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Biogenic Silica Production in Selected Alpine Plant Species and Plant Communities

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The biogenic silica extracted from samples of 28 alpine plant species belonging to 23 genera and nine 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 this study and from the literature have been used to predict the input made by different subalpine and alpine plant communities 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.

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 in the transpiration stream, and eventually deposited in 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 occupied by 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 secondary cell wall formation 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 reach concentrations up to five-times those in young tissues (Wyttenbach *et al*., 1991; Hodson *et al*., 1996; 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 (Raven, 1983; Hodson and Evans, 1995; 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 co-precipitation of AS and HAS may occur in plant tissues (Cocker *et al*., 1998). The co-deposition of Al and Si, recently documented in needles of four coniferous species, has been interpreted as a mechanism for sequestering aluminium (Hodson and Sangster, 1999). The co-deposition of silicon and heavy metals in plant tissues can function as a detoxifying mechanism in species that are resistant to heavy metals 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.) (Neumann *et al*., 1997; Bringezu *et al*., 1999). The active uptake of silicon has been demonstrated in sugar cane, horsetail, wheat and rice (Raven, 1983), although, in other species such as oat and barley, the content of silicon in the plant can be accounted for entirely in terms of supply in the transpiration 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 a structural and protective role, at a much lower energy cost than using lignin or polysaccharides (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 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 micrometres. The

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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. Piperno, 1988; Bozarth, 1993; Miller-Rosen, 1993; Pearsall, 1994; Fredlund and Tieszen, 1997; Barboni *et al*., 1999; Madella, 2000). However, if this methodology is to be applied to the reconstruction of long-term vegetation dynamics, more information on production, deposition and taphonomy of biogenic silica is 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 silicon.

Phytolith analysis can be a valuable tool in the study of the vegetation history in the Alps. Measurement of 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 climate 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 300 m 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 2500 m 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 was assessed. The plant silica content was then 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 in 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.

MATERIALS AND METHODS

Site descriptions

The plant material was collected from three sites in the Valais region of the Swiss Alps (Val d'Arpette, Furka Pass, and Belalp-Aletsch glacier region). In the study area, the soil types formed on acidic parent rock (gneiss) follow an altitudinal zonation: podzols are located between 2300 and 2550 m 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 2300 m a.s.l. at the study sites) and the alpine belt (between the treeline and the snow line i.e. 2300–3000 m 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 Ericaceae species (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. uliginosum, V. vitis-idaea, Arctostaphylos uva-ursi, Calluna vulgaris*); shrubs with *Alnus viridis* and *Salix helvetica*, 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*.

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 with the end of the growing season, the specimens were representative of the total annual silicon deposition in plant tissues. The species, sampling site and altitude at which they were collected are listed in Table 1. All the collected species are perennials. The woody taxa are evergreen with the exception of *Larix decidua*, *Vaccinium myrtillus* and *V. uliginosum*. The species selected are those most commonly occurring in the subalpine 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, 20–50 mm in diameter, were cut and collected. Leaves and stems of herbaceous plants were analysed together. In woody species, leaves and branches were analysed separately, 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 opal silica were made for each plant sample. Plant samples were washed several times in a solution of water and detergent (commercial washing-up liquid) and rinsed with de-ionized water. Mineral matter was removed by placing the samples in an ultrasound bath overnight (NEY, Ultrasonik 104X). Samples were then rinsed with de-ionized water, dried for 48 h 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

TABLE 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	Empetraceae
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
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 helvetica Vill.[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] Belalp-Aletsch Glacier.
L, Leaves, C, culms, W, woody branches.

change to other forms of silica; Piperno, 1988; Runge, 1998). The samples were burned for 4–12 h 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 3·5 N HCl. Residues were washed with de-ionized water and centrifuged at 1000 r.p.m. for 3 min, and the supernatant discarded (this step was repeated three times). The remaining biogenic silica residue was oven dried at 60 °C for 48 h and then weighed. The extracted biogenic silica was expressed as a percentage of the original plant dry weight.

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 polarized illumination at a magnification of ×504. 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 2). Since oxalates and carbonates had been removed, optically anisotropic particles were considered to be crystalline silica, alkaline 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[1], allowing for the different densities of the anisotropic and isotropic particles. The average density of 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 approximately the same.

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} $year^{-1}$) was calculated by taking the product of (1) 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}]; (2) the mean length of the growing season (d); and (3) the percentage of biogenic silica in the tissues of the species of the plant community (Table 3). The latter was calculated by taking into account

[1] 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 percentage of these impurities (*C. vulgaris*, *L. procumbens* and *E. nigrum*) all have very small leaves, either revoluted or embricated, where impurities can accumulate.

TABLE 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*

	LEAVES					WOOD				
Species	Ash %	B.S. %	s.d.	O.I. %	B.S. $\%_{corr}$	Ash %	B.S. %	s.d.	O.I. %	B.S. $\%_{corr}$
Monocotyledons*										
Calamagrostis villosa	8·96	5·90	0·841	100	5·9					
Carex curvula	—	1·03	0·177	93	0·96					
Carex sempervirens	4·78	2·31	0·354	99	2·29					
Festuca halleri	—	3·30	0·171	99	3·27					
Festuca puccinellii	5·59	2·96	0·160	100	2·96					
Festuca scabriculmis	—	2·52	0·222	96	2·41					
Nardus stricta	4·39	2·67	0·160	96	2·56					
Poa alpina	—	0·62	0·084	98	0·61					
Dicotyledons										
Alchemilla pentaphylla	—	0·05	0·012	80	0·04					
Alnus viridis	4·44	0·13	—	100	0·13	2·89	0·04	0·036	100	0·04
Arctostaphylos uva-ursi	0·25	0·04	0·010	70	0·03	2·59	0·25	0·013	85	0·21
Calluna vulgaris†	—	0·72	0·025	95	0·68					
Empetrum nigrum	3·05	0·19	0·011	84	0·16	1·40	0·11	0·011	—	0·11
Geum montanum	—	0·11	0·072	96	0·11					
Leontodon helveticus	—	0·00	0·000	—	0					
Loiseleuria procumbens	2·63	0·32	0·038	75	0·24	1·17	0·10	0·060	77	0·08
Rhododendron ferrugineum	2·79	0·04	0·019	89	0·04	1·76	0·02	0·011	73	0·01
Salix helvetica	—	0·06	0·046	75	0·04	—	0·50	0·181	87	0·43
Vaccinium myrtillus	—	0·04	0·037	97	0·04	2·42	0·04	0·011	77	0·03
Vaccinium uliginosum	4·92	0·10	—	—	0·1	1·51	0·08	0·017	100	0·08
Vaccinium vitis-idaea	2·83	0·04	0·043	67	0·03	2·46	0·03	0·017	84	0·03
Veronica bellidioides	—	0.00	0.000	—	0					
Conifers										
Abies alba	5·78	0·08	0·031	77	0·06					
Juniperus nana	3·44	0·08	0·022	83	0·07	7·04	0·15	0·060	—	0·15
Larix decidua	—	1·09	0·042	100	1·09	2·10	0·59	0·162	91	0·54
Picea abies	3·56	0·85	0·230	100	0·85	2·25	0·18	0·039	91	0·16
Pinus cembra	2·61	0·13	0·054	88	0·11	2·13	0·02	0·005	84	0·02
Pinus mugo	—	0·10	0·071	95	0·09	1·80	0·07	0·043	81	0·06

Data are means of three determinations.
*For monocotyledonous plants, leaves and culms are analysed together; † herbaceous stems and leaves.

the mean abundance of the species and, for heaths only, the different production of biogenic silica in herbaceous and woody tissues.[2]

As it was not possible to obtain data for *Festuca scabriculmis*, its APP was assumed to be of the same order as that of *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 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 3. The silica input by conifer stands has been underestimated because the contribution of the wood was not taken into account.

[2] The relative abundance of a species (a) was defined as $a = A/A_{tot}$, where A is the percentage cover of the species and A_{tot} is the sum of percentage cover of all species. To take into account the biomass of the species, 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 $H = a \times ph \times BS\%_{corr}$ (where $ph = h/(h + w)$ and $BS\%_{corr}$ 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 $W = a \times pw \times BS\%_{corr}$ (where $pw = w/(h + w)$ and $BS\%_{corr}$ is the silica content in the woody tissues as in Table 2. The total production of biogenic silica of a given community ($BS_{H,W}$) was calculated as the sum of all the contributions from the herbaceous and woody tissues of each species ($BS_{H,W} = H_{tot} + W_{tot}$).

RESULTS

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 plants of this family was 3 %. The biogenic silica content of *Carex sempervirens* and *C. curvula* was 2·29 % and 0.96 %, respectively.

TABLE 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 (d)	Above-ground productivity (g d. wt. m^{-2} d^{-1})	Biogenic silica content (% on d. wt. basis)	Predicted biogenic silica input (g m^{-2} $year^{-1}$)
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 uliginosum-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 *et al.* (1998)
[b] From Klug-Pümpel (1989)
[c] From Schmidt (1977)
[d] From Onipchenko (1994) and Onipchenko *et al.* (1998)
[e] From Klug-Pümpel (1978)
[f] Rehder (1970)
[g] From Pornon and Doche (1995)
[h] Litterfall from Bray and Gorham (1964). The annual litterfall is expressed here on a daily basis for easier comparison
[#] Leaves and wood mean of the ratio herbaceous/woody for above-ground productivity and the mean ratio between the dominant species in the plant community
[~] Estimated values

Dicotyledons

The mean content of biogenic silica in the leaves and wood of the dicotyledons analysed (0·1 %) was much lower than that for monocotyledons. Among the six species of the family Ericaceae, the highest percentage of silica was extracted 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* contained quantities of biogenic silica ranging from 0·03 % to 0·04 %. In general, the wood samples of the Ericaceae had 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 had similar values of biogenic silica in both leaves (0·16 %) and wood (0·11 %), *Alnus viridis* (with values of 0·13 % in leaves and 0·04 % in wood) and *Salix helvetica*, which accumulated higher quantities of silica in the wood (0·43 %) than in the leaves (0·04 %). The percentage of 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.

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 % 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 %.

Estimate of biogenic silica input into the soil

The estimated annual biogenic silica production of the subalpine and alpine plant communities is summarized in Table 3.

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 tended to have similar opal silica contents, there were several exceptions. The following discussion considers data from the present study and from the literature (Table 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.

Monocotyledons

Several studies on biogenic silica in grasses, in particular cereals, have been carried out and there is extensive literature on phytolith morphology for these plants (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 % biogenic silica, and *P. chaixi* only about 0·8 % (Table 4). Our values for *Calamagrostis villosa* are in the range of those reported in the literature for this species (3·3–7·4 %) (Table 4) and data from other species in the same genus are: *Calamagrostis rubescens*, 3·29 %, *C. inexpansa* 3·8 % and *C. epigeios*, 4–6·3 %. Samples of *Festuca halleri* and *F. puccinellii* contained around 3 % biogenic silica. Variation 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).

Sedges (Cyperaceae family) can be an important constituent of alpine pastures and grasslands. There have been few investigations into the silica content of above-ground tissues of sedges, although 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 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 found in *C. curvula* (Table 4).

Dicotyledons

Considerably less biogenic silica was extracted from dicotyledonous specimens than from 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). The other *Ericaceae* specimens studied 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). The opal content in *Alnus viridis* (0·13 %) and *Salix helvetica* (0·04 %) was low. An extremely wide range of opal silica content (0·01–8·8 %) has been reported for arborescent dicotyledons belonging to different families (43 species) of temperate regions (Table 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 % silica (Jones and Handreck, 1967), significantly less than monocotyledons.

Conifers

Larix decidua and *Picea abies* accumulated about ten-times more silica (by weight) than the other conifers analysed. Percentages 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). Needles of *Picea abies* 'pumila' and *P. abies* 'diffusa' contained between 2·35 and 2·78 % 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 mineralization in *Picea* is related to age. One-year-old needles of *P. abies* contained only 0·14 % of silica, but an increasing quantity was 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 '0-year-old' needles) up to 1·95 % (for 5-year-old needles) (Hodson *et al.*, 1996). This variability should 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 % (Table 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 0·18 and 0·13 % (Klein and Geis, 1978) while four other *Abies* species had opal silica percentages ranging from 0·12 to 0·84 % (Hodson *et al.*, 1996).

In this study, the opal silica content of needles was always higher than that of wood. *Pinus elliotti* and *Juniperus virginiana* are the only conifers for which it was possible to find data in the literature on the opal silica content of wood (Table 4). The values are similar to those for *Pinus* and *Juniper* wood analysed in this study.

TABLE 4. *Published data on percentage content of biogenic silica in some Angiosperms and Gymnosperms*

Taxonomic group	Species	Tissue	Biogenic silica (% of dry weight)	Authors
Monocotyledons	*Calamagrostis epigeios* (L.) Roth.	Above-ground parts	4–6.3	1
	Calamagrostis inexpansa Gray	Above-ground parts	3.80	2
	Calamagrostis rubescens Buckley	Above-ground parts	3.29	2
	Calamagrostis villosa (Chaix.) Gmelin	Above-ground parts	3.3–7.4	3
		Above-ground parts	5.90	Present paper
	Carex atherodes Spreng.	Above-ground parts	2.71	2
	Carex curvula All.	Above-ground parts	0.96	Present paper
	Carex filifolia Nutt.	Above-ground parts	2.76	2
	Carex sempervirens Vill.	Above-ground parts	2.29	Present paper
	Festuca halleri All.	Above-ground parts	3.27	Present paper
	Festuca idahoensis Elmer	Above-ground parts	3.59	2
	Festuca puccinellii Parl.	Above-ground parts	2.96	Present paper
	Festuca rubra L.	Above-ground parts	2.82	2
	Festuca scabrella Thurb.	Above-ground parts	3.15	2
	Festuca sylvatica (Pollich) Vill.	Above-ground parts	0.7–1.1	4
	Poa alpina L.	Above-ground parts	0.61	Present paper
	Poa chaixi Vill.	Above-ground parts	0.7–0.9	3
	Poa secunda J. S. Presl	Above-ground parts	2.63	2
Dicotyledons	*Alnus viridis* (Chaix) DC	Leaves	0.13	Present paper
	Calluna vulgaris L.	Leaves	0.68	Present paper
		Leaves	0.3–1.7	3
		Leaves	0.4–0.6	4
	Vaccinium myrtillus L.	Leaves	0.04	Present paper
		Leaves	0.1–0.3	3
	Salix helvetica Vill.	Leaves	0.04	Present paper
	Salix spp.	Leaves	0.5	2
	36 deciduous trees and shrubs	Leaves	0.01–3.79	5
	7 deciduous tree species [a]	Leaves	0.9–8.8	6
Conifers	*Abies alba* Miller	Needles	0.06	Present paper
	Abies balsamea (L.) Mill	Needles	0.182	7
	Abies fraseri (Pursh.) Poir,	Needles	0.129	7
	Abies grandis (Douglas) Lindley	Needles	0.84	8
	Abies mariesii Mast.	Needles	0.12	8
	Abies nordmanniana (Steven) Spach	Needles	0.39	8
	Abies procera Rehder	Needles	0.93	8
	Juniperus communis L.	Needles	0.04	8
	Juniperus nana Willd.	Needles	0.08	Present paper
	Juniperus virginiana L.	Needles and wood	0.10	9
	Larix decidua Mill.	Needles	1.09	Present paper
		Needles	1.372	7
		Needles	2.21	8
		Needles	0.9–1.0	3
	Picea abies (L.) Karsten	Needles	0.85	Present paper
		Needles	0.3–3.7	3
		1-year-old needles	0.1423	10
	Picea abies 'pumila'	Needles	2.35	8
	Picea abies 'diffusa'	Needles	2.78	
	Picea glauca (Moench.) Voss	Needles	1.048	7
		0-year-old needles	0.37	8
		5 -year-old needles	1.95	
	Picea mariana (Mill.) B. S. P.	Needles	0.168	7
	Picea rubens Sarg.	Needles	0.434	7
	Pinus (12 species)[b]	Needles	0.01–0.73	8
	Pinus banksiana Lamb.	Needles	0.184	7
	Pinus cembra L.	Needles	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.	Needles	0.83	7
	Pinus strobus L.	Needles	0.085	7
	Pinus sylvestris L.	Needles	0.05–0.1	3
		Needles	0.183	7

[a] *Quercus alba* L., *Acer saccharum* Marsh., *Fagus grandifolia* Ehr. *Ulmus rubra* Muhl., *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 *et al.* (1969)
2) Bezeau *et al.* (1966)
3) Bartoli and Souchier (1978)
4) Bartoli and Beaucire (1976)
5) Geis (1973)
6) Wilding and Drees (1971)
7) Klein and Geis (1978)
8) Hodson *et al.* (1996).
9) Lanning and Eleuterius (1983)
10) Wyttenbach *et al.* (1991)
11) Kalisz and Stone (1984)

Input and durability of biogenic silica particles in the soil

Estimates of the annual contribution of alpine plant communities (Table 3) stress the importance of grasslands in the biocycle of silicon in alpine and subalpine ecosystems. The mean silica production of subalpine grassland communities (9·4 g m^{-2} $year^{-1}$) is about one order of magnitude higher than that of upper alpine grassland communities (1·2 g m^{-2} $year^{-1}$), heaths (0·54 g m^{-2} $year^{-1}$), shrub formations (0·48 g m^{-2} $year^{-1}$) and litterfall of conifer forests (1·6 g m^{-2} $year^{-1}$). These estimates were made with the intention of assessing the biogenic silica production in different plant communities and exploring possible implications for palaeoecological studies. In calculating the input of biogenic silica several approximations were applied. The lack of precise data on the ecology of the alpine communities introduces significant uncertainty in the absolute measures of silica production. However, valid comparisons 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 grass communities at Trelease Grasslands (Illinois, USA) is 18 g m^{-2} $year^{-1}$ (Geis, 1978). For *Pinus sylvestris* woodlands, an input of only 0·2 ± 0·1 g m^{-2} $year^{-1}$ of silica from needles and 0·1 g m^{-2} $year^{-1}$ from wood has been calculated (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 underestimation 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 by 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 this 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 of relevance to alpine plant-soil ecosystems can be outlined. The stock of phytoliths present in the soil seems to be determined mainly 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 mineralization 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 rate of dissolution 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 the characteristics of the soil-plant ecosystem, including the physical, chemical and biological processes active in the soil (Bartoli and Souchier, 1978). In different ecosystems the estimated rates of turnover 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 this value was only 15 % in a coniferous forest on humus-ferruginous podzol (Bartoli, 1983). In alpine soils, the turnover of biogenic silica 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 does 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 lower horizons of the soil (Alexandre *et al.*, 1997).

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 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 palaeoecological 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

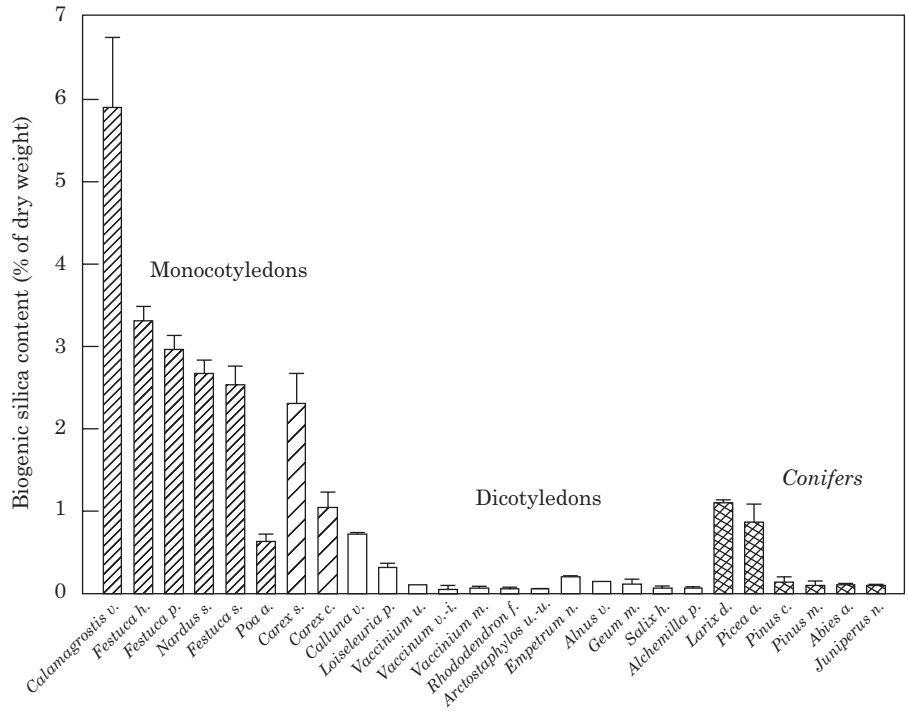

FIG. 1. Biogenic silica content of non-woody tissues of plants collected from subalpine and alpine zones in the Swiss Alps. The vertical bars indicate s.d.

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/shrub 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 woodland, heath and grassland 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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