

Edaphic influences of ophiolitic substrates on vegetation in the Western Italian Alps

Michele E. D'Amico · Franco Previtali

Received: 29 November 2010 / Accepted: 20 July 2011 / Published online: 1 October 2011
© Springer Science+Business Media B.V. 2011

Abstract

Background and aims Soils derived from serpentinite (serpentine soils) often have low macronutrient concentrations, exceedingly low Ca:Mg molar ratios and high heavy metal concentrations, typically resulting in sparse vegetative cover. This combined suite of edaphic stresses is referred to as the “serpentine syndrome.” Although several plant community-level studies have been conducted to identify the most important edaphic factor limiting plant growth on serpentinite, the primary factor identified has often varied by plant community and local climate. Few studies to date have been conducted in serpentinite plant communities of alpine or boreal climates. The goal of our study was to determine the primary limiting edaphic factors on plant community species composition and productivity (cover) in the alpine and boreal climate of the Western Alps, Italy.

Methods Soil properties and vegetation composition were analyzed for several sites underlain by serpentinite, gabbro, and calc-schist substrates and correlated using direct and indirect statistical methods.

Results Boreal forest soils were well-developed and tended to have low pH throughout the soil profile resulting in high Ni availability. Alpine soils, in comparison, were less developed. The distinct serpentinite plant communities of the Western Alps are most strongly correlated with high levels of bioavailable Ni associated with low soil pH. Other factors such as macronutrient deficiency, low Ca:Mg molar ratio and drought appear to be less important.

Conclusions The strong ecological influence of Ni is caused by environmental conditions which increase metal mobilization.

Keywords Bioavailable Nickel · CART · CCA · GLM · Serpentine syndrome · Soil-vegetation relationships

Abbreviations

CA Cluster Analysis
CART Classification Tree
CCA Canonical Correspondence Analysis
GLM Generalized Linear Models

Responsible Editor: Hans Lambers.

M. E. D'Amico (✉) · F. Previtali
Department of Environmental Sciences,
University of Milano Bicocca,
Piazza della Scienza 1,
20126 Milan, Italy
e-mail: ecomike77@gmail.com

Introduction

Serpentinite (ultramafic) rock is a relatively rare rock type consisting of hydrothermally-altered oceanic crust and upper mantle (ophiolite sequence) that has been emplaced on land within continental crustal

rocks (Alexander et al. 2007; Brooks 1987; Malpas 1992). Serpentinite (henceforth referred to as serpentine) has an unusual mineral composition being composed primarily of ferro-magnesium silicates. Serpentine weathers to produce soils with extreme adverse chemical and physical properties for plant productivity (Alexander et al. 2007; Kruckeberg 1984; Brooks 1987). Adverse chemical properties include low macronutrient (N, P, K) concentrations, extremely low Ca and high Mg concentrations resulting in a low Ca:Mg molar ratio, and high heavy metal (Ni, Cr, Co) concentrations. Adverse physical properties include susceptibility to drought as a result of dark colour, coarse soil texture, rockiness, and shallow soil depth. These adverse serpentine soil properties have a profound influence on the plant species that they support. This combined suite of edaphic stresses is referred to as the “serpentine syndrome” (Kruckeberg 1984).

The unique vegetation of serpentine soils has long fascinated biologists. Although this vegetation is typically sparse and stunted, plant diversity is often high with abundant endemic plant species (Kruckeberg 1984; Brooks 1987). Many studies have examined the numerous edaphic stresses of the serpentine syndrome to identify the primary factor influencing plant community species composition and cover (Carter et al. 1987; Chiarucci et al. 1998, 2001; Kayama et al. 2005; Krám et al. 1997; Nagy and Proctor 1997; Roberts 1992; Robinson et al. 1996; Verger et al. 1993). The relative strength and role of each edaphic factor has been found to vary greatly depending upon plant community and local climate (Proctor and Nagy 1991; Lazarus et al. 2011). Heavy metals (particularly Ni) are often the edaphic factor of greatest focus in such studies due to their toxicity. The role of heavy metals in influencing serpentine vegetation is unclear. Some researchers have reported that Ni has strong negative effects on plant cover on serpentine (Lee 1992; Chardot et al. 2007), whereas others have reported little to no effect (Nagy and Proctor 1997; Chiarucci et al. 2001).

Few studies examining the effects of multiple serpentine edaphic factors on plant community species composition and cover have been conducted in alpine or boreal climates. In the high elevation Ayas Valley in western Italy, Ni was found in high concentrations in plants growing on serpentine soil, however, no other edaphic factors were examined in the study (Vergnano Gambi 1992). In nearby valleys,

soil pH was found to be the primary factor influencing species composition on serpentine soils (Verger et al. 1993). Relatively nutrient-rich, weakly-alkaline serpentine soils in boreal (subalpine) climate supported understory plant species typical of neutral pH soils. The serpentine soil did not support the subalpine *Picea excelsa* and *Pinus cembra* forest, as typical at the same elevation on nonserpentine soils. Neutral pH serpentine soils in the alpine climate supported plant species typical of neutral pH or alkaline soils. The influence of heavy metals was not examined. Recent studies conducted on serpentine soils of Mont Avic Natural Park, Aosta Valley, western Italy have revealed that acidic soils are dominant and the plant community species composition in montane, subalpine forest and alpine climate is typical of acidic soils (D’Amico 2006a, b). Heavy metal stress was identified in both microbial and microarthropod communities, suggesting that acidic soil pH increases the bioavailability of heavy metals (D’Amico et al. 2009).

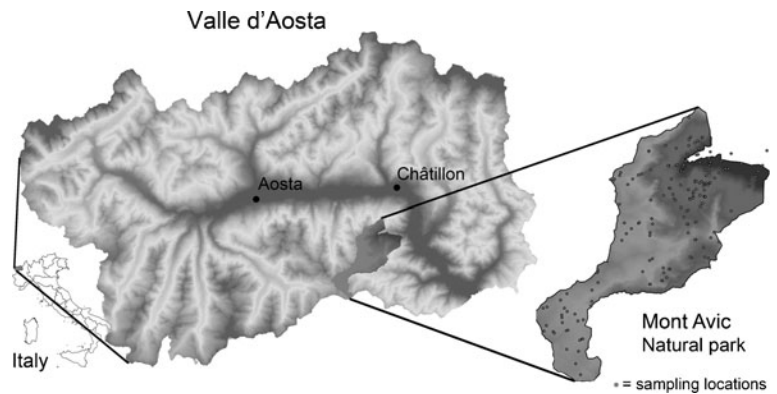
The purpose of this study was to determine the primary limiting edaphic factors of serpentine, gabbro, and calc-schist on plant community species composition and productivity (cover) in the alpine and forest habitats of the Western Alps, Italy. Focus was placed on the common edaphic factors of the serpentine syndrome, including macronutrient availability, Ca:Mg molar ratio, heavy metal availability, and rockiness.

Study area description

Mont Avic Natural Park spans the Chalamy and Champorcher Valleys of the Alps in Aosta Province, Italy (Fig. 1). The climate is sub-continental with Mediterranean influence. Altitude ranges from 1000 m. to 2900 m. Average annual temperature decreases from 5° to - 3°C and precipitation increases from 700 to 1200 mm between 1000 m. and 2600 m elevation (Mercalli 2003). Most precipitation falls in autumn and spring. Summers are quite dry, but not dry enough to induce significant plant drought stress.

Mont Avic Natural Park is included in the Piedmontese Ophiolite Complex. Serpentinite (mainly composed of antigorite minerals) is the primary rock type in the study area, associated with small outcrops of mafic metagabbros and amphibolites (Occhipinti 1997). Calc-schists emerge in the southern portion of the park above 2400 m. Pleistocene glaciers com-

Fig. 1 Study area in the Western Italian Alps



pletely covered the area until 12,000–15,000 years BP. Glaciation has resulted in soil parent material in the area being composed primarily of glacial till. The glacial till is of mixed lithology and contains serpentine rock in varying quantities. Subalpine (boreal) soils are podzolized (though not always classified as Spodosols) with deep acidification (D'Amico et al. 2008). Cryoturbation is a common feature in the alpine zone and permafrost is present on north-facing slopes above 2600 m. Cryoturbation and sparse vegetative cover largely inhibit development of alpine soils as the rate of soil erosion exceeds soil formation (Sirois and Grandtner 1992); the soil chemical properties are strictly dependant on the parent material. In small areas of the alpine zone where vegetative cover is sufficient to protect soil from erosion, organic matter has accumulated along with soil acidification.

Serpentine vegetation in Mont Avic Natural Park differs markedly with slope aspect and elevation (Fig. 2). Common herbaceous understory species growing on serpentine soil in the subalpine conifer

forests include *Noccaea alpestris* subsp. *sylvium* (commonly known as *Thlaspi sylvium*) and *Carex fimbriata* (D'Amico 2006a, b). The dominant herbaceous species on serpentine in the alpine zone is *Caricetum fimbriatae* while *Carex curvula* is the dominant species on metagabbro and calc-schist (Bovio and Broglio 2007; Buffa et al. 1998; D'Amico 2006a).

Materials and methods

Field data collection, soil sampling and analysis

Data collection was conducted in July and August 2008. 198 sites were subjectively chosen according to geology and vegetation (from existing cartography and field observations), following altitudinal and lithological transects. Some plots had previously been characterized (D'Amico 2006a, b). A non-random sampling design was followed to obtain data on uncommon habitats which had the potential of being missed with a random selection of sampling plots.

A phytosociological survey was completed in homogeneous areas of 16 m², estimating the cover (%) of each species. The following data were collected: altitude (m.), slope steepness (%), aspect, surface rockiness (SR, %), drainage, cryoturbation intensity (scale 1–5), erosion (qualitative), herbaceous species cover (%), and tree cover (%). SR, herbaceous species and tree cover were determined by visual area estimation. Drainage was estimated on the basis of standing water, redoxymorphic features (mottling and gleying) indicative of waterlogging in the soil horizons and on the presence of wetland indicator plant species. Cryoturbation intensity was qualitatively classified above the treeline, using observations of

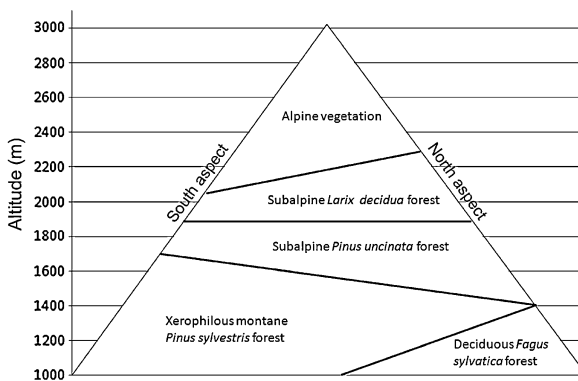


Fig. 2 Vegetation change with altitude and aspect in the study area

lichen cover on cobbles and boulders, the presence of mud bursts, mud flows in solifluction affected areas, discontinuities in plant cover (Hjort and Luoto 2009), the presence of plant species and vegetation types indicators of soil instability. Plant species were identified according to Pignatti (1992).

Soil pits were excavated in the middle of each plot down to the C or R horizon (parent material) and the soil profile was examined to assess soil development and pedogenic factors. Approximately 1 kg of soil was collected from the majority of the genetic horizons. All samples were air-dried and sieved to <2 mm, followed by physical and chemical analysis according to the methods of MPAF (2000). Soil texture was determined by pipette method. Soil pH was determined by soil to KCl solution ratio of 1:2.5: pH determined in KCl solution gives more stable results compared to H₂O measurements, but the values are lower than water pH (0.3–0.8 in the studied soils). Total acidity was determined with BaCl₂-TEA extraction followed by titration with 0.1 M HCl. Total C (TOC) and Total N (TON) were determined by micro-Dumas dry combustion using a Thermo Fisher Flash EA 1112 CN Analyzer (Thermo Fisher Scientific, Waltham, Massachusetts, USA). Available P was determined by extraction with NaHCO₃ (Olsen). Exchangeable K⁺, Na⁺, Ca²⁺, Mg²⁺, and Ni²⁺ (later on, Ca, Mg, Ni) were determined by extraction with CH₃COONH₄ (ammonium acetate; 1 M). Cation Exchange Capacity (CEC) was calculated as the sum of exchangeable bases and acidity. Rock fragments >5 mm were cleaned with (NaPO₃)₆ (sodium hexametaphosphate), sorted according to the lithology, and weighed, to semi-quantitatively characterize the parent material of the soil horizons.

Data analysis

Data analysis was performed using R2.11.1 software (R Foundation for Statistical Software, Institute for Statistics and Mathematics, Vienna, Austria). Montane and subalpine conifer forest and alpine data sets were treated separately. Deciduous forest (*Fagus*) stands and anthropogenic grasslands (outliers) were omitted. In forest habitats, trees and shrubs were omitted, as their distribution depends primarily on altitude.

Vegetation types were classified through Cluster Analysis (CA). Some agglomeration criteria were examined (single, average (1) and complete linkage, median, centroid, Ward), but only (1) was chosen for

later analysis owing to its highest cophenetic correlation value (Sneath and Sokal 1973). The best dissimilarity algorithm (Bray-Curtis) was selected according to the function *rank index* in the *Vegan* package (Oksanen 2007), which correlates many dissimilarity algorithms with a given gradient (in this case, soil-environmental properties).

To facilitate the ecological interpretation of the clusters, indicator species for each cluster were obtained with the help of the ISAMIC function, based on Dufrêne and Legendre (1997).

The number of clusters was chosen according to their ecological significance. Cluster stability was assessed through the “bootstrap” noise-adding and subsetting methods (Hennig 2007). These results are the Clusterwise Jaccard mean. If the mean is below 0.5, the cluster is regarded as “dissolved” and not significant, while the mean is regarded as “stable” and significant if the value is above 0.75.

A correlation analysis was performed on the soil-environmental properties, to recognize co-linearities (R^2 above 0.8) and select a subset of independent variables to be used in the following elaborations. The selected variables were altitude, slope steepness, aspect, surface rockiness (SR), drainage, cryoturbation intensity, soil pH, TOC, TON, P, Ca, molar Ca: Mg ratio, Ni, herbaceous species cover (%), and tree cover (%). Altitude, TON, P, Ca, and Ni were log-transformed prior to analysis.

In order to detect the relationships between plant communities (obtained from the CA) and soil-environmental properties, the Classification Tree method (CART) was used. CART is more adept at discerning the environmental factors involved in cluster separation than general discriminant analysis (De’Ath and Fabricious 2000).

Canonical Correspondence Analysis (CCA, Ter Braak 1987) was used to highlight the important factors correlated with the vegetation gradients. We used biplot scaling focused on inter-species distances, without transforming species cover or downweighting rare ones. Sampling sites were labelled on the biplot with the number of the cluster they were included in, to show the dependence of plant communities on soil-environmental (causal) factors. The statistical significance was verified with Montecarlo permutation tests.

The relationships between some serpentine species (presence-absence data) and soil-environmental properties were detected through Generalized Linear

Models (GLM, binomial distribution) and CART. GLMs are better than canonical ordinations when considering single common species (Guisan et al. 1999), while CART shows the optimal distribution ranges (Vayssières et al. 2000).

Results

Soils

Chemical properties of soils on the different substrates were highly variable (Figs. 3 and 4). Soil pH

was generally lowest on gabbro soils, but subalpine serpentine soils were deeply acidified and desaturated as well, characterized by low biological activity mor and moder humus forms. Soil pH increased with altitude and disturbance on all substrates in the alpine zone. K (not shown) and TON concentrations did not vary significantly on the different substrates. P concentration was highly variable across all substrates. Soil TOC was highly positively correlated with soil TON and P concentrations (Table 1), and thus was omitted from the statistical analysis.

Ca was unexpectedly high in the serpentine soils, particularly in soils rich in TOC. Mg was

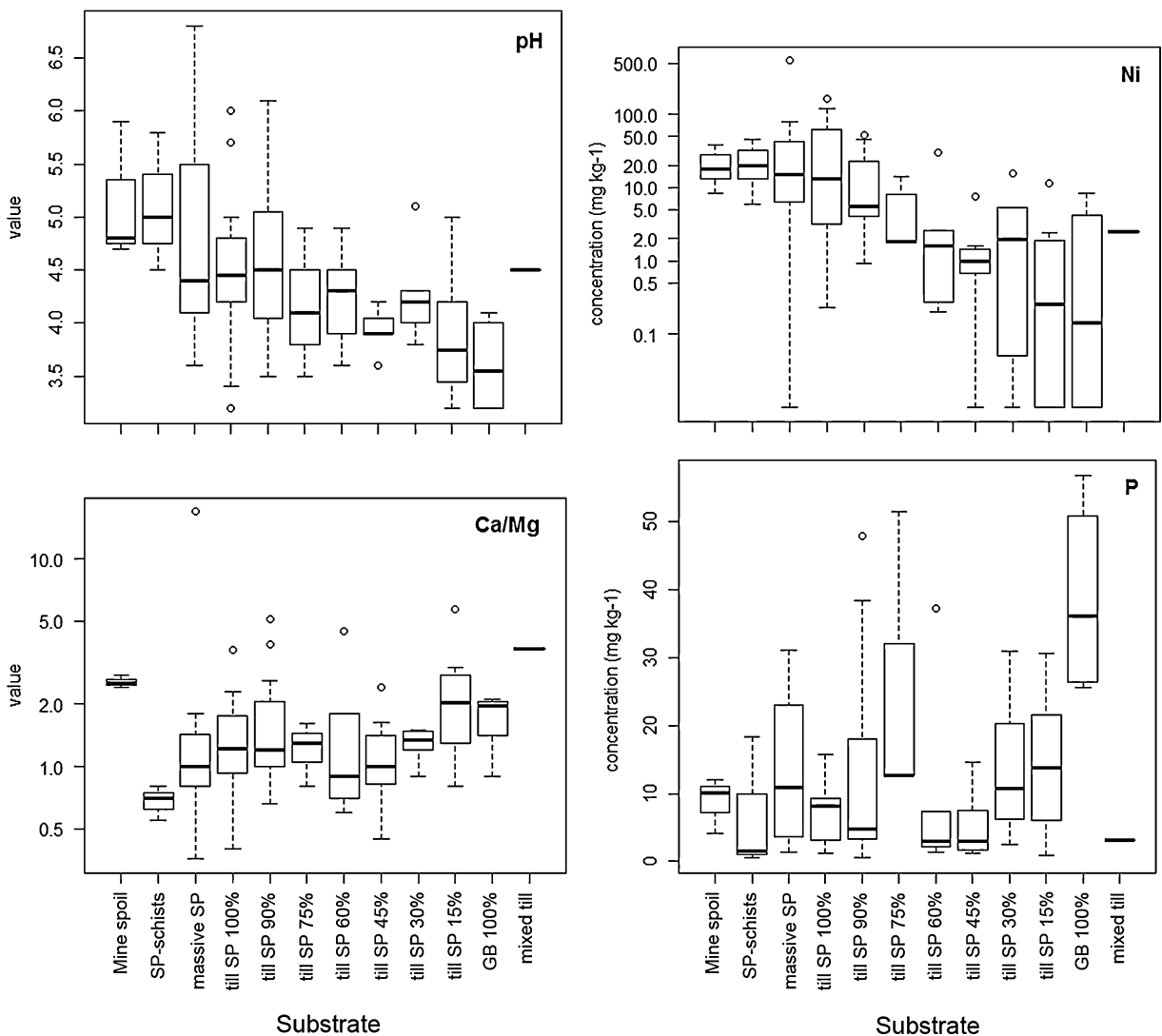


Fig. 3 Average values and variance of pH, Ni, Ca:Mg molar, and P in forest soils, formed on different substrates (SP=serpentine, GB=gabbro)

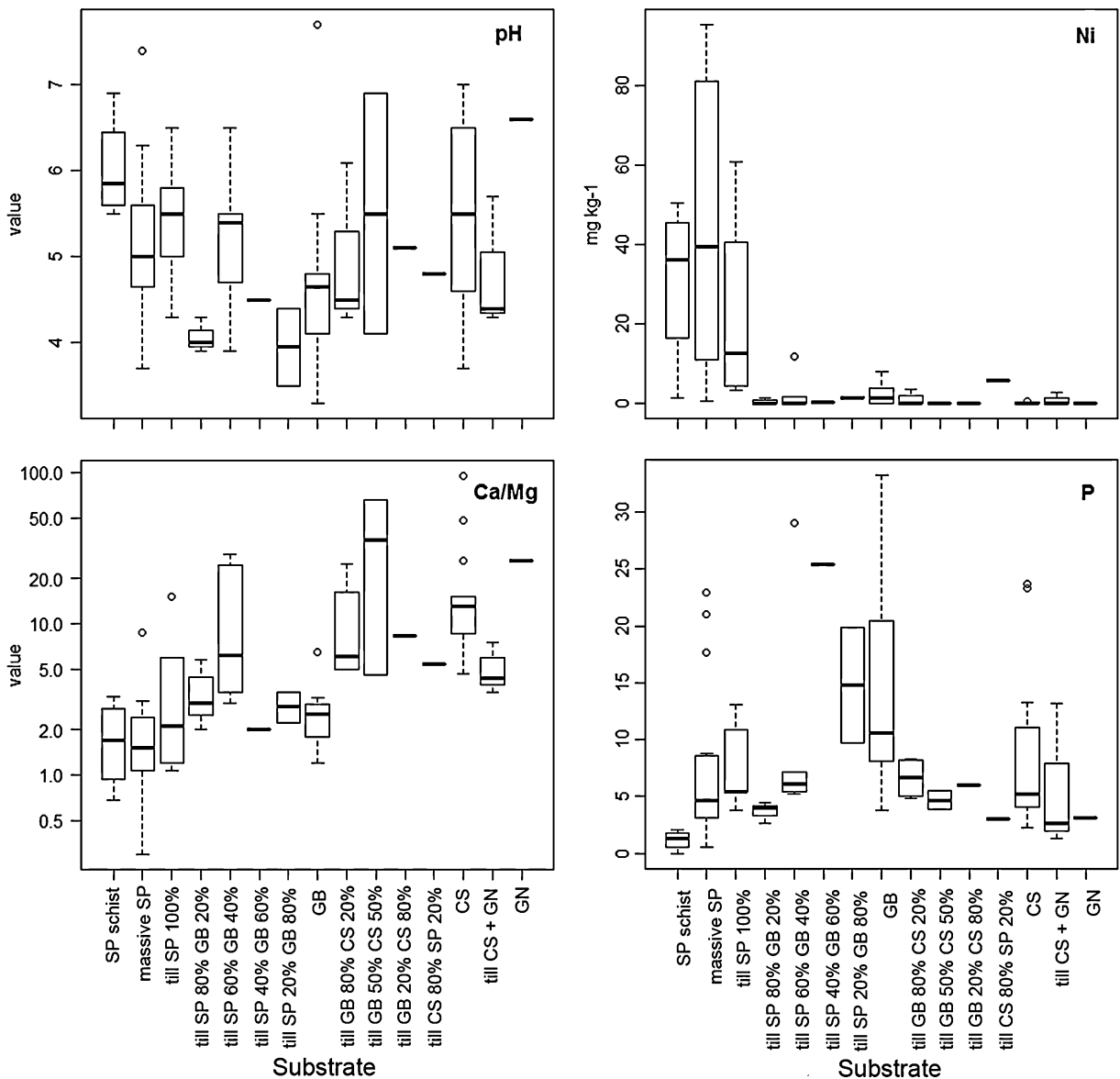


Fig. 4 Average values and variance of pH, Ni, molar Ca:Mg and P in alpine soils, formed on different substrates (SP=serpentine, GB=gabbro, CS=calcschists, GN=gneiss)

low particularly at low soil pH (in agreement with Lee et al. 2001). Consequently, the Ca:Mg molar ratio of serpentine soils included in the study varied from 0.2 in low organic E horizons in subalpine soils, up to 5 in the A horizons of some alpine and forest soils. The extreme value (16) was found in a subalpine serpentine crevice colonized by serpentine endemic species.

Serpentine soil Ni concentration was also highly variable, but was often positively correlated with soil

Ca concentration. Soil horizons rich in TOC often contained high Ni concentrations. High soil exchangeable Ni concentrations also occurred in serpentine scree as a result of elevated total Ni content derived from the incipient weathering of serpentine parent material (Carter et al. 1987). Ni concentration was typically low in strongly acidic subalpine serpentine soils.

The high weatherability of serpentine minerals resulted in higher clay and silt contents in

Table 1 Correlation matrix between soil and environmental properties in the forest soils (white cells) and in alpine soils (gray cells). Significant values are underlined (p -value <0.05)

	pH	alt	aspect	Ca:Mg	Ca	Ni	drain	slope	t.cover	SR	TON	TOC	P	Cover	Cryo
pH		0.05	-0.17	<u>0.42</u>	0.38	0.17	-0.03	0.37		0.37	-0.28	-0.28	<u>-0.43</u>	-0.36	0.22
Alt	-0.31		-0.12	0.33	0.09	-0.29	0.33	-0.06		-0.04	-0.15	-0.15	-0.1	0.00	<u>0.54</u>
Aspect	0.1	0.19		-0.34	-0.29	0.15	-0.18	0.2		-0.07	-0.16	-0.2	-0.19	0.06	-0.12
Ca:Mg	0.25	-0.08	0.03		<u>0.49</u>	-0.21	0.22	0.04		0.03	0.06	0.07	-0.04	-0.05	0.29
Ca	<u>0.49</u>	-0.21	0.07	0.6		-0.05	0.09	0.09		-0.08	<u>0.42</u>	0.38	0.1	0.22	0.1
Ni	0.39	-0.02	-0.05	0.09	0.3		-0.19	0.35		0.3	-0.02	-0.06	-0.2	-0.3	-0.15
Drain	0.15	-0.2	-0.02	0.1	-0.02	0.13		-0.29		<u>-0.42</u>	-0.05	-0.08	-0.01	0.24	0.22
Slope	0.21	-0.22	0.11	0.38	0.34	0.32	0.03			0.34	-0.15	-0.16	-0.22	-0.27	-0.12
t.cover	-0.03	<u>-0.56</u>	-0.04	-0.03	0.04	-0.16	0.04	0.17							
SR	0.37	-0.01	-0.11	0.24	0.2	0.39	0.15	0.38	-0.23		-0.36	-0.33	-0.31	<u>-0.81</u>	0.23
TON	0.09	0.1	0.02	<u>0.58</u>	0.52	0.26	0.11	0.15	-0.31	0.14		<u>0.98</u>	<u>0.7</u>	<u>0.54</u>	-0.39
TOC	0.03	-0.07	-0.07	<u>0.49</u>	0.43	0.2	0.2	0.08	-0.18	0.18	<u>0.87</u>		<u>0.74</u>	<u>0.5</u>	-0.34
P	-0.16	-0.13	-0.06	0.17	0.19	-0.05	-0.03	-0.1	0.06	-0.17	<u>0.48</u>	<u>0.61</u>		0.37	-0.2
Cover															<u>-0.41</u>

serpentine soils, which were mostly loamy or loamy skeletal.

Vegetation

Forest vegetation data

Forest vegetation is grouped into 10 ecologically meaningful clusters (Fig. 5a). Characteristic plant

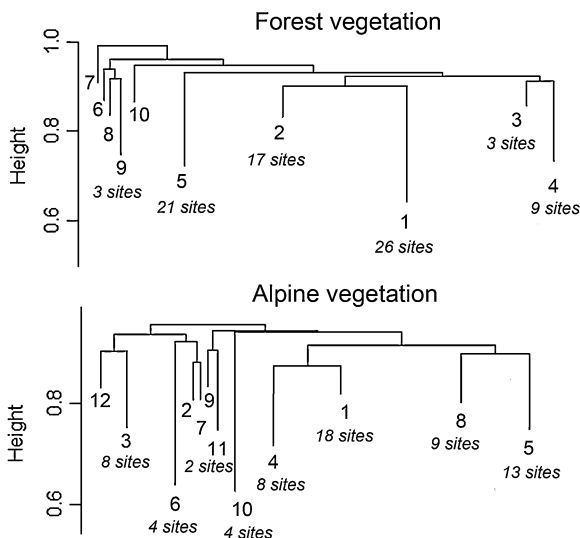


Fig. 5 Average linkage clusters (Bray-Curtis distance) of Forest vegetation and Alpine vegetation

species associated with the Forest vegetation clusters are listed in Table 2. Only a few of the clusters were statistically stable due to species in the plant communities being similarly associated with acidic soils (dominant condition of forest soils) and due to the lack of variation in plant community species composition across the different environments.

Clusters 1 and 2 were similar and included open subalpine *Pinus uncinata* and *Larix decidua* forest vegetation. Cluster 1 included sites on serpentine above 1800 m, enriched in serpentine-endemics including *Carex fimbriata* and *Noccaea alpestris subsp. sylvium*, and in the local serpentine indicator, *Plantago serpentina*. Cluster 2 included similar subalpine communities developed on gabbro, serpentine and mixed parent materials, devoid of serpentine species. Cluster 3 included species-poor sites developed in closed subalpine forests. Clusters 4 and 5 represented species-rich montane and subalpine sites. Cluster 5 included *Pinus sylvestris* forests, stream banks, rock crevices and scree containing several serpentine endemics or strong serpentine indicators such as *Noccaea alpestris subsp. sylvium*, *Cardamine plumieri*, *Biscutella laevigata*, *Asplenium adulterinum* and *A. viride*. Cluster 9 included riverbeds on serpentine, dominated by serpentine endemic and strong serpentine indicator species. The remaining groups included species-poor sites such as mine spoils and gabbro rock crevices.

Table 2 Indicator species according to the Dufrene-Legendre index (Dufrene and Legendre 1997), ordered according to the clusters of forest herbaceous vegetation. The smallest clusters are omitted, as well as the species growing in less than 30% of the sites belonging to single clusters

Species	Family	Clusters								
		1 Open subalpine forest on serpentine	2 Typical subalpine forest	3 Species-poor subalpine closed forests	4 Montane <i>Pinus sylvestris</i> forest	5 Montane species-rich serpentine forests	9 Riverbeds on serpentine			
<i>Astrantia minor</i>	Apiaceae	0.32	0.27	0.66	0.22	0.11	0	0	0	
<i>Chaerophyllum villarsii</i>	Apiaceae	0.04	0.11	0	0.11	0	0.66	0	0.66	
<i>Antennaria dioica</i>	Asteraceae	0.4	0.05	0	0.22	0.11	0	0	0	
<i>Arnica montana</i>	Asteraceae	0.36	0.22	0	0	0	0	0	0	
<i>Carduus defloratus</i>	Asteraceae	0	0	0	0	0.11	0.33	0	0.33	
<i>Hieracium murorum</i> subsp. <i>lachenalii</i>	Asteraceae	0.36	0.55	1	0.88	0.5	0.66	0	0.66	
<i>Homogyne alpina</i>	Asteraceae	0.56	0.27	0.33	0	0.11	0	0	0	
<i>Solidago virgaurea</i> subsp. <i>minuta</i>	Asteraceae	0.24	0.22	0.33	0.22	0.05	0	0	0	
<i>Biscutella laevigata</i>	Brassicaceae	0.56	0.11	0	0.22	0.33	0	0	0	
<i>Cardamine plumieri</i>	Brassicaceae	0.16	0.05	0	0.11	0.27	0.66	0	0.66	
<i>Noccaea alpestris</i> subsp. <i>sylvium</i>	Brassicaceae	0.4	0.05	0	0.33	0.5	0	0	0	
<i>Noccaea caerulea</i>	Brassicaceae	0.04	0	0	0	0.05	0	0	0	
<i>Campanula rotundifolia</i>	Campanulaceae	0.04	0.11	0.33	0	0	0	0	0	
<i>Campanula scheuchzeri</i>	Campanulaceae	0.12	0.11	0.33	0.11	0.22	0	0	0	
<i>Carex echinata</i>	Cyperaceae	0.08	0.16	0	0.11	0	0.33	0	0.33	
<i>Carex fimbriata</i>	Cyperaceae	0.68	0.11	0	0	0.11	0	0	0	
<i>Carex sempervirens</i>	Cyperaceae	0.72	0.11	0	0.33	0.11	0.33	0	0.33	
<i>Athyrium filix-foemina</i>	Dryopteridaceae	0	0.16	0	0.33	0.11	0	0	0	
<i>Loiseleuria procumbens</i>	Ericaceae	0.36	0	0	0	0	0	0	0	
<i>Gentiana acaulis</i>	Gentianaceae	0.72	0.16	0.66	0.22	0.05	0	0	0	
<i>Luzula nivea</i>	Juncaceae	0.04	0	0	0	0.16	0.33	0	0.33	
<i>Luzula sudetica</i>	Juncaceae	0.08	0	0.33	0	0.05	0	0	0	

<i>Luzula sylvatica</i>	Juncaceae	0.12	0.16	0	0.33	0	0	0
<i>Ajuga pyramidalis</i>	Lamiaceae	0.04	0	0	0	0	0.33	0
<i>Thymus polirichus</i>	Lamiaceae	0.32	0.05	0	0.11	0.38	0	0
<i>Pinguicula leptoceras</i>	Lentibulariaceae	0.32	0.05	0	0.11	0	0	0
<i>Lycopodium annotinum</i>	Lycopodiaceae	0.16	0.27	0	0.11	0.11	0.33	0.33
<i>Epilobium collinum</i>	Onagraceae	0	0	0	0.11	0	0.33	0.33
<i>Dactylorhiza maculata</i> subsp. <i>fuchsii</i>	Orchidaceae	0.16	0.22	0	0.22	0.11	0.33	0.33
<i>Pseudorchis albida</i>	Orchidaceae	0.04	0.05	0.33	0	0.05	0	0
<i>Oxalis acetosella</i>	Oxalidaceae	0	0.11	0	0.33	0	0	0
<i>Plantago serpentina</i>	Plantaginaceae	0.68	0.05	0	0.33	0.16	0	0
<i>Anthoxanthum odoratum</i>	Poaceae	0.44	0.38	0.33	0.33	0.27	0	0
<i>Brachipodium pinnatum</i>	Poaceae	0.08	0.11	0.33	0.55	0.11	0	0
<i>Calamagrostis arundinacea</i>	Poaceae	0.04	0.05	0	0	0.66	0.33	0.33
<i>Calamagrostis villosa</i>	Poaceae	0.08	0.88	0	0.11	0	0	0
<i>Deschampsia flexuosa</i>	Poaceae	0.44	0.33	0.66	0.55	0.16	0	0
<i>Deschampsia caespitosa</i>	Poaceae	0	0.05	0	0	0.05	0.33	0.33
<i>Festuca varia</i>	Poaceae	0.44	0.55	0	0.55	0.66	0	0
<i>Molinia caerulea</i>	Poaceae	0	0	0	0	0.05	0.66	0.66
<i>Nardus stricta</i>	Poaceae	0.72	0.22	0	0.11	0.16	0	0
<i>Rumex acetosella</i>	Polygonaceae	0.04	0	0	0	0.05	0.33	0.33
<i>Rumex scutatus</i>	Polygonaceae	0	0	0	0	0.27	0.33	0.33
<i>Primula hirsuta</i>	Primulaceae	0.28	0.05	0	0	0.05	0	0
<i>Soldanella verna</i>	Primulaceae	0.36	0.05	0	0	0	0	0
<i>Ranunculus acris</i>	Ranunculaceae	0	0.11	0	0.44	0.11	0.33	0.33
<i>Potentilla erecta</i>	Rosaceae	0.56	0.44	0.66	0.22	0.11	0.33	0.33
<i>Galium album</i>	Rubiaceae	0.08	0.05	0	0.33	0.27	0	0
<i>Maianthemum bifolium</i>	Ruscaceae	0.08	0.11	0	0.33	0	0	0
<i>Tofieldia calyculata</i>	Tofieldiaceae	0.16	0.05	0	0	0	0.33	0.33
<i>Viola biflora</i>	Violaceae	0.16	0.27	0.33	0.44	0.33	1	1
<i>Viola reichenbachiana</i>	Violaceae	0.2	0.11	0.33	0.33	0.27	0	0

Table 3 Indicator species according to the Dufrêne-Legendre index (Dufrêne and Legendre 1997), ordered according to the clusters of alpine vegetation. The single-site clusters are omitted, as well as the species growing in less than 30% of the sites belonging to single clusters

Species	Family	Clusters									
		1	3	4	5	6	8	10	11		
		Stable serpentine plots	Serpentine talus and outcrops	Stable on gabbro (rarely calc-schist)	High altitude on gabbro	High altitude gabbro, <i>Festuca varia</i>	High altitude on calc-schist	High altitude talus on serpentine	Stable on calc-schists		
<i>Astrantia minor</i>	Apiaceae	0.33	0	0	0	0	0	0	0		
<i>Ligusticum mutetina</i>	Apiaceae	0.16	0	0	0.38	0.25	0	0	0.5		
<i>Antennaria dioica</i>	Asteraceae	0.44	0.12	0.12	0.07	0.25	0	0	0.5		
<i>Arnica montana</i>	Asteraceae	0.11	0	0	0	0	0	0	0.5		
<i>Cirsium spinosissimum</i>	Asteraceae	0	0	0	0.07	0	0.11	0	0.5		
<i>Erigeron uniflorus</i>	Asteraceae	0	0	0.12	0.3	0	0.44	0	0.5		
<i>Gnaphalium supinum</i>	Asteraceae	0	0	0.12	0.07	0	0.11	0.5	0		
<i>Hieracium glanduliferum</i>	Asteraceae	0	0.12	0	0.07	0.5	0	0	0		
<i>Leontodon alpinum</i>	Asteraceae	0.11	0	0	0.15	0	0	0	0.5		
<i>Leontodon helveticum</i>	Asteraceae	0.33	0	0.37	0.07	0	0.11	0	0		
<i>Leucanthemopsis alpina</i>	Asteraceae	0.27	0	0.62	0.53	0	0.44	0.5	0.5		
<i>Botrychium lunaria</i>	Botrychiaceae	0	0	0	0	0.25	0	0	0.5		
<i>Arabis caerulea</i>	Brassicaceae	0	0	0	0	0	0	0.5	0		
<i>Biscutella laevigata</i>	Brassicaceae	0.33	0.5	0	0	0.25	0	0	0		
<i>Cardamine plumieri</i>	Brassicaceae	0.05	0.87	0	0	0	0	0.25	0		
<i>Noccaea alpestris</i> subsp. <i>sylvium</i>	Brassicaceae	0.22	0.75	0.12	0.15	0	0	0.25	0		
<i>Noccaea corymbosa</i>	Brassicaceae	0.05	0.25	0	0.07	0	0.33	0.75	0		
<i>Pritzelago alpina</i>	Brassicaceae	0	0	0.12	0	0	0.22	0.5	0		
<i>Campanula cochlearifolia</i>	Campanulaceae	0.05	0.62	0	0.15	0	0	0	0		
<i>Cerastium alpinum</i>	Caryophyllaceae	0.05	0	0	0.07	0	0	0	0.5		
<i>Cerastium arvense</i>	Caryophyllaceae	0	0.25	0	0.07	0	0	0.5	0		
<i>Cerastium uniflorus</i>	Caryophyllaceae	0	0	0	0.07	0	0.33	0.75	0		
<i>Minuartia recurva</i>	Caryophyllaceae	0	0	0	0	0.25	0.33	0	0		
<i>Minuartia verna</i>	Caryophyllaceae	0	0	0	0.15	0.5	0	0	0.5		
<i>Silene excapa</i>	Caryophyllaceae	0.33	0	0.37	0.76	0.5	0.66	0.5	0.5		
<i>Silene rupestris</i>	Caryophyllaceae	0.16	0.12	0	0.15	0.25	0	0	0.5		
<i>Silene vulgaris</i>	Caryophyllaceae	0	0.5	0	0	0	0	0	0		

<i>Seduma alpinum</i>	Crassulaceae	0.11	0.12	0.37	0.23	0	0.11	0.25	0
<i>Sempervivum montanum</i>	Crassulaceae	0.05	0	0.37	0.3	0.5	0	0	0
<i>Juniperus communis</i>	Cupressaceae	0.22	0.12	0	0	0.5	0	0	0
<i>Carex curvula</i>	Cyperaceae	0.22	0	1	0.69	0.5	0.22	0	0
<i>Carex fimbriata</i>	Cyperaceae	0.77	0.75	0	0.23	0	0.11	0.25	0
<i>Carex sempervirens</i>	Cyperaceae	0.44	0.12	0.12	0.46	0.75	0	0	0
<i>Loiseleuria procumbens</i>	Ericaceae	0.61	0	0.25	0.07	0	0	0	0
<i>Rhododendron ferrugineum</i>	Ericaceae	0.5	0.12	0.12	0	0.25	0	0	0
<i>Vaccinium myrtillus</i>	Ericaceae	0.05	0	0.12	0	0.5	0	0	0
<i>Vaccinium uliginosum</i>	Ericaceae	0.72	0	0.37	0.46	0.25	0	0.25	0
<i>Vaccinium vitis-idaea</i>	Ericaceae	0	0	0	0	0.5	0	0	0
<i>Lotus corniculatus</i>	Fabaceae	0.05	0	0.12	0.23	0.25	0.11	0	0.5
<i>Trifolium alpinum</i>	Fabaceae	0.11	0.37	0.37	0	0.75	0	0	0
<i>Trifolium nivale</i>	Fabaceae	0.11	0	0	0.07	0	0	0	0.5
<i>Gentiana acaulis</i>	Gentianaceae	0.22	0.12	0	0.07	0.5	0	0	0.5
<i>Gentiana campestris</i>	Gentianaceae	0	0	0	0	0	0	0	1
<i>Gentiana klusii</i>	Gentianaceae	0	0	0	0	0	0	0	0.5
<i>Gentiana ramosa</i>	Gentianaceae	0.22	0	0.12	0.46	0.25	0	0	0
<i>Gentiana verna</i>	Gentianaceae	0.05	0	0.25	0.3	0	0	0	1
<i>Juncus jacquini</i>	Juncaceae	0	0	0	0.53	0	0	0	0
<i>Juncus trifidus</i>	Juncaceae	0.22	0.12	0	0.23	0.5	0	0	0.5
<i>Juncus triglumis</i>	Juncaceae	0	0	0	0.15	0	0	0	0.5
<i>Luzula alpinopilosa</i>	Juncaceae	0.05	0	0.12	0.46	0	0.22	0.25	0
<i>Luzula lutea</i>	Juncaceae	0.33	0.62	0	0.07	0	0.11	0.25	0
<i>Luzula spicata</i>	Juncaceae	0	0	0.12	0.3	0	0	0	0.5
<i>Trichophorum caespitosum</i>	Juncaceae	0.33	0	0.37	0.07	0.25	0	0	0
<i>Thymus serpyllum</i>	Lamiaceae	0.11	0.37	0	0.07	0	0	0	0.5
<i>Plantago serpentina</i>	Plantaginaceae	0.27	0.12	0.12	0.07	0.25	0.11	0	0.5
<i>Armeria alpina</i>	Plumbaginaceae	0.38	0.25	0.25	0.61	0.25	0.33	0.25	0.5
<i>Agrostis rupestris</i>	Poaceae	0.77	0.37	0.25	0.46	0.25	0.33	0.5	0
<i>Anthoxanthum alpinum</i>	Poaceae	0.16	0	0.12	0.53	0.25	0	0	1
<i>Festuca halleri</i>	Poaceae	0.38	0	0.75	0.53	0	0.11	0.5	0.5
<i>Festuca quadriflora</i>	Poaceae	0	0	0.12	0.38	0	0.44	0.25	0
<i>Festuca varia</i>	Poaceae	0.22	0.5	0.12	0.15	1	0	0	0

Table 3 (continued)

Species	Family	Clusters								
		1 Stable serpentine plots	3 Serpentine talus and outcrops	4 Stable on gabbro (rarely calc-schist)	5 High altitude on gabbro	6 High altitude, <i>Festuca</i> <i>varia</i>	8 High altitude on calc-schist	10 High altitude talus on serpentine	11 Stable on calc-schists	
<i>Poa alpina</i>	Poaceae	0.27	0	0.62	0.69	0.25	0.44	0.75	0.5	
<i>Oxyria digyna</i>	Polygonaceae	0.11	0	0.12	0.15	0	0.11	0.5	0	
<i>Polygonum viviparum</i>	Polygonaceae	0.33	0	0.37	0.76	0	0.33	0	0.5	
<i>Primula hirsuta</i>	Primulaceae	0.61	0	0.25	0.15	0	0	0	0	
<i>Soldanella verna</i>	Primulaceae	0.27	0	0.12	0.3	0	0	0	0	
<i>Pulsatilla alpina</i>	Ranunculaceae	0	0.25	0	0.23	0.5	0	0	0	
<i>Ranunculus glacialis</i>	Ranunculaceae	0	0	0	0.3	0	0.33	0	0	
<i>Geum montanum</i>	Rosaceae	0.05	0	0.5	0.46	0.25	0	0	0.5	
<i>Potentilla grandiflora</i>	Rosaceae	0	0	0	0	0.5	0	0	0	
<i>Galium anysophyllum</i>	Rubiaceae	0.11	0.25	0	0.07	0	0	0	0.5	
<i>Salix foetida</i>	Salicaceae	0.11	0.12	0	0	0	0.11	0	0.5	
<i>Salix herbaceae</i>	Salicaceae	0.27	0	0.37	0.23	0.25	1	0	0	
<i>Salix reticulata</i>	Salicaceae	0	0	0	0.07	0	0.33	0	0.5	
<i>Tesium pyrenaicum</i>	Santalaceae	0	0	0	0.07	0	0.11	0	0.5	
<i>Saxifraga exarata</i> subsp. <i>moschata</i>	Saxifragaceae	0.11	0.25	0.37	0.23	0	0.55	0	0	
<i>Saxifraga oppositifolia</i>	Saxifragaceae	0.38	0.12	0.37	0.46	0	0.44	0	0	
<i>Euphrasia minima</i>	Scrophulariaceae	0.11	0	0.12	0.53	0	0.66	0	0	
<i>Euphrasia rohostikoviana</i>	Scrophulariaceae	0.05	0	0	0.07	0.25	0.11	0	0.5	
<i>Myosotis alpina</i>	Scrophulariaceae	0	0	0.25	0.15	0	0	0	0.5	
<i>Pedicularis kernerii</i>	Scrophulariaceae	0.33	0	0.5	0.69	0.25	0.22	0	0.5	
<i>Veronica bellidoides</i>	Scrophulariaceae	0	0	0.37	0	0.5	0	0	0	
<i>Athamantha cretensis</i>	Umbelliferae	0	0.37	0	0	0	0	0	0	
<i>Valeriana celtica</i>	Valerianaceae	0.55	0	0.75	0.61	0	0.11	0	0.5	
<i>Viola biflora</i>	Violaceae	0.11	0.37	0	0	0.25	0	0.25	0	

Alpine vegetation data

Alpine vegetation was grouped into 12 ecologically meaningful and (usually) statistically stable clusters, with two major divisions (Fig. 5b). Characteristic plant species associated with the Alpine vegetation clusters are listed in Table 3.

The highest division isolated Clusters 12, 3, 6, 2, 7 from the other clusters. Cluster 3 included serpentine outcrops or talus, rich in the serpentine endemics *Cardamine plumieri*, *Noccaea alpestris* subsp. *sylvium* and *Carex fimbriata*. Cluster 12 is similar, but enriched in species strongly associated with alkaline soils due to the presence of calc-schist outcrops upstream. Cluster 6 included high-altitude plant communities dominated by *Festuca varia* on meta-gabbro, strongly associated with acidic soils.

On the other side of the highest division are Clusters 9, 11, 10, 4, 1, 8, and 5. Cluster 9 consisted of steep, vegetated talus on mafic rocks. Plant species strongly associated with acidic, unstable soils, of Cluster 9 include *Oxyrietum digynae*. Cluster 11 included calc-schist slopes supporting *Curvuletum*, a vegetation type normally associated with acidic soils, but here containing also alkaline soil species. Cluster 10 consisted of high altitude talus vegetation on serpentine supporting *Thlaspietum rotundifolii* and characterized by the Ni hyperaccumulator *Noccaea corymbosa* (commonly known as *Thlaspi rotundifolium* subsp. *corymbosum*). Cluster 4 consisted of gabbro and calc-schist typically supporting, strictly acidophilous *Curvuletum*. Cluster 1 included serpentine dominated by *Carex fimbriata*, as well as other plant species strongly associated with acidic soils (Ericaceae shrubs). Clusters 8 and 5 represented calc-schist and gabbro talus dominated by plant species strongly associated with acidic soils, but also contained some species normally associated with alkaline soils.

Soil-vegetation relationships

Forest vegetation data

The average values and variance of some edaphic properties under the vegetation clusters are shown in Fig. 6.

Serpentine plant communities of Mont Avic Natural Park were most strongly influenced by habitat

factors, such as altitude, tree cover and surface rocks, and by soil Ni and pH values, which were the most important chemical factors correlated with vegetation differences. Other factors such as slope, drainage, Ca, Ca:Mg, P had a weaker correlation with vegetation changes, as revealed by CCA (Fig. 7b; Table 4). Ca and Ca:Mg were positively correlated with the presence of serpentine species and plant communities. The first axis could be interpreted as an altitude/tree cover gradient, while the second as a disturbance gradient. The low proportion (22.6%) of the inertia explained by the model is due to the disorder typical of ecological systems (Chiarucci et al. 2001), associated with a weak differentiation in species composition or to the omission of important environmental properties (e.g., bare soil, hydrography, winter snow depth, etc.) which deeply influence vegetation in mountain ecosystems (Guisan et al. 1998).

Serpentine vegetation (Clusters 9, 1, and 5) was often associated with low tree cover (Fig. 7a). Low Ca values characterized subalpine plant communities on all substrates (Clusters 1, 2, and 3), due to strong leaching. Low Ca:Mg characterized typical, stable subalpine vegetation, devoid of serpentine endemic species (Cluster 2), compared to the analogous vegetation on serpentine soils (Cluster 1). Serpentine endemic rich plant communities (Cluster 5) were associated with Ni and, often, high Ca and low P soils (Fig. 7a).

Alpine vegetation data

Disturbed, pioneer plant communities (Clusters 3 and 10 on serpentine, 5 and 8 on gabbro and calc-schist) grew on soils characterized by higher pH, Ni, Ca, and lower P and N values than climax, stable plant communities on similar substrates (Clusters 1, 4, 6 and 11). Comparing similar well-developed and stable habitats, serpentine plant communities grew on soils characterized by a much higher Ni and a slightly lower N content than elsewhere. Ca was highest in the *Curvuletum* plant community developed on calc-schists (Fig. 8).

Plant cover, altitude and slope were effective in differentiating plant communities (Fig. 9a). Low cover, high SR and Ni characterized serpentinic clusters (Clusters 1 and 3). *Carex fimbriata* associations grew on strongly acidic soils (Cluster 1). A

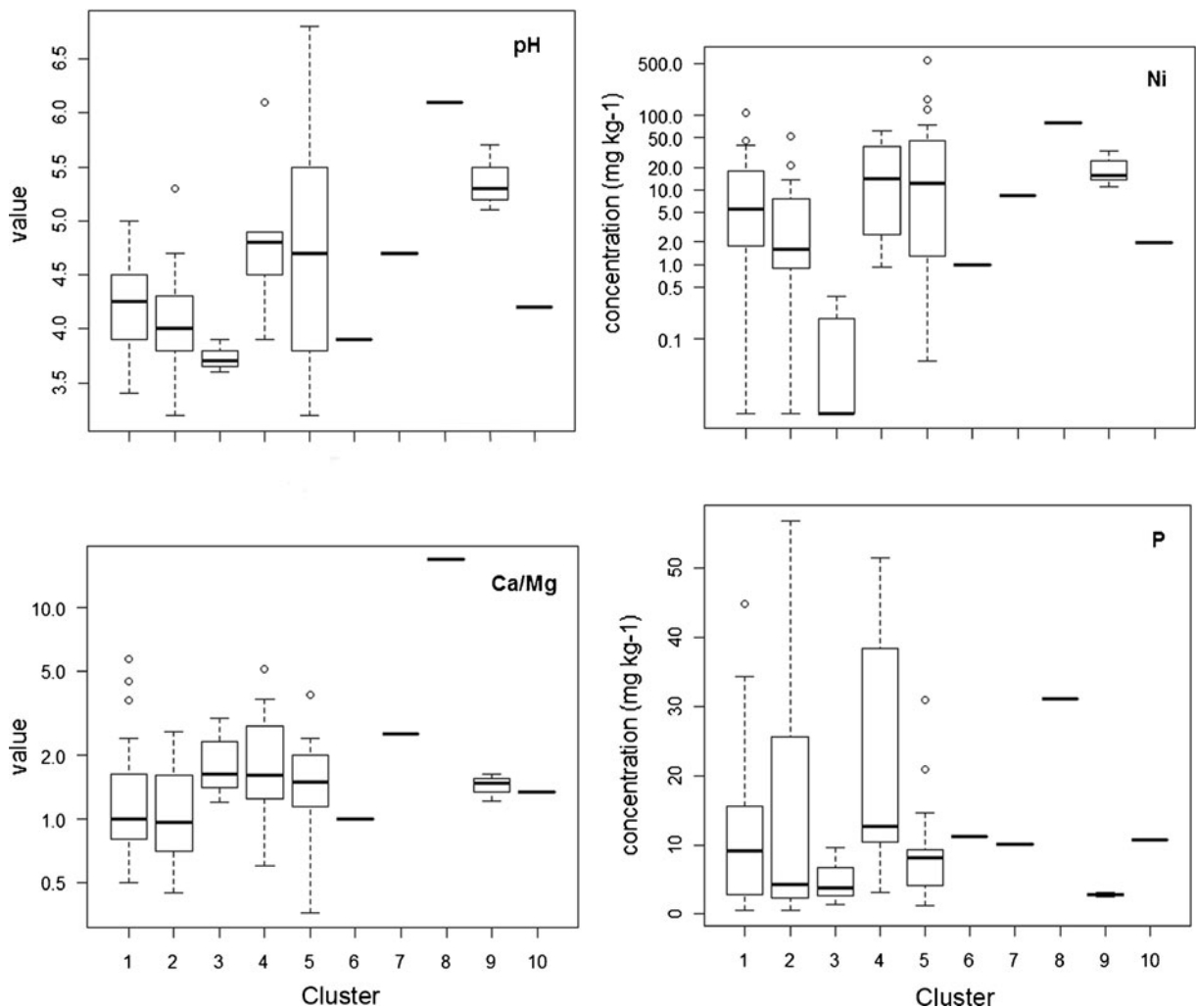


Fig. 6 Average values and variance of soil pH, Ni, molar Ca:Mg and P in forest plant associations (represented by the cluster numbers)

lower N content (not shown) separated high altitude stands on serpentine (Cluster10) from the ones on other substrates (Cluster8).

The low proportion of inertia explained by the CCA model (25%) was due to the same reasons discussed in the previous section. Axis 1 was correlated with slope, SR, drainage and Ni and could be interpreted as a drainage gradient (Table 4, Fig. 9b). The second axis is mostly related with aspect, cryoturbation, Ni, Ca and Ca:Mg (partially corresponding to a “disturbance” gradient). Most edaphic and environmental factors were correlated with both axes. Soil pH and Ni were the most influential chemical properties (long arrows, Ter Braak 1987). The CCA separated the clusters quite well along the species-environment gradients.

Notes on some species

GLMs (Table 5) and CART, applied to some common species, showed interesting correlation with the chemical soil properties. The serpentine endemics *Carex fibrariata*, *Noccaea alpestris* subsp. *sylvium*, *Noccaea corymbosa*, *Cardamine plumieri* and the local serpentine indicators *Luzula lutea* and *Biscutella laevigata* appeared to be strongly correlated with high soil Ni concentration (Fig. 10a–c, Table 5). High soil pH was also strongly correlated with *Noccaea corymbosa* and *Cardamine plumieri*. Additionally, *Noccaea corymbosa* and *Luzula lutea* were strongly correlated with low soil Ca:Mg.

Carex sempervirens was preferentially distributed on serpentine soils with intermediate concentrations

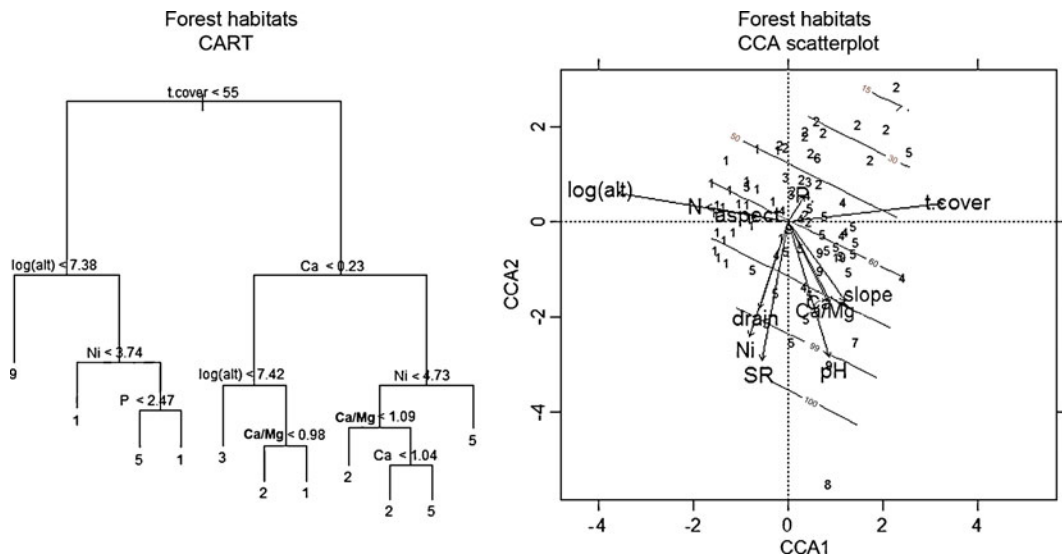


Fig. 7 CART and CCA scatterplot of forest habitats. It is possible to see the primary edaphic factors involved in forest vegetation differentiation (abbreviations: log(alt), log-transformed altitude; Ni, log(Ni); cover, plant cover above the

treeline). Ca is expressed in cmol/kg. The first axis of the CCA scatterplot represents an altitude gradient, the second a stability gradient. Substrate (serpentine %) is indicated by the *curves*

of Ni and low Ca:Mg. Common alpine species such as *Carex curvula* (Fig. 10d) and *Luzula spicata* were negatively correlated with Ni, emphasizing their absence on serpentine soils at Mont Avic.

Silene vulgaris grows on different soil types at Mont Avic. On serpentine sites with extreme physical and chemical soil properties, the species manifests unique morphological characteristics including short stature and thickened, blue-violet leaves. It may represent a unique serpentine adapted ecotype of the species.

Discussion

Forest habitats

Forest soils in Mont Avic Natural Park are generally well-developed influenced by the podzolization process on stable sites (D'Amico et al. 2008), or they are Entisols in steep or disturbed areas. N concentrations were found to be variable and not dependent upon parent material. P concentration was lowest in the most acidic, leached, and well-developed Spodosols. Forest serpentine soils exhibit bioaccumulation of Ca in the A horizon as a result of biocycling and organic matter accumulation. Ca is included in organic compounds and is also preferentially bound to

exchange sites of organic molecules (Rodenkirchen and Roberts 1993). In the most acidic soils, Ca is leached from the soil profile on all parent materials, while it is not bioaccumulated on serpentine. Mg is always depleted in surface organic layers of the forest soils, unlike that observed on serpentine soils of humid conifer forests in the Pacific Northwest, USA (Burt et al. 2001).

Soil pH, Mg and Ni concentration were found to be inversely dependent upon the degree of soil development, which in turn, is related to soil moisture and stable, acidifying vegetative cover. Low soil pH, combined with high humidity, has resulted in substantial leaching of Ni. This is similar to the findings of Chardot et al. (2007). An opposite trend with respect to soil Ni concentration (increased Ni availability at low pH) has often been observed (Chiarucci et al. 1998; Lee and Hewitt 1982; Robinson et al. 1996; Tsiripidis et al. 2010), possibly resulting from a warmer and drier Mediterranean climate (less precipitation and leaching; Chiarucci et al. 1998; Tsiripidis et al. 2010).

In boreal forests, serpentine habitats often stand out as treeless, barren islands, with isolated colonies of arctic or alpine plant species at the lower altitudinal limit of their distribution (Rune and Westerbergh 1991). In Mont Avic Natural Park, forest vegetation of the serpentine soils is generally dense without any

Table 4 The canonical scores of the environmental factors and the eigenvalues of the first 3 canonical axes. *: significant values or models (p value <0.01)

		CCA1	CCA2	CCA3	
Forest habitats *	eigenvalue	0.55	0.38	0.36	
	Inertia explained	4.57	3.02	2.97	
	Scores				
	pH*	-0.20	-0.60	0.34	
	Log(Altitude)*	-0.90	0.15	0.01	
	Tree cover*	0.82	0.10	-0.03	
	Log(Ni)	-0.21	-0.60	0.34	
	Ca:Mg	0.20	-0.42	0.13	
	Drainage*	-0.15	-0.45	-0.26	
	Aspect	-0.20	0.03	-0.35	
	Log(Ca)	0.22	-0.42	0.29	
	Slope	0.29	-0.41	-0.52	
	Log(P)	0.08	0.13	0.45	
	Log(N)	-0.43	0.08	0.04	
	SR	-0.14	-0.73	-0.32	
	Alpine habitats *	Eigenvalue	0.50	0.44	0.42
		Inertia explained (%)	3.86	3.37	3.22
Scores					
pH*		-0.40	0.37	-0.47	
Log(Alt)*		0.51	0.12	-0.75	
Slope*		-0.58	-0.26	-0.39	
Log(Ni)*		-0.36	0.56	0.35	
Log(Ca)		0.00	0.27	-0.32	
Cryo		0.19	0.35	-0.38	
Ca:Mg		0.16	0.14	-0.38	
Drain*		0.59	0.18	0.03	
Aspect		-0.26	-0.52	-0.10	
Cover		0.53	-0.45	0.08	
SR		-0.55	0.40	-0.12	
Log(P)		0.21	-0.21	0.20	
Log(N)		0.18	-0.27	0.31	

marked stunting of growth. The lack of characteristic vegetation stunting and sparse vegetative cover (serpentine syndrome) of the forest serpentine soils may be the result of extensive leaching of Mg (relative to Ca) and Ni. Mg and Ni leaching would result in a higher Ca:Mg molar ratio and lower Ni concentration (less chemical stress) than typical serpentine soils, as seen in this study. A similar weakening of the serpentine syndrome on forest soils has also been documented in coniferous forests of northern California (Alexander 1988). In that case, higher forest productivity on well developed, ancient soils was attributed to the progressive leaching of Mg and other heavy metals such as Ni. In Japan (Nakata

and Kojima 1987) the humid climate induced a strong leaching of Mg from the podzolic soils, which supported a closed coniferous forest.

Subalpine serpentine vegetation of Mont Avic typically consists of acidophilous *Vaccinietum* with interspersed serpentine endemic or indicator plant species including *Noccaea alpestris* subsp. *sylvium*, *Biscutella laevigata*, and *Carex fimbriata*. Serpentine endemic plant species were generally found to be more abundant on less developed serpentine soils at Mont Avic. A similar trend has been found for serpentine vegetation at other sites in Italy (Chiarucci et al. 1998), where the greater proportion of serpentine endemics was attributed to weaker nutrient

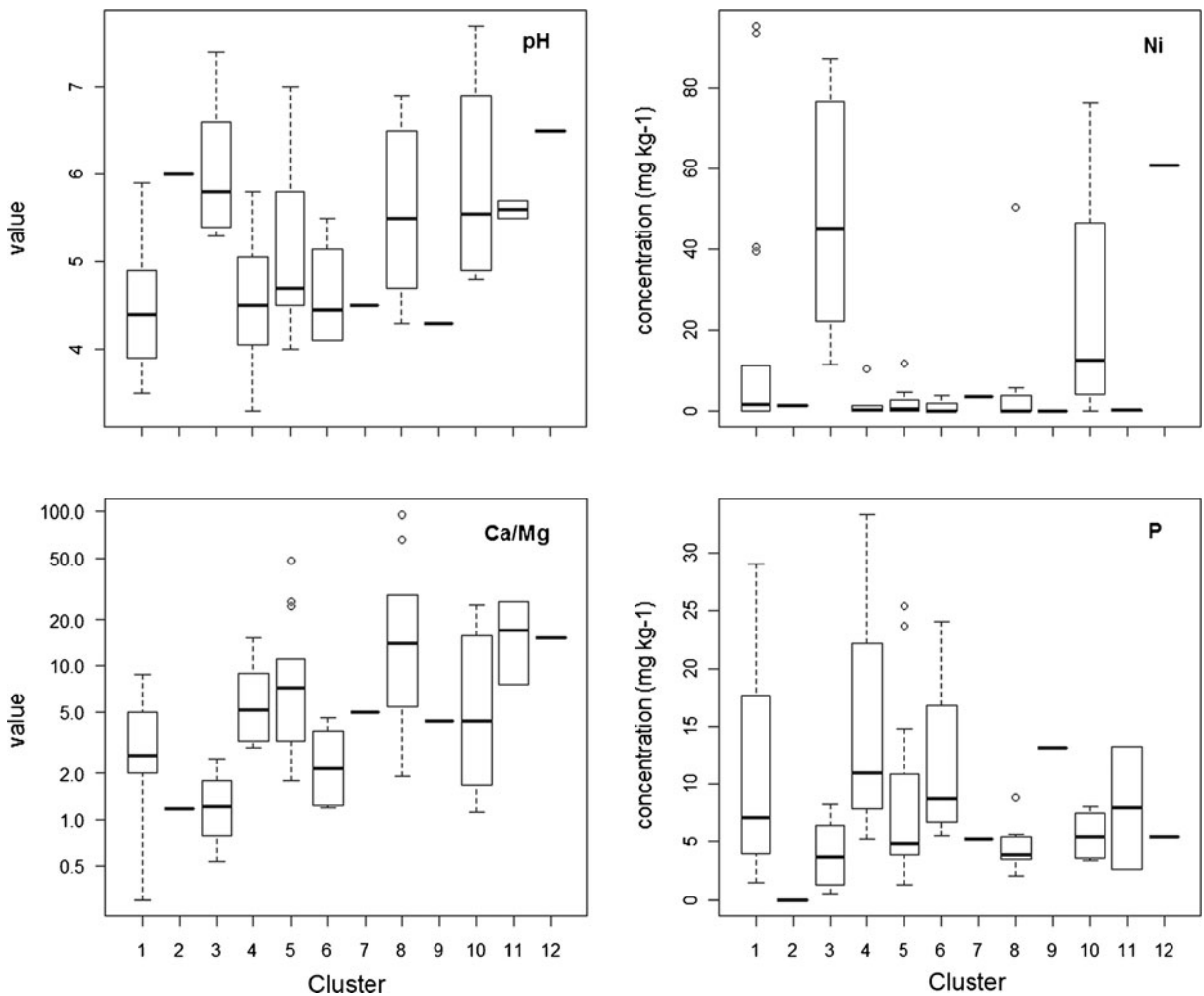


Fig. 8 Average values, variances and extreme values of pH, Ni, molar Ca:Mg and P, associated with alpine plant associations (represented by the cluster numbers)

cycling (compared to well developed forest soils) rather than to cation leaching. Cation (Mg and Ni) leaching appears to be the most important soil process at Mont Avic, determining the distribution/absence of serpentine endemics. Another reason explaining the smaller frequency of serpentine species in closed forests can be the high competition for light, space and soil resources which normally characterizes forest habitats. However, open forests on serpentine often host large numbers of some serpentine species, despite the high development degree of the soils and the dense herb and shrub cover.

At Mont Avic, highest soil Ni concentrations were found where soil development was inhibited by steep slope (rock crevices, talus), or where occasional

flooding along river beds deposits fresh serpentine alluvium, or along dry depressions, where subsurface waters enrich the soil in water-soluble cations (Lee et al. 2001) or in organo-metallic compounds (Sommer et al. 2000). In these habitats serpentine species grew most abundantly (Cluster 5). Similar poorly developed sites on mafic rocks host an analogous vegetation devoid of serpentine endemics.

P and N were sometimes lower where serpentine species grew in montane or disturbed soils than in similar gabbro sites, from which they were excluded. However, in stable habitats, nutrients were more abundant in soils supporting serpentine endemic rich communities than in the serpentine or gabbro soils not supporting serpentine species. Thus, their importance

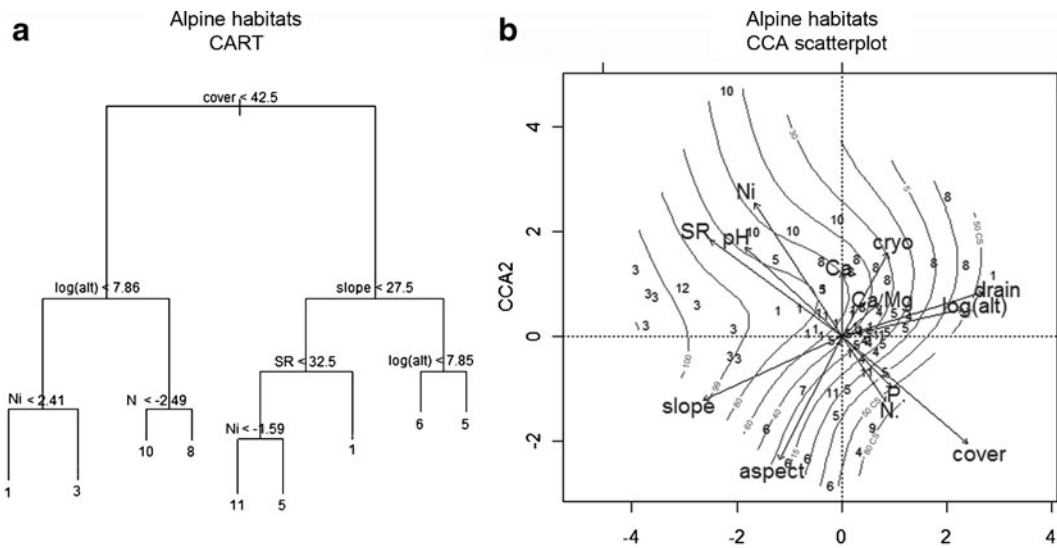


Fig. 9 CART and CCA scatterplot of alpine habitats, with the first two axes showing plant community distribution along species-environmental gradients. The first axis is mainly a

in differentiating vegetation on serpentine in montane climates seems negligible, when compared to their ability to differentiate vegetation on serpentine in mediterranean (Chiarucci et al. 2003) and boreal climates (Proctor 1992).

Low N and P, Mg toxicity and low Ca:Mg molar ratio are often considered key components of the “serpentine syndrome”; however, their effects upon

drainage/humidity gradient, the second can be interpreted as a stability/altitude gradient. Substrate is indicated by the curves, as defined in Fig. 4. Abbreviations and units are indicated in Fig. 4

plant communities dominated by serpentine endemics appear to be negligible in the Mont Avic area. Distinct serpentine plant communities were only found where exchangeable soil Ni concentration was $>2 \text{ mg kg}^{-1}$ in surface horizons, both in primitive soils and in well developed, stable forest ones. Increased soil Ni concentration was positively correlated with the presence and abundance of serpentine endemic and indicator plant species at Mont Avic.

Statistical methods were not able to detect herb or shrub species excluded from high Ni serpentine soils. However, elevated soil Ni concentrations, along with other adverse chemical and physical conditions of the habitat, may act to exclude less adapted species, thereby favoring the dominance of highly-adapted, serpentine endemic plant species. Moreover, a positive effect of high soil Ni on the metabolism of some serpentine endemic Brassicaceae has been demonstrated by Gabbriellini et al. (1989) and by Bani et al. (2011).

The lack of a significant change in drainage and soil moisture among serpentine species rich habitats and similar environments devoid of serpentine endemics indicates that subalpine serpentine vegetation is not strongly controlled by drought on the western Alps. This appears to be in contrast to the factors influencing serpentine vegetation in humid boreal (Carter et al. 1987) or Mediterranean habitats (e.g., Chiarucci et al. 2003).

Table 5 GLM coefficients between *Carex fimbriata*, *Noccaea alpestris* subsp. *sylvium*, and *Cardamine plumieri*, with respect to soil and environmental properties. Underlined values are significant at p -value <0.05

	<i>Carex fimbriata</i>	<i>Noccaea alpestris</i> subsp. <i>sylvium</i>	<i>Cardamine plumieri</i>
Intercept	65.41	96.45	52.39
pH	-0.44	0.29	<u>4.31</u>
Log(Alt).	-7.99	-12.32	4.25
Log(Ni)	<u>0.12</u>	<u>2.09</u>	<u>0.74</u>
Log(Ca)	<u>0.03</u>	-0.48	-0.28
Plant cover	0.01	-0.01	-0.04
Ca:Mg	0.00	-0.10	1.14
Drain.	-0.70	0.99	0.01
Aspect	0.07	-1.68	0.11
Slope	-0.02	0.09	-0.03
Log(P)	-1.04	-0.61	-0.96
Log(N)	0.69	3.66	1.01

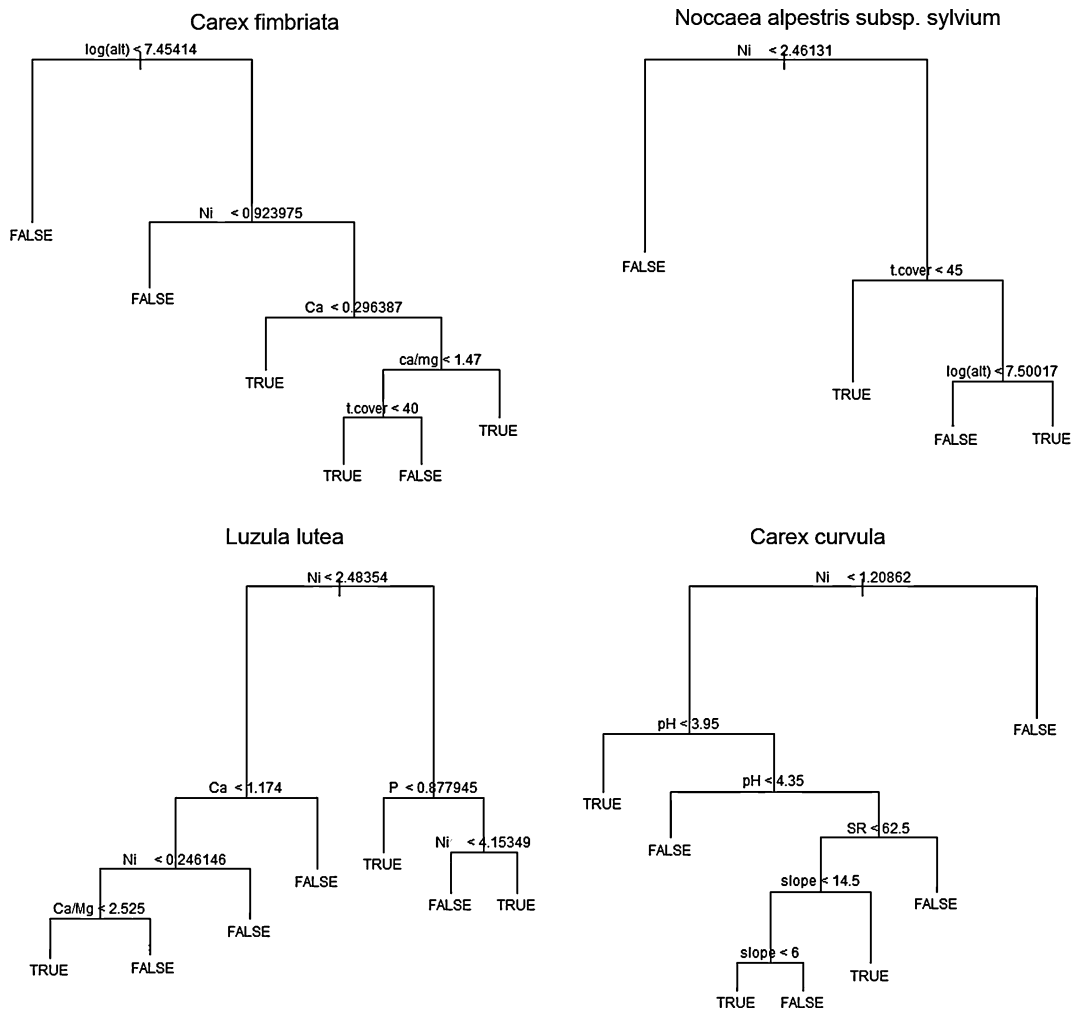


Fig. 10 Tree classification showing the primary edaphic and environmental factors involved in the distribution of *Carex fimbriata* and *Noccaea alpestris subsp. sylvium* in forest habitats, *Luzula lutea*, and *Carex curvula* in alpine habitat

Norway spruce (*Picea excelsa*) is absent from serpentine on Mont Avic, even though it is the dominating subalpine tree in nearby valleys on non-serpentine substrates. The lack of some conifer species on serpentine in Japan and Czech Republic, which are abundant on nonserpentine substrates, was attributed to Ni and/or Mg toxicity (Kayama et al. 2005; Kràm et al. 1997). Non adapted tree species are also excluded from acidified serpentine soils in New Zealand due to high Ni availability (Robinson et al. 1996).

Alpine habitats

Alpine soils of Mont Avic Natural Park are generally classified as Entisols or Inceptisols. Soil profiles are

poorly developed due to poor vegetative cover, cryoturbation and high erosion rates. Cryoturbation, erosion and deposition frequently introduce unweathered substrate to the soil surface, which readily weathers releasing cations to the surface soil materials. Vegetation type in the alpine zone is highly dependent upon substrate and surface stability (steepness, erosion-deposition and cryoturbation processes). Serpentine vegetation is usually markedly different from nearby nonserpentine communities, both in physiognomy (stunted appearance) and species composition.

Alpine serpentine soils on stable surfaces accumulate organic matter, resulting in lower pH and elevated Ca:Mg molar ratio from Mg leaching. Despite the extremely low total Ca:Mg ratio, the available Ca:Mg ratio is

often greater than 1, similar to underdeveloped, cryoturbated and eroded soils. Similar values have been observed in other young, skeletal and disturbed serpentine soils on the Western Alps (Vergnano Gambi et al. 1987). In Mont Avic Natural Park, soil pH is often lower than in similar high altitude or arctic soils (Proctor 1992; Roberts 1992; Kataeva et al. 2004), possibly due to soil waterlogging during snowmelt, which can cause severe base leaching (Sirois and Grandtner 1992), or because of mineral differences which modify the weathering processes.

Soil Ni concentration at Mont Avic is up to 100 times higher than that of high altitude serpentine soils in Spain (Sanchez-Marañon et al. 1999). Increased soil Ni at Mont Avic as compared to high altitude serpentine in Spain may be the result of increased mineral weathering from greater soil moisture. Similar Ni availability has been found by Rune and Westerbergh (1991) in Sweden, and on the Scottish Highlands by Proctor (1992).

High soil Ni concentration at Mont Avic was highly correlated with the presence of serpentine endemic and serpentine indicator species. The serpentine endemics *Noccaea alpestris* subsp. *sylvium*, *Cardamine plumieri*, and *Biscutella laevigata* all grew where Ni was above 10–20 mg kg⁻¹. *Carex fimbriata*, an endemic species dominating alpine prairies on serpentine soils, was also positively correlated with exchangeable Ni. Some common alpine plant species such as *Carex curvula* and *Luzula spicata* were intolerant of serpentine at these elevated soil Ni concentrations. The stronger ecological role of high soil Ni concentrations in alpine as compared to Mediterranean habitats was previously documented (Vergnano Gambi and Gabbrielli 1981; Vergnano Gambi et al. 1987; Vergnano Gambi 1992) and soil Ni likely plays an important role in determining the distribution of serpentine endemic plant species at Mont Avic Natural Park.

The trend in ecological influence of metals in other alpine or subarctic habitats is unclear. In the UK, soil Ni was determined to not have a significant effect on vegetation, despite extremely high concentrations (Carter et al. 1987; Proctor 1992). Likewise Ni does not appear to have a detrimental effect on vegetation in Newfoundland (Dearden 1979).

The “serpentine syndrome” is normally visible on coarse, eroded and cryoturbated soils in humid boreal serpentine habitats (e.g., Proctor 1992), but in the

Western Alps some serpentine endemic species (*Carex fimbriata*, *Noccaea alpestris* subsp. *sylvium*, *Noccaea caerulea*) also grew in dense plant communities on well-developed and extremely acidic soils. They are usually regarded as indifferent to soil pH (Richard 1985; Verger et al. 1993), but it is here demonstrated that soil pH and base status are weakly involved in their distribution. In high altitude, humid climates drought does not appear to be a key factor for plant distribution on serpentine (Brady et al. 2005), nor for enhanced metal toxicity (Chiarucci et al. 2001). Disturbances inhibiting soil development are able to maintain high metal availability. Therefore, disturbed sites generally support more endemic, heavy metal adapted, Ni-hyperaccumulator species.

The stunted appearance of serpentine vegetation in Scotland was mainly attributed to P scarcity. In the study area, available P was unable to discriminate between similarly developed communities on different substrata, but between stable and unstable (P-poor) sites. This good correlation between available P and soil stability—development degree is in agreement with the P biocycling and bioaccumulation on serpentinite (Bonifacio and Barberis 1999).

Conclusions

In the Alps, pedogenic processes change dramatically from forest to alpine habitats, influencing element availability. Forest acidic soil vegetation usually changes only slightly on the different substrates due to extreme acidification, podzolization, cation leaching and bioaccumulation of nutrients, while alpine vegetation strikingly depends on substrate type, and manifestation of the “serpentine syndrome” becomes readily apparent. However, similar edaphic and environmental factors can be included or excluded from the “serpentine factor”, above and below the treeline.

The physical properties (coarse texture, excessive drainage, shallowness and dark colour) do not specifically characterize serpentine habitats. In fact, soil texture is finer on serpentine than on other rocks, because of its higher weatherability. Drainage and soil thickness are related with topography, erosion, aspect and altitude, and not with substrate type. Soil colour depends only on TOC content in surface horizons. However, the physical factors can be important in differentiating vegetation on

similar materials (for example, influencing the distribution of closed forest communities).

Some chemical properties including the macronutrients N, P, K, and Ca can be excluded as factors influencing serpentine vegetation as well. These soil nutrients were observed to be more abundant under serpentine vegetation than elsewhere. The high variance of the Ca:Mg ratio in soils supporting serpentine endemic species and communities is evidence of its low impact on the local plant ecology; only few species are positively correlated with low Ca:Mg ratio.

Higher pH values were often found under serpentine vegetation (likely in relation with skeletal and disturbed soils), but only few species were correlated with this factor. Available Ni is correlated with serpentine species and plant communities. It is likely the most important ecological factor involved in community differentiation among the different substrates, which consists of the presence of a few metal-adapted species on serpentinite in forest habitats. Above the treeline, Ni is related with the lower plant cover and the different species composition. The effect of heavy metals is particularly intense where soil development is inhibited by erosion, deposition and cryoturbation, which may maintain elevated concentrations in surface horizons.

Deep snow cover in winter and spring and humid summers which characterize the European Alps facilitate faster mineral weathering, element release and leaching, compared to Mediterranean habitats. Ni availability is increased by strong acidification, while the elevated rate of Mg leaching is counterbalanced by Ca bioaccumulation. Other possible causes of the different elemental balance in other humid, boreal or oceanic habitats may be related to mineralogical differences in the ultramafic parent material.

Acknowledgements This study was performed thanks to the funds of the Mont Avic Natural Park and the logistic help provided by its Director, Dr. Massimo Bocca. We also thank Dr. Fabio Moia for many laboratory analyses. We also thank Ryan O'Dell and another anonymous reviewer for the precious comments to previous version of this study.

References

Alexander EB (1988) Morphology, fertility and classification of productive soils on serpentinitized peridotites in California (U.S.A.). *Geoderma* 41:337–351

- Alexander EB, Coleman RG, Keeler-Wolf T, Harrison SP (2007) *Serpentine geoecology of western North America*. Oxford University Press, New York, 512 pp
- Bani A, Echevarria G, Skura E, Morel JL, Sulce S (2011) The role of edaphic factors on the growth and Ni accumulation in *Alyssum murale*. In: 7th International conference on serpentine ecology. Abstract Book
- Bonifacio E, Barberis E (1999) Phosphorus dynamics during pedogenesis on serpentinite. *Soil Sci* 164 (12):960–968
- Bovio M, Broglio M (2007) *La flora del Parco Naturale Mont Avic*. Libreria Saint Etienne, Aosta
- Brady KU, Kruckeberg AR, JrHD B (2005) Evolutionary ecology of plant adaptation to serpentine soils. *Ann Rev Ecol Evol Syst* 36:243–266
- Brooks RR (1987) *Serpentine and its vegetation. A multidisciplinary approach*. Dioscorides Press, Portland
- Buffa G, Miserere L, Montacchini F (1998) Aspetti della vegetazione d'altitudine del Parco Naturale del Mont Avic. *Rev Valdotaie Hist Nat* 52:35–48
- Burt R, Fillmore M, Wilson MA, Gross ER, Langridge RW, Lammers DA (2001) Soil properties of selected pedons on ultramafic rocks in Klamath Mountains, Oregon. *Comm Soil Sci Plant An* 32(13):2145–2175
- Carter SP, Proctor J, Slingsby DR (1987) Soil and vegetation of the Keen of Hamar serpentine, Shetland. *J Ecol* 75 (1):21–42
- Chardot V, Echevarria G, Gury M, Massoura S, Morel JL (2007) Nickel bioavailability in an ultramafic toposequence in the Vosges Mountains (France). *Plant Soil* 293:7–21
- Chiarucci A, Robinson BH, Bovini I, Petit D, Brooks RR, De Dominicis V (1998) Vegetation of Tuscan ultramafic soils in relation to edaphic and physical factors. *Folia Geobot* 33:113–131
- Chiarucci A, Rocchini D, Leonzio C, De Dominicis V (2001) A test of vegetation-environment relationships in serpentine soils of Tuscany, Italy. *Ecol Res* 16:627–639
- Chiarucci A, Bovini I, Fattorini L (2003) Community dynamics of serpentine vegetation in relation to nutrient addition and climatic variability. *J Med Ecol* 4:19–27
- D'Amico ME (2006a) Suoli ed ambienti del Parco Naturale del Mont Avic (Ao) – 1: il piano subalpino superiore e il piano alpino. *Rev Valdôtaine Hist Nat* 60:1–28
- D'Amico ME (2006b) Suoli ed ambienti del Parco Naturale del Mont Avic (Ao) – 2: le foreste. *Rev Valdôtaine Hist Nat* 60:29–52
- D'Amico ME, Julitta F, Previtali F, Cantelli D (2008) Podzolization over ophiolitic materials in the western Alps (Natural Park of Mont Avic, Aosta Valley, Italy). *Geoderma* 146:129–136
- D'Amico ME, Calabrese F, Rossetti A, Previtali F (2009) Heavy metals and biological properties of subalpine soils on Ophiolites in the Italian Western Alps. *Northeast Nat* 16:193–214
- De'Ath G, Fabricious KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81(11):3178–3192
- Dearden P (1979) Some factors influencing the composition and location of plant communities on a serpentine bedrock in Western Newfoundland. *J Biogeogr* 6(1):93–104

- Dufrène M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Mon* 67:345–366
- Gabbriellini R, Grossi L, Vergnano O (1989) The effects of nickel, calcium and magnesium on the acid phosphatase activity of two *Alyssum* species. *New Phytol* 111:631–636
- Guisan A, Theurillat JP, Kienast F (1998) Predicting the potential distribution of plant species in an alpine environment. *J Veg Sci* 9(1):65–74
- Guisan A, Weiss SB, Weiss AD (1999) GLM versus CCA spatial modelling of plant species distribution. *Plant Ecol* 143:107–122
- Hennig C (2007) Cluster-wise assessment of cluster stability. *Comp Stat Data Anal* 53:258–271
- Hjort J, Luoto M (2009) Interaction of geomorphic and ecologic features across altitudinal zones in a subarctic landscape. *Geomorph* 112:324–333
- Kataeva MN, Alexeeva-Popova NV, Drodzova IV, Beljaeva AI (2004) Chemical composition of soils and plant species in the Polar Urals as influenced by rock type. *Geoderma* 122:257–268
- Kayama M, Quoreishi AM, Uemura S, Koike T (2005) Differences in growth characteristics and dynamics of elements absorbed in seedlings of three spruce species raised on serpentine soil in Northern Japan. *Ann Bot* 95:661–672
- Krám P, Hruška J, Wenner B, Driscoll CT, Johnson CE (1997) The biogeochemistry of basic cations in two forest catchments with contrasting lithology in the Czech Republic. *Biogeochemistry* 37:173–202
- Krückeberg AR (1984) California serpentines: Flora, vegetation, geology, soils, and management problems. University of California Press, Berkeley, 180 pp
- Lazarus BE, Richards JH, Claassen VP, O'Dell RE, Ferrel MA (2011) Species specific plant-soil interactions influence plant distribution on serpentine soils. *Plant Soil*. doi:10.1007/s11104-010-0698-2
- Lee WG (1992) The serpentinized areas of New Zealand, their structure and ecology. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 375–417
- Lee WG, Hewitt AE (1982) Soil changes associated with development of vegetation on an ultramafic scree, north-west Otago, New Zealand. *J Royal Soc New Zealand* 12:229–242
- Lee BD, Graham RC, Laurent TE, Amrhein C, Creasy RM (2001) Spatial distribution of soil chemical condition in a serpentinic wetland and surrounding landscape. *Soil Sci Soc Am J* 65:1183–1196
- Malpas J (1992) Serpentine and the geology of serpentinized rocks. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 31–73
- Mercalli L (2003) *Atlante climatico della Val d'Aosta*. SMI eds
- MPAF (Ministero delle Politiche Agricole e Forestali) (2000) *Metodi di Analisi Chimica dei Suoli*. In: Violante P, Sequi P (eds) *Collana di Metodi Analitici per l'Agricoltura*. Franco Angeli (Ed.), Milano, pp 1–474
- Nagy L, Proctor J (1997) Plant growth and reproduction on a toxic alpine ultramafic soil: adaptation to nutrient limitation. *New Phytol* 137:267–274
- Nakata M, Kojima S (1987) Effects of serpentine substrate on vegetation and soil development with special reference to *Picea glehnii* forests in Teshio District, Hokkaido, Japan. *For Ecol Manag* 20:265–290
- Occhipinti S (1997) *Prime note sulla geologia e geomorfologia della valle del torrente Chalamy*. Biblioteca del Parco Naturale del Mont Avic, Champdepraz
- Oksanen J (2007) Multivariate analysis of ecological communities. In R: vegan tutorial. January 12, 2007. <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>. Accessed 04 April 2010
- Pignatti S (1992) *Flora d'Italia*, vol 1–3. Edagricole, Bologna
- Proctor J (1992) Chemical and ecological studies on the vegetation of ultramafic sites in Britain. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 135–167
- Proctor J, Nagy L (1991) Ultramafic rocks and their vegetation: an overview. In: *The Vegetation of Ultramafic (Serpentine) soils*. Proceedings of the First International Conference on Serpentine Ecology. University of California, Davis, 19–22 June 1991
- Richard JL (1985) Observations sur la sociologie et l'écologie de *Carex fimbriata* Schkuhr dans les Alpes. *Bot Helv* 95–2:157–164
- Roberts BA (1992) Ecology of serpentinized areas, Newfoundland, Canada. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 76–113
- Robinson BH, Brooks RR, Kirkman JH, Gregg PEH, Gremigni P (1996) Plant-available elements in soils and their influence on the vegetation over ultramafic ("serpentine") rocks in New Zealand. *J Royal Soc New Zealand* 26 (4):457–468
- Rodenkirchen H, Roberts BA (1993) Soils and plant nutrition on a serpentinized ridge in South Germany. I. Soils. *Pflanzenernähr Bodenkd* 156:407–410
- Rune O, Westerbergh A (1991) Phytogeographic aspects of the serpentine flora of Scandinavia. In: *The Vegetation of Ultramafic (Serpentine) soils*. Proceedings of the First International Conference on Serpentine Ecology. University of California, Davis, 19–22 June 1991
- Sanchez-Marañón M, Sanchez-Marañón M, Gámiz E, Delgado G, Delgado R (1999) Mafic-ultramafic soils affected by silicic colluvium in the Sierra Nevada Mountains (southern Spain). *Can J Soil Sci* 79:431–442
- Sirois L, Grandtner MM (1992) A phyto-ecological investigation of the Mount Albert serpentine plateau. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 115–133
- Sneath PHA, Sokal RR (1973) *Numerical Taxonomy*. Freeman, San Francisco
- Sommer M, Halm D, Weller U, Zareai M, Stahr K (2000) Lateral podzolization in a granite landscape. *Soil Sci Soc Am J* 64:1434–1442
- Ter Braak CJF (1987) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179

- Tsiripidis I, Papaioannou A, Sapounidis V, Bergmeier E (2010) Approaching the serpentine factor at a local scale – a study in an ultramafic area in northern Greece. *Plant Soil* 329:35–50
- Vayssières MP, Plant RE, Alen-Diaz BH (2000) Classification trees: an alternative non-parametric approach for predicting species distribution. *J Veg Sci* 11:679–694
- Verger JP, Cadel G, Rouiller J, Souchier B (1993) Végétations forestières et alpines du haut Val d'Aoste sur roches ophiolitiques et gneiss. *Rev Ecol Alp* 2:43–72
- Vergnano Gambi O (1992) The distribution and ecology of the vegetation of ultramafic soils in Italy. In: Roberts BA, Proctor J (eds) *The ecology of areas with serpentinized rocks, a world view*. Kluwer, Dordrecht, pp 217–247
- Vergnano Gambi O, Gabbrielli R (1981) La composizione minerale della vegetazione degli affioramenti ofiolitici dell'alta Valle d'Ayas. *Rev Valdotaine d'Hist Nat* 35:51–61
- Vergnano Gambi O, Pedani R, Gabbrielli R (1987) Ulteriori dati sulla composizione minerale della vegetazione degli affioramenti ofiolitici dell'alta Valle d'Ayas. *Rev Valdôtaine Hist nat* 41:99–110