abies* (L.) Karst, *Larix decidua* Miller, *Pinus cembra* L. and *Pinus mugo* Turra), heaths with ericoid species (*Rhododendron ferrugineum* Linn., *Vaccinium myrtillus* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., *Arctostaphylos uva-ursi* Spreng., *Calluna vulgaris* L.) and shrubs with *Alnus viridis* (Chaix.) DC and *Salix helvetica* Vill. The subalpine vegetation is also represented by swards dominated by *Carex sempervirens* Vill. and *Nardus stricta* L. The *alpine* vegetation belt – the zone where trees are absent – is situated between the tree line and the snow line at 2300 – 3000m a.s.l., and is dominated by dwarf shrub heaths with *Loiseleuria procumbens* Desf., *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher and *Vaccinium uliginosum* L., or by swards with *Carex curvula*.

Samples were collected from a soil section located at 2370m a.s.l. (BA 1), on a S-SE facing slope dominated by alpine acidic grasslands.

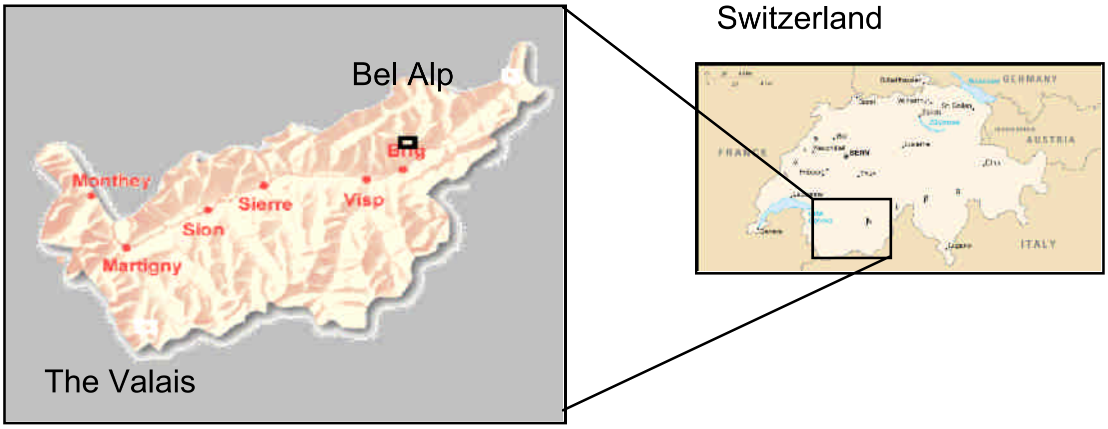


Fig. 1 Site location

Soil and phytolith analyses

The soil was described according to the "Référentiel pedologique" (AFES, 1998) and the methodological details are reported in VADI, 1999 . The parent rock material is constituted by gneiss.

About 5g of soil from each sediment sample were processed for phytolith analysis (MADELLA *et al*., 1998). Permanent microscope slides of the extracted phytoliths were mounted with Eukitt (refractive index: 1.5 at 20 °C) and observed under a microscope equipped with phase contrast optics and polarised illumination at a magnification of x504. For the purpose of the present research, it was decided to count only two categories of phytolith morphotypes: Gramineae *short cells* (METCALFE, 1960) and *polyhedrons*. Polyhedrons are morphotypes with an irregular polyhedral shape that may have different histologic origin, such as epidermis or mesoderm. They might also originate from the breakage of other morphotypes. The choice of short cells and polyhedrons was dictated by the need to trace the presence of two distinct vegetation structures: prairies and woodlands. Short cells are unique to grasses and make excellent tracers for this type of plants. Polyhedrons are predominant (though not exclusive) in woody species tissues.

The concentration of phytolith morphotypes in the soil (number of phytoliths /g dry soil) was also calculated (modified from ALBERT *et al*., 1999).

RESULTS

The soil is a podzol and the soil horizons are in general well developed and no evidence of pedoturbation or solifluction is present. The profile shows a sequence E/BPs, with a progressive transition of the eluvial zone into the illuvial zone (Fig 2). The humus is of eumoder type. The organic horizon OF is clearly defined, unlike the OH, and consists mainly of roots and faecal pellets. The horizon AE is rather compact: the texture is silt-sand with low to medium porosity, and its transition to Eh is gradual. The Eh horizon is rather compact, the texture is silt-sand, the porosity is low, and the transition with the underlying horizon is abrupt. The horizon EhBPs has a polyhedral structure with low stability containing about 10% gravel. Horizon BPs has micropolyhedral structure with low stability, medium porosity and gravel up to 20 %. The transition with the underlying layer BPsC is abrupt. The structure of BPsC is polyhedral with low stability, the texture is silt-sand, porosity is low and gravel is about 30-40%. The horizon C1 has similar characteristics but a medium porosity and gravel up to 60%. The deepest horizon, C2, is strongly altered with micropolyhedral structure, gravel is 90%, and porosity high. The roots are present in the first 60-70cm, of soil, but decrease remarkably after 30cm of depth. Soil pH is on average 5. The potential acidity (ΔpH) is high in all the profile (>1), and especially so in the illuvial zone.

The biogenic silica content of the various soil horizons (expressed as percentage of soil dry weight) is displayed in Fig. 3. The percentage of opal silica is very low in the top horizons. It is higher within the horizons AE and Eh, where it is constant, and increases constantly in EhBPs and BPs. The concentration from the horizon BPsC down to the base of the profile is nearly constant, with only a slight decrease in C1.

The concentration of grass short cell phytoliths in the top organic horizons is very low. The frequency of short cells has a peak in the AE horizon, followed by an abrupt diminution in the eluvial horizon Eh. In the deepest horizons the short cell phytoliths content is remarkably constant. The percentage of total biogenic silica is not correlated with the short cell concentrations.

The concentrations of polyhedrons shows a much wider variability and a depletion zone in the eluvial horizons can be observed. There is a tendency for polyhedron accumulation towards the deepest horizons.

DISCUSSION

The results here discussed are part of an on going multidisciplinary research project in which data supplied by pollen, plant macrofossil, soil, charcoals, and biogenic silica analyses are combined to investigate the fluctuations of the treeline during the Holocene in the Central Swiss Alps. The dynamic of the alpine treeline in the last Postglacial, has been investigated mainly by pollen and plant macrofossil analysis from peat bogs. It is considered that, in the European Alps, the forested subalpine zone and the Kampfzone, attained their highest elevation in the climatic optimum of the Atlantic period (5000 to 6000 BP). The forest is estimated to have been 100 to 300 m higher than the present potential timberline (e.g. (VORREN *et al*., 1993)). In the central Valais region (Swiss Central Alps) it is inferred from pollen and plant macrofossil analysis, that the treeline maximum altitude was 2400m a.s.l. (TINNER and AMMANN, 1996). However, recent findings in the Zermatt region of the Swiss Central Alps (Thinon, unpublished data) of charcoals of *Larix decidua* Miller and *Pinus cembra* Lin the upper alpine zone, as high as 2900 - 3000 m a.s.l.. show that the treeline for areas with continental climate could have been much higher.

Much of the palaeobotanical reconstruction in the Alps has been based on pollen and plant macrofossils. . These techniques present several advantages especially when undisturbed lacustrine sedimentary records offer a great continuity in time. Also, lacustrine palaeoenvironmental archives have been investigated extensively and therefore a large comparative data set is available (AMMANN, 1995). The identification of pollen grains offers a regional perspective to the identification of ancient floras or vegetation. At the local scale more reliable indicators of past treelines are the analysis of pollen concentrations and influxes, and plant macrofossil (including stomata of conifers). However, all these methods lack of spatial continuity at higher altitudes where *wet archives* are extremely scattered or missing. Soil analysis, on the contrary, allows a virtually complete spatial continuity and is therefore suitable to investigate gradients of environmental factors (such as altitude/temperature) by means of transects. Soils are a source of palaeoenvironmental information as horizons, colour, textures and micromorphology can be preserved for long time even if the processes that have originated them are not active anymore. The use of soil bio-sequences (suites of soils where the abiotic factors are similar) has been pioneered in the Valais region (Swiss Central Alps) by Tinner and Amman (1996). These authors demonstrated that soil analysis of carefully selected sites , can be a useful tool in the investigation of the ancient treelines. The Holocene treeline maximum has been reconstructed on the basis of a multidisciplinary approach that applied the analysis of soil profiles along altitudinal transects, soil charcoals, plant-macrofossil and pollen sequences.

An innovative and complementary approach can be found in the study of alpine soils and the plant micro- and macrofossils preserved in these *dry archives*. Charcoals and phytoliths are, indeed, common components of the soil. The study of charcoals particles in soils (pedoantrachology) has been employed to reconstruct the evolution of ligneous vegetation in fire-affected environments (PAYETTE and GAGNON, 1985; TALON *et al*., 1998), by identifying and dating the charred wood recovered from soils. Assuming that the presence of charcoals is a direct proof of the presence of ligneous species - an assumption that is not widely accepted yet- pedoantrachology is a method with a very high spatial resolution. The occurrence of charcoals in the soil, however, is the result of an event limited in space and time and for that reason, lacks the temporal continuity offered by pollen records. After a fire event, charcoals are fragmented and buried in the soil as a consequence of biotic and abiotic factors. In general, the particles depth of burial should be a function of time though this is not always the case because in soils with intense biological activity the pedofauna and small vertebrates may cause pedoturbations (CARCAILLET and TALON, 1996). The spatial resolution of micro-charcoals is still an open issue. Only few experimental studies different ecosystems are available on the transport of charred wood after fire events (THINON, 1992; CLARK, 1988). By convention pedoanthracology only considers fragments of > 400 µm of size, in order to exclude small airborne fragments. The taxonomic potential of charcoals for alpine taxa is high since they can be normally identified at the genus level. However, a rather long and very detailed anatomical analysis is required because of the very small size of most of the fragments. Charcoal analysis has been employed in different palaeoenvironmental studies of palaeo-treelines in different biomes such as the French Alps (CARCAILLET and THINON, 1996) and the forest-tundra ecocline (PAYETTE and GAGNON, 1985).

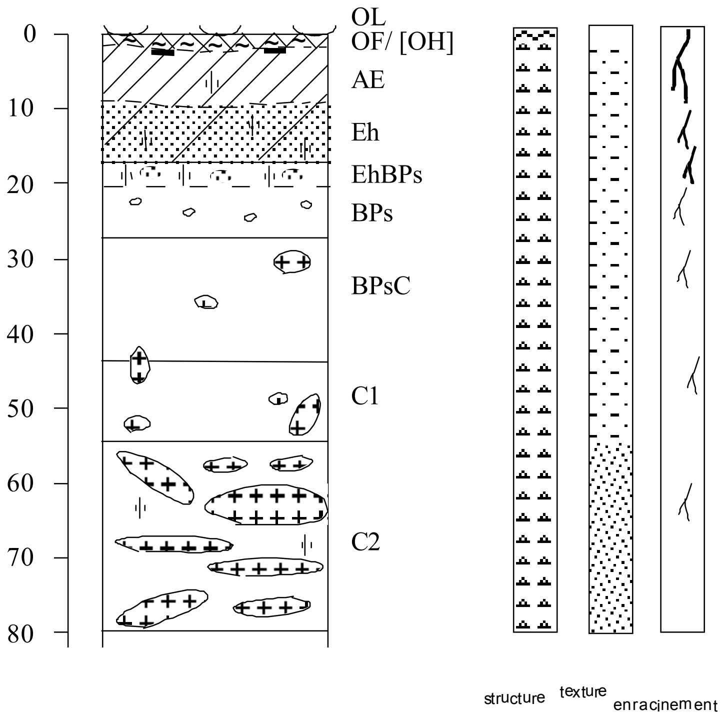
Data from the silica production in alpine plant communities in Northwestern Caucasus (BLINNIKOV, 1994) and the preliminary result discussed in the present work, show that phytoliths analysis can contribute to the reconstruction of the vegetation history of alpine soils. In particular, this approach can offer a high degree of spatial resolution and a more detailed image of the herbaceous vegetation that is recorded by charcoals and often very approximate in pollen assemblages. Plant communities (e.g. grasslands vs. woodlands) can have a remarkable different production of opal silica (CARNELLI ET AL, in press) and the variability in concentration of biogenic silica content in the soil has been employed to reconstruct past vegetation (WITTY and KNOX, 1964;

BAKEMAN and NIMLOS, 1985).The time integrated biogenic silica input of plant communities can be calculated (e.g. CARNELLI *et al.*, in press) and the predicted values can be compared with the actual content of biogenic silica of a soil and its age, to reconstruct the history of vegetation of a site. In the plant communities from the Alps, the annual input of biogenic silica of subalpine grasslands is predicted to be one order of magnitude higher than the one of woody species (CARNELLI *et al.*, in press). It should be therefore possible to trace the fluctuations of the forest-grassland boundary by measuring the content of opal in alpine soils.

In the soil profile analysed, the distribution of biogenic silica seems to be driven mainly by soil leaching processes. Opal is depleted in the eluvial horizons and accumulated in the illuvial ones. The processes that phytoliths undergo once deposited in the soil have not yet been investigated thoroughly. A bi-compartimental model (ALEXANDRE *et al.*, 1997) seems to be able to describe the distribution of total biogenic silica in the horizons BA1. It is hypothesised that a first fraction of phytoliths is dissolved in the horizon BPs and then leached with ground water, while a residual fraction, constituted of phytoliths with longer life-span, is dislocated towards the bottom of the profile. Data on the resistance of biogenic silica to dissolution in natural conditions are lacking. However, under experimental conditions it was shown that grass phytoliths were less resistant than that of dicotyledon and gymnosperm (BARTOLI and WILDING, 1980). The distributions of short cells and polyhedral phytoliths seem to be in agreement with those findings: the grass short cells already appear to be subjected to dissolution while at the top of the soil profile, since their concentration drops at the basis of the eluvial horizons. Only a small fraction of short cells is preserved in the deepest horizons. On the contrary, polyhedral phytolith concentration does vary significantly and increases at the base of the profile. The higher variability of the concentration of polyhedral phytoliths along the profile is potentially the result of a mixed histologic origin for these morphotypes. Furthermore, a fraction of this group may also originate from the fragmentation of other morphotypes. Polyhedral phytoliths are very common in the tissues of dicotyledon and gymnosperm species of the alpine and subalpine vegetation (Carnelli, unpublished data on reference collection material of alpine plants), and they constitute the majority of morphotypes produced by ligneous tissues (see also ALBERT *et al.*, 2000). It can be speculated that the increase in polyhedral phytoliths in the deeper soil horizon may be associated with the presence of woody vegetation in the past. However other independent evidence is necessary to substantiate this hypothesis.

To investigate the origin of the polyhedral phytoliths, a non-morphological approach was adopted. This comprised the elemental analysis of the biogenic silica by means of an x-ray microanalitical technique. Data from reference collection material of subalpine and alpine plants occurring in the study area showed that phytoliths containing aluminium are present principally in woody species (CARNELLI *et al.* submitted). These findings are consistent with the early works of Bartoli (BARTOLI and WILDING, 1980) and more recently of Hodson and Sangster (1999). Preliminary tests carried out during the present study indicated that also in soil-born phytoliths the presence of aluminium in biogenic silica could be detected and therefore employed as tracer for phytolith origin.

Fig. 2 Soil profile BA1



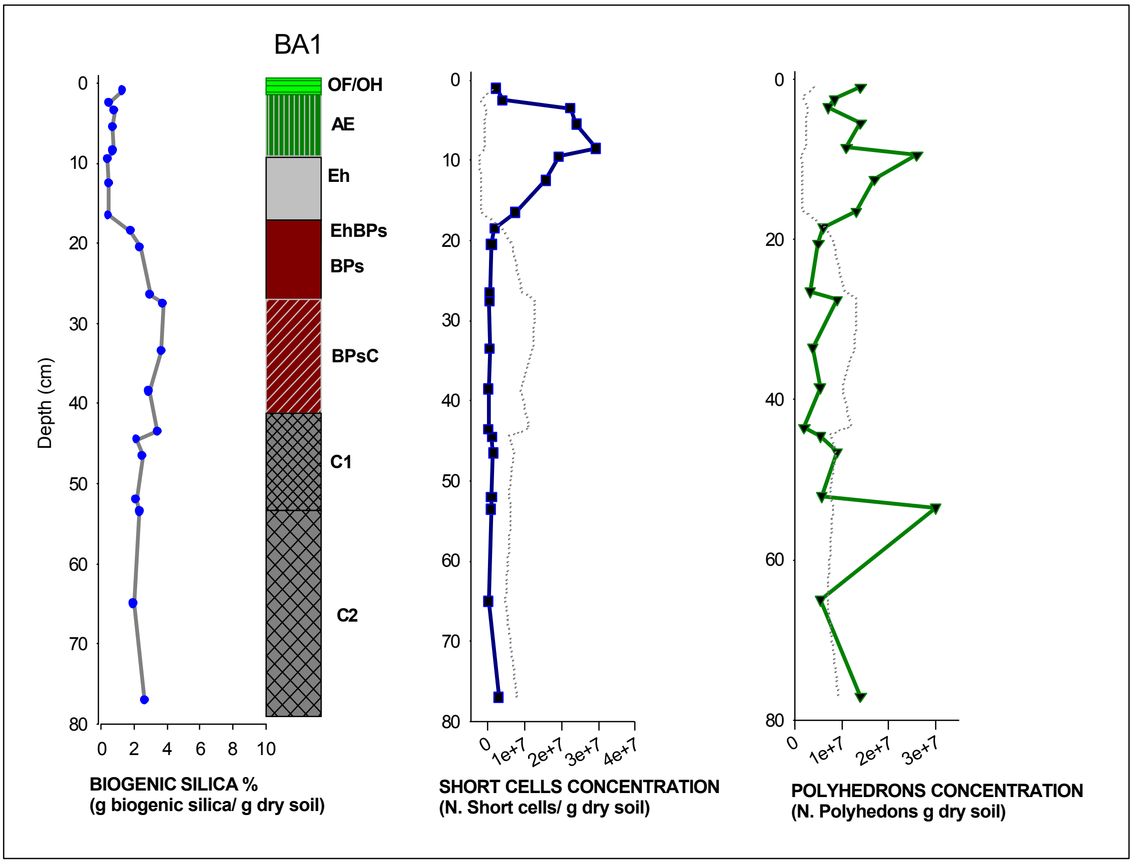


Fig.3
Biogenic silica, short cells and polyhedrons concentrations in BA1

CONCLUSIONS

The potential of soil phytoliths as tracers of alpine vegetation history in dry terrestrial environments has been discussed. The biogenic silica content in the soil profile shows a minimum in the eluvial horizon and increases towards the bottom of the profile. The grass *short cells* concentration shows a peak in the upper part of the profile then decreases drastically at the base of the eluvial horizon. Polyhedral phytoliths are the most common morphotypes at the base of the soil profile. Their abundance can be explained by the dissolution of the more soluble opal of monocotyledons or it could be a genuine signature of arboreal species presence in the past. This second hypothesis is confirmed by means of EDX-analysis, which is shown to be a powerful tool to distinguish not-idiomorfic morphotypes.

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