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VEGETATION OF TUSCAN ULTRAMAFIC SOILS IN RELATION TO EDAPHIC AND PHYSICAL FACTORS

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Abstract: Vegetation and soil sampling were carried out in 80 plots located in five different ultramafic (serpentine) sites of Tuscany, central Italy. The physical and chemical features of each plot were determined and the species composition and cover recorded. The exchangeable fraction of soil metals was analysed because it gives a measure of their concentrations available to plants. The plots were classified by cluster analysis and ANOVA was used to compare the environmental variables of the groups of plots. Canonical correspondence analysis was used to detect the principal factors for gradients of species composition within the plant communities. A higher content of exchangeable metals was found under the more evolved and structured plant communities, suggesting that serpentine vegetation of Tuscany is not strongly limited by soil metals, such as chromium, cobalt, nickel and magnesium, typically associated with ultramafic soils. The low nutrient content of the soils and drought stress mainly due to topographical features, appear to have a more significant role in determining the typical scattered vegetation of the Tuscan ultramafics.

INTRODUCTION

Ultramafic (serpentine) soils host a distinctive flora and vegetation. The stunted plants and patches of bare soil have been attributed to the chemical and physical features of ultramafic soils. These typically contain high concentrations of heavy metals such as nickel, chromium, cobalt, and manganese, low concentrations of nutrients and a large excess of magnesium over calcium; moreover these soils are shallow, well drained and prone to erosion (BROOKS 1987, BAKER et al. 1992, ROBERTS & PROCTOR 1992). However, large variations exist in the soil features of the different sites. PROCTOR & NAGY (1992) suggested that the factors controlling ultramafic flora might differ from site to site.

There are several ultramafic outcrops in Tuscany, Italy, and their flora and vegetation have been widely studied by botanists and ecologists (see VERGNANO GAMBI 1992). The most typical plant community of Tuscan ultramafic soils is a garigue, described as the *Armerio-Alyssetum bertolonii* association, which is characterised by low ground cover and several endemic species (ARRIGONI et al. 1983, CHIARUCCI et al. 1995). This vegetation type occurs, differentiated into two sub-associations, over all ultramafic outcrops of Tuscany (CHIARUCCI et al. 1995). Tall scrub or woodland plant communities have also been reported

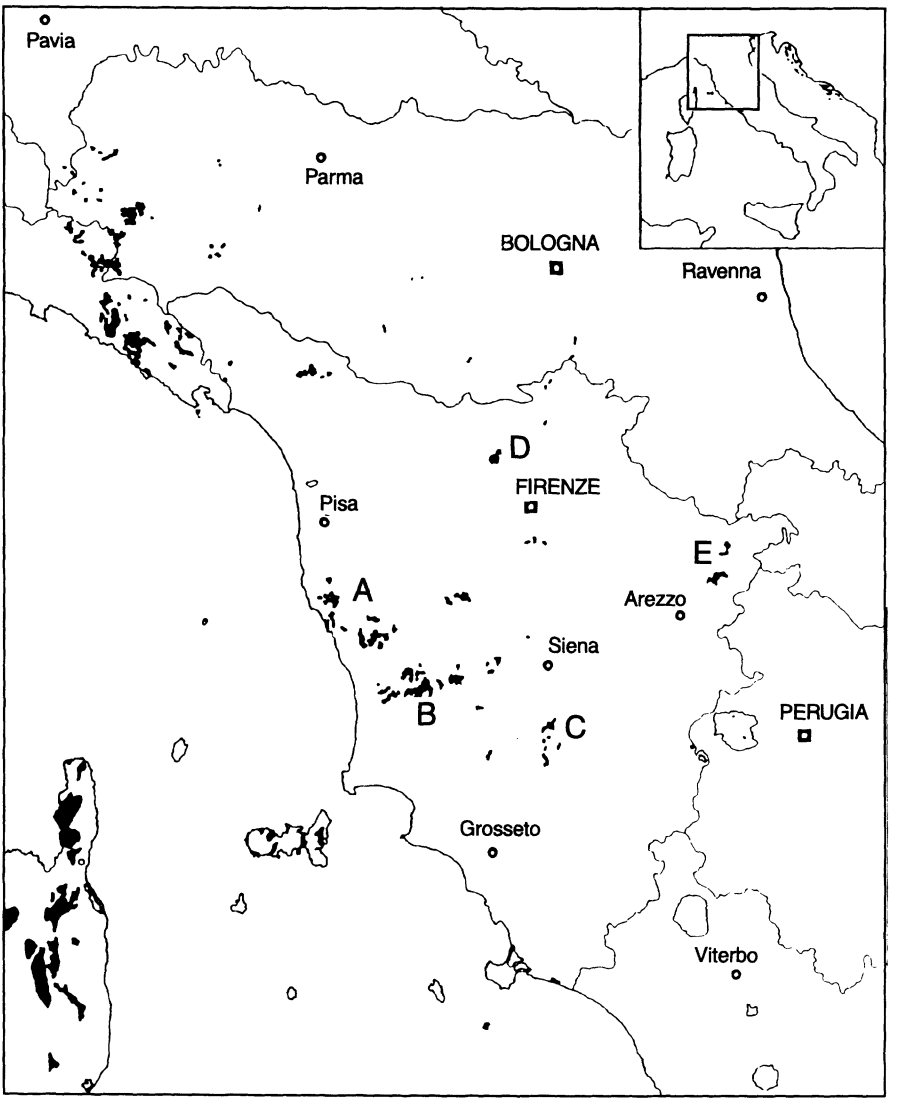

Fig. 1. Distribution of the ultramafic outcrops (black) of Corsica and central-northern Italy with indications of study areas. A – Livorno hills; B – Cecina Valley and surrounding areas; C – Murlo area; D – Mt. Ferrato; E – Upper Tiber Valley.

and are widespread in some sites (MESSERI 1936, PICHI-SERMOLLI 1948, MARCHIORI & TORNADORE MARCHIORI 1977, CHIARUCCI 1994). Some authors (e.g. SASSE 1979a, b, ARRIGONI et al. 1983, VERGNANO GAMBI 1992) have claimed that soil metal content negatively affects plant communities. Others have hypothesised that soil metal content does not affect vegetation when nutrients are available (CHIARUCCI & DE DOMINICIS 1995, CHIARUCCI 1996). In spite of the several papers published on the flora, vegetation and metal uptake by plants, only a few studies have thoroughly investigated the relations between environmental features and vegetation composition and structure (CHIARUCCI et al. 1998).

The aim of the present paper was to describe the species diversity and composition of the plant communities growing over the most important ultramafic outcrops of Tuscany in relation to the main environmental features, with particular attention to the exchangeable soil metal content.

MATERIALS AND METHODS

Study areas and vegetation sampling

Five of the largest ultramafic areas in Tuscany were selected as study sites (Fig. 1): the hills near Livorno, the Cecina Valley and surrounding areas, the Murlo area, Mt. Ferrato and the upper Tiber Valley. Some 15–20 100 m^2 plots, representing all the main vegetation types, were sampled in each area in June 1996. The cover of all vascular species was estimated in each vegetation layer. The following features were recorded: altitude (m), aspect, slope (°), cover (%) and height (m) of the tree layer, cover (%) and height (m) of the shrub layer, field layer cover (%), rockiness (%) and stoniness (%). The index of normalised insolation (BARTORELLI 1967) was used as a heat index, summarising the interactive effects of latitude, slope and aspect on determining the amount of solar radiation that each plot receives during the year. This index based on the hours per year of overhead sunlight, is a measure of the radiation the site actually receives in one year, given its aspect, slope, and latitude. Plant nomenclature follows PIGNATTI (1982) for most species, CHIARUCCI et al. (1995) for serpentinophytes and MORALDO (1986) for the genus *Stipa*.

Soil sampling and analysis

A composite soil sample was taken in each plot at about 10 cm of depth. Soil samples were air dried and passed through a 2 mm sieve. A 1 : 2.5 soil-water suspension was used to measure pH; organic matter was estimated by measuring loss on ignition (LOI) after heating soil subsamples to 450 °C overnight. Exchangeable cations were determined by adding 30 ml of 1M CH_3COONH_4 to 3 g of soil in a polythene container and shaking the containers overnight. The solutions were filtered and analysed by flame atomic absorption spectroscopy. The exchangeable fraction, as opposed to the total metal concentration, was determined because it gives a measure of the concentration available to plants.

Data analysis

Because of the climatic and phytogeographic differences between the Mediterranean (the first three sites) and the inland (Mt. Ferrato and Upper Tiber Valley) sites (ARRIGONI 1980, CHIARUCCI et al. 1995), the data-set was divided in two parts. The total cover of each species (not subdivided into three layers) was used for analysis. The plots were classified by a homogeneity-optimising procedure. Cluster analysis, using MNSSQ as agglomeration criterion, was applied to a distance matrix constructed on the basis of the similarity ratio (PODANI 1994). Data processing was performed with the SYN-TAX 5.0 program package (PODANI 1993). For the groups of plots identified by cluster analysis, soil and environmental data were compared by one-way ANOVA; statistical differences between groups were tested by the Duncan multiple-range test at $P < 0.05$. To satisfy the normality assumptions of statistical analysis, the variables LOI, rockiness, stoniness, and exchangeable cations were logarithmically transformed.

Table 1. Structural features and species diversity data (mean ± s.e.) of plots belonging to the six groups identified by cluster analysis in the Mediterranean data-set.

Cluster/Group	A/1	A/2	B/3	B/4	C/5	C/6
n	9	8	7	7	7	12
Tree layer cover (%)	–	–	–	–	11.4 ± 11.4	55.0 ± 12.0
Shrub layer cover (%)	3.8 ± 1.5	12.8 ± 2.2	70.7 ± 5.2	83.6 ± 2.6	73.4 ± 12.2	51.6 ± 9.8
Field layer cover (%)	13.8 ± 2.1	14.0 ± 2.4	25.0 ± 4.4	17.7 ± 6.3	15.7 ± 9.6	2.1 ± 0.5
Total species richness	32.5 ± 1.2	29.6 ± 2.2	26.4 ± 2.3	26.4 ± 1.7	26.6 ± 2.0	15.9 ± 1.1
Tree layer richness	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.9	3.3 ± 0.8
Shrub layer richness	3.2 ± 0.6	4.7 ± 0.6	9.6 ± 1.0	13.0 ± 0.8	11.1 ± 0.9	8.8 ± 0.8
Field layer richness	29.7 ± 1.5	25.0 ± 2.1	16.9 ± 2.3	13.6 ± 1.4	15.0 ± 2.6	5.6 ± 0.7

To detect gradients in species composition and in species-environment relations, canonical correspondence analysis (CCA) (TER BRAAK 1986) was performed by the program package CANOCO 3.11 (TER BRAAK 1988). Cover data were log-transformed and rare species were downweighted. A Monte Carlo permutation test was applied to test the significance of the eigenvalue corresponding to the first CCA canonical axis (TER BRAAK 1988).

RESULTS

191 vascular plant species were found in the eighty 100 m^2 plots, of which 142 species were in the Mediterranean data set and 127 in the inland data set. The average species richness per plot was 25.1. The results are reported separately for the two data sets.

Mediterranean data set

Species composition and richness

The main cluster divisions (not shown) were linked to floristic characters reflecting vegetation structure and diversity (Tab. 1). All groups contained plots from the three sites. Species frequency and cover in the six groups are reported in Tab. 2.

Cluster A contained the vegetation types with low ground cover: the plots of Group 1 were sampled in typical garigues of the ultramafic sites of Mediterranean Tuscany, belonging to the *Armerio-Alyssetum bertolonii euphorbietosum spinosae* (CHIARUCCI et al. 1995), with a very low shrub cover. This vegetation type is characterised by several endemic plants, the most abundant of which is the nickel hyperaccumulator *Alyssum bertolonii* (ARRIGONI et al. 1983, CHIARUCCI et al. 1995). Group 2 included similar plant communities, but with a higher shrub cover mainly due to *Juniperus oxycedrus* subsp. *oxycedrus* and *Phillyrea latifolia*.

Cluster B contained the plots sampled in xerophilous shrublands. The plots of Group 3 were in open juniper scrub communities, dominated by *Juniperus oxycedrus* subsp. *oxycedrus*, in which *Cistus salvifolius*, *Quercus ilex*, *Phillyrea latifolia* and *Erica arborea* were also abundant. The field layer was dense and rich, being characterised both by garigue species (*Centaurea aplolepa* subsp. *carueliana*, *Galium corrudifolium*, *Stachys recta* subsp. *serpentini*, *Thymus striatus* var. *ophioliticus*, *Trinia glauca*, *Linum trigynum*, *Anthericum liliago*) and xerophilous perennial graminoids (*Bromus erectus*, *Festuca inops*, *F. robustifolia*, *Carex humilis*). The plots of Group 4 were sampled in closed juniper scrub communities, in which the broad-leaved evergreen species (*Quercus ilex*, *Arbutus unedo*, *Phillyrea latifolia*) were more abundant than *J. oxycedrus* subsp. *oxycedrus*. Cover and richness of the field layer were

Table 2. Species frequency (F) according to a five point scale (I, < 20%; II, 20–40%; III, 40–60%; IV, 60–80%; V, 80–100%) and mean cover (C) in the six groups of plots identified by cluster analysis in the Mediterranean data-set. +, mean cover less than 0.01. Species endemic to serpentine or locally exclusive to serpentine are indicated in bold.

Cluster/Group	A/1		A/2		B/3		B/4		C/5		C/6	
	F	C	F	C	F	C	F	C	F	C	F	C
Tree layer												
Erica scoparia	.	.	.	.	.	.	.	.	I	0.43	.	.
Juniperus oxycedrus	.	.	.	.	.	.	.	.	I	2.14	I	0.42
Fraxinus ornus	.	.	.	.	.	.	.	.	I	5.71	III	13.08
Arbutus unedo	.	.	.	.	.	.	.	.	I	0.71	III	8.75
Phillyrea latifolia	.	.	.	.	.	.	.	.	I	0.71	III	2.08
Quercus ilex	.	.	.	.	.	.	.	.	I	3.57	IV	30.42
Erica arborea	.	.	.	.	.	.	.	.	.	.	III	2.83
Quercus pubescens	.	.	.	.	.	.	.	.	.	.	I	1.25
Rhamnus alaternus	.	.	.	.	.	.	.	.	.	.	I	0.83
Hedera helix	.	.	.	.	.	.	.	.	.	.	I	0.08
Quercus suber	.	.	.	.	.	.	.	.	.	.	I	0.83
Smilax aspera	.	.	.	.	.	.	.	.	.	.	I	0.25
Sorbus torminalis	.	.	.	.	.	.	.	.	.	.	I	0.33
Shrub layer												
Genista januensis	II	0.02	III	0.15	V	0.36	III	0.23	III	0.17	.	.
Cistus incanus	II	0.02	II	0.31	II	1.79	II	0.74	II	1.00	.	.
Clematis flammula	.	.	I	0.03	.	.	.	.	.	.	.	.
Osyris alba	.	.	.	.	.	.	I	0.06	.	.	.	.
Cistus salvifolius	II	0.10	IV	0.91	IV	7.64	V	1.24	I	0.01	I	0.02
Juniperus oxycedrus	V	2.02	V	6.88	V	42.86	V	24.00	V	8.29	III	3.00
Erica arborea	II	0.22	II	0.33	V	5.64	V	4.21	V	14.43	III	6.33
Erica scoparia	II	0.49	II	1.50	III	4.43	IV	14.57	III	3.86	III	3.67
Myrtus communis	II	0.78	I	0.13	II	4.29	III	2.93	II	7.14	III	2.08
Phillyrea latifolia	II	0.48	IV	3.50	V	5.86	V	12.29	V	13.29	IV	5.08
Fraxinus ornus	I	0.02	I	0.03	III	1.90	V	3.76	IV	1.01	III	3.92
Quercus ilex	I	0.06	II	0.44	V	6.86	V	24.00	IV	11.44	V	26.83
Pistacia lentiscus	.	.	I	0.19	I	0.04	III	2.40	I	0.14	I	0.04
Arbutus unedo	.	.	.	.	IV	0.46	V	8.93	IV	16.00	III	3.29
Smilax aspera	.	.	.	.	II	0.73	IV	0.24	III	0.27	V	1.87
Lonicera implexa	.	.	.	.	III	0.06	IV	0.21	III	0.14	II	0.13
Asparagus acutifolius	.	.	.	.	II	0.01	I	0.01	III	0.13	III	0.11
Rhamnus alaternus	.	.	.	.	I	0.71	I	0.14	III	5.03	.	.
Viburnum tinus	.	.	.	.	II	0.04	II	0.44	I	0.07	III	1.42
Genista pilosa	.	.	.	.	II	0.04	II	0.11	.	.	I	0.03
Quercus pubescens	.	.	.	.	.	.	II	0.30.	.	.	.	.
Tamus communis	.	.	.	.	.	.	I	0.01	I	0.01	.	.
Calicotome villosa	.	.	.	.	.	.	.	.	I	0.43	.	.
Sorbus aria	.	.	.	.	.	.	I	0.04	.	.	I	0.04
Spartium junceum	.	.	.	.	.	.	I	0.03	.	.	I	0.03
Ruscus aculeatus	.	.	.	.	.	.	I	0.29	III	2.96	III	1.58
Cytisus villosus	.	.	.	.	.	.	II	0.09	I	0.04	I	0.02
Lonicera caprifolium	.	.	.	.	.	.	I	0.01	I	0.03	I	0.03
Rubus ulmifolius	.	.	.	.	.	.	.	.	II	0.13	II	0.28
Juniperus communis	.	.	.	.	.	.	.	.	II	0.57	I	0.13
Rosa sempervirens	.	.	.	.	.	.	.	.	I	0.07	I	0.04
Sorbus domestica	.	.	.	.	.	.	.	.	I	0.03	I	0.08

Cluster/Group	A/1		A/2		B/3		B/4		C/5		C/6	
	F	C	F	C	F	C	F	C	F	C	F	C
Rubia peregrina	.	.	.	.	.	.	.	.	.	.	I	0.06
Pyrus pyraster	.	.	.	.	.	.	.	.	.	.	I	0.01
Field layer												
Jasione montana	II	0.01	.	.	.	.	.	.	.	.	.	.
Linum* cf. *alpinum	II	0.03	.	.	.	.	.	.	.	.	.	.
Lathraea squamaria	II	0.01	.	.	.	.	.	.	.	.	.	.
Ceterach officinarum	II	0.01	.	.	.	.	.	.	.	.	.	.
Anthemis* cf. *montana	I	0.04	.	.	.	.	.	.	.	.	.	.
Euphorbia nicaeensis* subsp. *prostrata	I	0.28	.	.	.	.	.	.	.	.	.	.
Festuca arundinacea	I	0.01	.	.	.	.	.	.	.	.	.	.
Polygonum patulum	I	+	.	.	.	.	.	.	.	.	.	.
Psilurus incurvus	I	+	.	.	.	.	.	.	.	.	.	.
Sanguisorba minor	I	0.01	.	.	.	.	.	.	.	.	.	.
Scrophularia canina	I	0.06	.	.	.	.	.	.	.	.	.	.
Onosma echioides	V	0.62	I	0.25	.	.	.	.	.	.	.	.
Sedum album	IV	0.11	III	0.18	.	.	.	.	.	.	.	.
Anthyllis vulneraria subsp. *praepropera*	III	0.04	IV	0.16	.	.	.	.	.	.	.	.
Silene paradoxa	III	0.03	II	0.01	.	.	.	.	.	.	.	.
Armeria denticulata	III	0.06	III	0.26	.	.	.	.	.	.	.	.
Allium moschatum	II	0.01	I	0.06	.	.	.	.	.	.	.	.
Alyssum montanum	II	0.04	I	0.04	.	.	.	.	.	.	.	.
Inula viscosa	II	+	II	0.02	.	.	.	.	.	.	.	.
Reichardia picroides	II	0.01	I	0.04	.	.	.	.	.	.	.	.
Stipa etrusca	II	0.49	II	0.39	.	.	.	.	.	.	.	.
Aira elegans	I	+	I	+	.	.	.	.	.	.	.	.
Medicago minima	I	+	I	+	.	.	.	.	.	.	.	.
Arenaria serpyllifolia	I	+	.	.	I	+	.	.	.	.	.	.
Teucrium montanum	V	0.27	V	0.45	III	0.08	.	.	.	.	.	.
Herniaria glabra	V	0.04	IV	0.03	I	0.01	.	.	.	.	.	.
Iberis umbellata	V	0.03	III	0.02	II	0.01	.	.	.	.	.	.
Linum trigynum	IV	0.04	IV	0.06	IV	0.01	.	.	.	.	.	.
Cheilanthes marantae	III	0.04	II	+	I	+	.	.	.	.	.	.
Allium sphaerocephalon	III	0.01	III	0.01	I	+	.	.	.	.	.	.
Convolvulus cantabrica	III	0.03	I	+	II	0.01	.	.	.	.	.	.
Hypochoeris achyrophorus	II	0.01	II	0.01	I	+	.	.	.	.	.	.
Echium vulgare	II	0.01	I	+	II	0.01	.	.	.	.	.	.
Asperula cynanchica	V	0.02	III	0.02	.	.	I	+	.	.	.	.
Genista januensis	III	0.07	.	.	.	.	I	0.01	.	.	.	.
Anagallis arvensis	.	.	II	+	.	.	.	.	.	.	.	.
Agrostis gigantea	.	.	I	0.01	.	.	.	.	.	.	.	.
Briza media	.	.	I	+	.	.	.	.	.	.	.	.
Bromus hordeaceus	.	.	I	+	.	.	.	.	.	.	.	.
Bromus madritensis	.	.	I	+	.	.	.	.	.	.	.	.
Catapodium rigidum	.	.	I	+	.	.	.	.	.	.	.	.
Rubus ulmifolius	.	.	I	+	.	.	.	.	.	.	.	.
Sherardia arvensis	.	.	I	+	.	.	.	.	.	.	.	.
Trifolium stellatum	.	.	I	+	.	.	.	.	.	.	.	.
Brachypodium distachyum	.	.	II	0.01	.	.	.	.	.	.	.	.
Genista pilosa	.	.	I	0.01	.	.	.	.	.	.	.	.
Hieracium pilosella	.	.	I	0.01	.	.	I	+	.	.	.	.
Scabiosa columbaria	.	.	I	+	I	+	I	0.01	.	.	.	.

Cluster/Group	A/1		A/2		B/3		B/4		C/5		C/6	
	F	C	F	C	F	C	F	C	F	C	F	C
Knautia arvensis	.	.	.	.	I	+	II	0.05	.	.	.	.
Prasium majus	.	.	.	.	.	.	I	+	.	.	.	.
Cerastium ligusticum	IV	0.06	III	0.01	.	.	.	.	I	+	.	.
Dianthus sylvestris subsp. *longicaulis*	V	0.05	V	0.12	II	0.01	.	.	I	0.01	.	.
Cuscuta epithymum	III	0.02	II	+	II	+	.	.	I	+	.	.
Helichrysum italicum	III	0.84	III	0.47	III	0.09	.	.	I	0.01	.	.
Sedum rupestre	V	0.35	IV	0.23	I	0.01	.	.	II	0.04	.	.
Iris chamaeiris	II	0.03	III	0.09	I	0.01	.	.	II	0.02	.	.
Anthericum liliago	V	0.03	IV	0.03	III	0.01	III	0.01	I	+	.	.
Plantago holosteum	IV	0.80	III	0.30	II	0.03	I	0.03	I	0.57	.	.
Stachys recta* subsp. *serpentini	IV	0.11	III	0.09	V	0.12	I	0.01	I	0.01	.	.
Alyssum bertolonii	V	0.58	V	0.36	II	0.02	I	0.01	II	0.02	.	.
Centaurea aplolepa* subsp. *carueliana	V	1.38	V	1.11	IV	0.11	III	0.04	II	0.24	.	.
Thymus striatus* var. *ophioliticus	V	0.63	V	0.64	III	0.14	I	0.01	III	0.15	.	.
Festuca robustifolia	V	0.46	III	0.43	V	1.21	IV	0.74	III	0.12	.	.
Galium corrudifolium	IV	0.14	V	0.21	V	0.55	IV	0.11	III	0.05	.	.
Trinia glauca* subsp. *glauca	IV	0.15	IV	0.17	V	0.08	V	0.27	III	0.03	.	.
Koeleria splendens	III	0.19	III	0.11	I	0.01	I	0.04	III	0.09	.	.
Euphorbia spinosa	I	0.22	III	1.88	II	1.50	II	0.08	I	0.36	.	.
Linum tenuifolium	I	0.01	I	0.01	I	0.01	I	+	I	+	.	.
Centaurium pulchellum	I	0.06	I	+	II	0.06	I	+	I	0.01	.	.
Bromus erectus	IV	0.89	IV	1.61	V	14.43	V	7.07	IV	1.31	.	.
Potentilla hirta	II	0.17	V	0.19	II	0.02	II	0.03	III	0.02	.	.
Vincetoxicum hirundinaria	I	+	I	0.01	II	0.02	I	+	III	0.02	.	.
Cistus salvifolius	II	0.36	.	.	.	.	.	.	I	0.01	.	.
Biscutella pichiana* subsp. *pichiana	II	0.01	.	.	.	.	.	.	I	+	.	.
Sesleria* cf. *tenuifolia	II	1.00	.	.	.	.	.	.	I	5.71	.	.
Centaurium erythraea	I	+	.	.	.	.	.	.	I	+	.	.
Dorycnium hirsutum	II	0.06	.	.	II	0.01	IV	0.04	II	0.01	.	.
Dactylis hispanica	I	0.02	.	.	II	0.16	II	0.43	II	0.12	.	.
Danthonia alpina	II	0.12	.	.	.	.	II	1.43	I	2.14	.	.
Cytisus decumbens	I	0.01	.	.	.	.	I	+	I	0.01	.	.
Fumana procumbens	.	.	I	0.05	.	.	.	.	I	0.01	.	.
Cytinus hypocistis	.	.	I	0.01	II	0.01	I	+	I	0.01	.	.
Staehelina dubia	.	.	I	0.13	.	.	I	0.01	I	0.01	.	.
Teucrium polium	.	.	I	0.01	.	.	.	.	I	0.03	.	.
Hieracium piloselloides	.	.	.	.	I	0.01	II	0.02	I	0.01	.	.
Brachypodium sylvaticum	.	.	.	.	I	0.01	.	.	II	0.29	.	.
Centaurea nigra	.	.	.	.	I	0.01	.	.	I	+	.	.
Melittis melissophyllum	.	.	.	.			.	.	I	0.01	.	.
Polygala flavescens	.	.	.	.	I	0.03	I	0.01	I	0.01	.	.
Carex hallerana	.	.	.	.	I	0.21	I	0.43	I	0.07	.	.
Leontodon villarsii	.	.	.	.	.	.	.	.	I	+	.	.
Festuca inops	IV	1.92	V	3.91	IV	1.47	III	0.21	II	0.29	I	+
Carex humilis	II	0.44	II	0.14	III	4.47	II	0.29	III	0.36	I	0.08
Stachys officinalis	I	+	.	.	.	.	II	0.05	III	0.05	III	0.03
Asparagus acutifolius	.	.	I	+	I	0.01	.	.	II	0.03	II	0.02
Rubia peregrina	.	.	.	.	II	0.04	V	0.29	IV	0.29	V	0.88
Brachypodium rupestre	.	.	.	.	I	0.21	III	4.57	IV	3.96	III	0.36
Cyclamen repandum	.	.	.	.	I	0.01	II	0.79	III	0.15	IV	0.36
Tanacetum corymbosum	.	.	.	.	II	0.07	II	0.09	III	0.08	I	+
Filipendula vulgaris	.	.	.	.	I	0.01	I	0.04	.	.	I	+
Serratula tinctoria	.	.	.	.	I	+	.	.	I	0.01	I	+

Cluster/Group	A/1		A/2		B/3		B/4		C/5		C/6	
	F	C	F	C	F	C	F	C	F	C	F	C
Carex flacca	.	.	.	.	.	.	III	0.30	III	0.59	I	+
Viola alba subsp. *dehnhardtii*	.	.	.	.	.	.	I	+	III	0.02	II	0.01
Asplenium onopteris* f. *serpentini	.	.	.	.	.	.	I	+	.	.	I	0.06
Viburnum tinus	.	.	.	.	.	.	I	0.01	.	.	I	+
Tamus communis	.	.	.	.	.	.	.	.	I	0.01	II	0.01
Bromus ramosus	.	.	.	.	.	.	.	.	I	+	I	0.01
Peucedanum cervaria	.	.	.	.	.	.	.	.	I	+	I	+
Hedera helix	.	.	.	.	.	.	.	.	.	.	II	0.28
Melica uniflora	.	.	.	.	.	.	.	.	.	.	I	+
Ruscus aculeatus	.	.	.	.	.	.	.	.	.	.	I	0.07
Carex distachya	.	.	.	.	.	.	.	.	.	.	I	0.01
Cephalanthera rubra	.	.	.	.	.	.	.	.	.	.	I	+
Cerastium arvense	.	.	.	.	.	.	.	.	.	.	I	+
Silene nutans	.	.	.	.	.	.	.	.	.	.	I	+
Smilax aspera	.	.	.	.	.	.	.	.	.	.	I	+

Table 3. Soil and environmental data (mean ± s.e.) for the six groups identified by cluster analysis in the Mediterranean data-set. When analyses were applied to log-transformed data the standard error range is given in brackets. Different letters indicate significant differences between groups of plots. Duncan multiple-range test at $P < 0.05$.

Cluster/Group	A/1	A/2	B/3	B/4	C/5	C/6
n	9	8	7	7	7	12
Rockiness (%)	26.4 ± 7.8	18.5 ± 5.8	9.4 ± 1.9	4.3 ± 1.1	8.0 ± 4.7	1.1 ± 0.5
Stoniness (%)	51.7 ± 6.8	56.3 ± 7.8	17.0 ± 5.5	4.9 ± 2.6	6.6 ± 4.1	1.3 ± 0.4
Insolation	2139 ± 131 ab	2230 ± 121 a	2318 ± 88 a	2247 ± 143 a	1933 ± 143 ab	1833 ± 100 b
LOI	10.6 a (9.7–1.5)	10.2 a (9.5–0.9)	18.4 b (16.0–18.1)	17.0 b (15.8–21.5)	20.3 b (18.3–22.5)	21.0 b (18.7–23.6)
pH	7.4 ± 0.1 a	7.2 ± 0.1 ab	6.9 ± 0.1 c	6.9 ± 0.1 bc	6.7 ± 0.1 c	6.7 ± 0.1 c
Ca	444 a (340–579)	577 ac (439–758)	899 ab (614–1318)	1028 ab (877–1205)	1651 b (1140–2392)	1332 bc (1105–1605)
Mg	1253 ab (983–1597)	799 a (687–928)	1696 ab (1192–2414)	1506 ab (1296–1750)	2598 b (1700–3969)	1768 ab (1516–2062)
Mg/Ca	2.9 ± 0.3 a	1.9 ± 0.4 b	1.9 ± 0.1 b	1.8 ± 0.4 b	1.7 ± 0.2 b	1.6 ± 0.2 b
Cu	0.2 (0.2–0.3)	0.2 (0.2–0.3)	0.3 (0.3–0.3)	0.4 (0.3–0.4)	0.3 (0.3–0.4)	0.5 (0.3–0.6)
Fe	2.2 (2.0–2.5)	2.3 (2.1–2.6)	2.8 (2.2–3.4)	2.7 (2.5–3.0)	3.2 (2.7–3.7)	3.4 (3.0–3.7)
K	45 a (32–63)	39 a (32–46)	106 ab (69–162)	100 ab (83–122)	136 b (82–225)	171 b (127–229)
Mn	3.1 a (2.5–3.7)	2.7 a (1.9–3.7)	8.5 b (7.0–11.3)	19.8 c (17.0–23.0)	7.9 b (5.8–10.7)	10.0 bc (7.3–13.6)
Ni	3.4 a (2.8–4.0)	3.6 a (2.8–4.6)	8.2 b (7.4–9.1)	6.4 b (7.6–7.0)	8.8 b (7.9–9.8)	6.6 b (5.6–7.8)

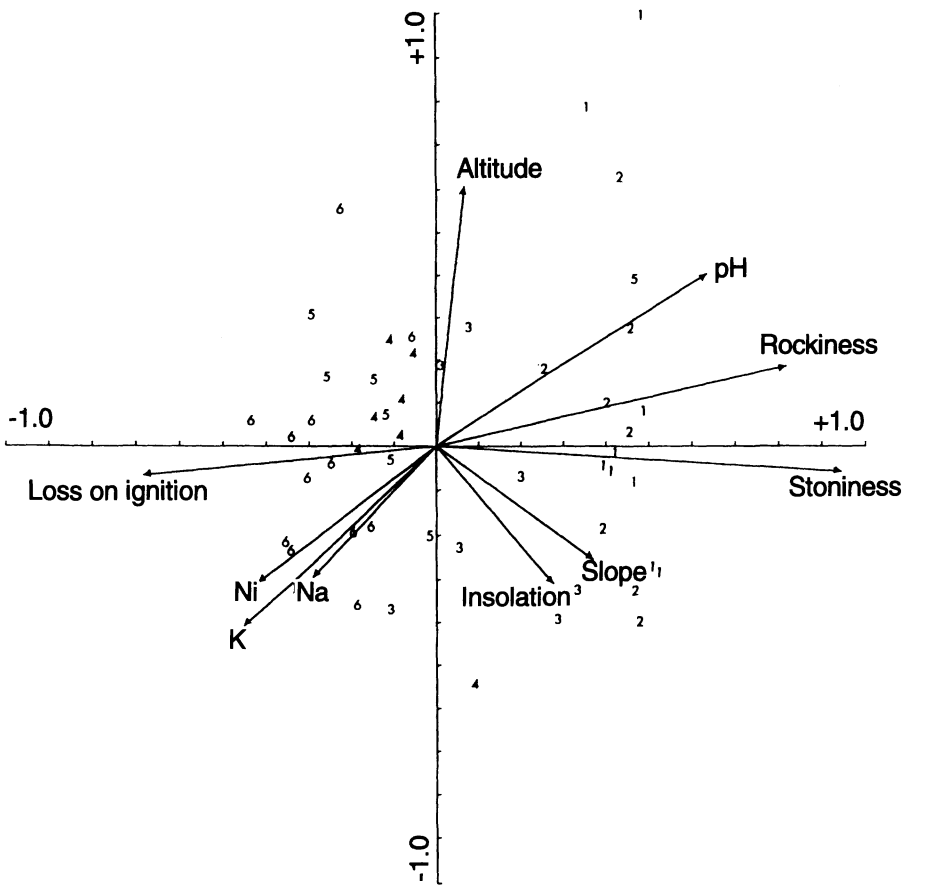

Fig. 2. CCA ordination diagram of the environmental variables and 50 plots of the Mediterranean data-set. The numbers refer to the group of plots (see text). The environmental variables Mg, Ca, Mn, Cu and Fe are not shown, because of their short length.

reduced because of the higher shrub cover. The garigue species and the xerophilous graminoids were almost totally absent, being partly replaced by *Brachypodium rupestre* and *Rubia peregrina*. The vegetation of these two groups has not yet been described from a phytosociological point of view.

Cluster C, linked to cluster B, contained closed woody communities. Group 5 combined the plots sampled in closed maquis a few metres high, locally called "forteto", in which the Mediterranean broad-leaved evergreen species, together with *Erica scoparia* and *E. arborea*, played the main structural role, whereas *J. oxycedrus* subsp. *oxycedrus* was scarce. The field layer consisted of *Brachypodium rupestre* and several woodland species (*Rubia peregrina*, *Stachys officinalis*, *Cyclamen repandum*, *Viola alba* subsp. *dehnhardtii*). This vegetation type has been referred to the *Viburno-Quercetum ilicis ericetosum* (MARCHIORI & TORNADORE MARCHIORI 1977, CHIARUCCI 1994). The plots of Group 6 were in the most evolved communities, similar to Group 5 but with a structure often differentiated into three layers. This vegetation type was assigned to the *Viburno-Quercetum ilicis ornetosum* (MARCHIORI

Table 4. Intraset correlations of environmental variables with the first two axes of CCA ordination in the Mediterranean data-set. Statistically significant values are indicated in bold.

Variable	Correlation coefficients Axis 1	Axis 2
Altitude	0.063	**0.515**
Slope	0.353	-0.263
Insolation	0.263	-0.263
Rockiness	**0.780**	0.156
Stoniness	**0.900**	-0.049
LOI	**-0.648**	-0.056
pH	**0.605**	0.343
Ca	-0.380	-0.091
Cu	-0.268	-0.020
Fe	-0.362	0.018
K	-0.429	-0.348
Mg	-0.273	-0.168
Mn	-0.454	-0.047
Na	-0.276	-0.250
Ni	-0.399	-0.260

& TORNADORE MARCHIORI 1977, CHIARUCCI 1994). The field layer had a very low cover and low species richness.

Soil and physical environment

The main soil features are reported in Tab. 3. The results show that organic matter content and availability of metals increased from garigue to woodland vegetation types, whereas the pH, rockiness and stoniness decreased. Insolation was higher in the shrubland community than in maquis and woodlands. In the garigue it had intermediate values. Chromium, which usually has high total concentrations in ultramafic soils (BROOKS 1987), was below the detection limit (< 0.5 μg/g) in the soil extracts. The Mg/Ca quotient, which has been regarded as important in controlling some serpentine floras (PROCTOR & NAGY 1992), was significantly higher only under the garigue vegetation.

Gradient analysis

The CCA ordering of plots and environmental variables is shown in Fig. 2. The cumulative percentage of variance explained by the first two axes accounted for 25.4% (19.9% and 5.5%) of the species data and 56.8% (44.6% and 12.2%) of the species-environment relations; the eigenvalue of the first canonical axis was highly significant ($P < 0.01$). The plot scattering according to the first two axes (Fig. 2) showed an evolutive trend from garigues to garigues with shrubs, open juniper scrub, closed juniper scrub, maquis and woods, from the positive to the negative values on the first axis. The first axis was positively correlated with rockiness, stoniness and pH and negatively with loss on ignition, whereas the second axis was positively correlated with altitude (Tab. 4). Exchangeable cations were negatively, but not significantly, correlated with the first axis, indicating increasing availability of these elements in the soil from the less to the more evolved communities.

Inland data set

Species composition and richness

The two main clusters (not shown) pertained to the plant communities with high (A) and low (B) degrees of bare soil, differing in structure and species diversity (Tab. 5). The two groups of cluster A corresponded to Groups 1 and 2 of the Mediterranean data set but were slightly different in terms of flora (Tab. 6). In fact, the plots of Group 1 belonged to the *Armerio-Alyssetum bertolonii typicum*, which is reported for all the ultramafic sites of inland Tuscany (CHIARUCCI et al. 1995). Group 2 pertained to similar vegetation but with a higher ground cover and with a higher shrub cover, *Juniperus oxycedrus* subsp. *oxycedrus* and *Fraxinus ornus* being the most abundant shrubs.

Table 5. Structural features and species diversity data (mean ± s.e.) of plots belonging to the six groups identified by cluster analysis in the inland data-set.

Cluster/Group	A/1	A/2	B/3	B/4	B/5
n	7	6	7	6	4
Tree layer cover (%)	0.7 ± 0.7	–	22.9 ± 5.9	14.2 ± 3.0	75.0 ± 2.0
Shrub layer cover (%)	2.8 ± 1.1	35.9 ± 12.3	45.0 ± 13.7	13.8 ± 11.3	32.5 ± 11.1
Field layer cover (%)	30.7 ± 6.4	49.5 ± 10.1	85.0 ± 2.7	75.8 ± 6.0	14.3 ± 6.2
Total species richness	24.7 ± 1.8	28.3 ± 2.0	21.6 ± 0.9	25.7 ± 2.3	20.8 ± 0.9
Tree layer richness	0.1 ± 0.1	0.0 ± 0.0	0.9 ± 0.1	1.0 ± 0.0	2.8 ± 0.8
Shrub layer richness	1.0 ± .4	4.3 ± 0.6	5.4 ± 1.0	3.0 ± 0.7	8.8 ± 1.1
Field layer richness	23.6 ± 2.0	24.0 ± 1.9	15.7 ± 1.1	22.2 ± 1.7	11.5 ± 1.2

Table 6. Species frequency (F) according to a five point scale (I, < 20%; II, 20–40%; III, 40–60%; IV, 60–80%; V, 80–100%) and mean cover (C) in the five groups of plots identified by cluster analysis in the inland data-set. + mean cover less than 0.01. Species endemic to serpentine or locally exclusive are indicated in bold.

Cluster/Group	A/1		A/2		B/3		B/4		B/5	
	F	C	F	C	F	C	F	C	F	C
Tree layer										
Pinus pinaster	I	0.71	.	.	V	20.71	V	14.17	.	.
Fraxinus ornus	.	.	.	.	.	.	.	.	V	6.75
Quercus pubescens	.	.	.	.	.	.	.	.	V	55.75
Ostrya carpinifolia	.	.	.	.	.	.	.	.	II	12.50
Quercus cerris	.	.	.	.	.	.	.	.	II	3.75
Sorbus aria	.	.	.	.	.	.	.	.	II	2.50
Shrub layer										
Erica scoparia	I	0.50	I	0.13	III	17.86	II	11.80	.	.
Erica arborea	I	0.07	.	.	IV	26.43	III	0.25	.	.
Rosa agrestis	.	.	II	0.17	.	.	.	.	.	.
Juniperus oxycedrus subsp. *oxycedrus*	III	2.29	V	34.17	I	0.09	I	0.03	V	2.38
Fraxinus ornus	I	+	V	2.45	II	0.13	.	.	V	10.13
Sorbus aria	.	.	I	0.50	.	.	.	.	II	0.50
Quercus pubescens	.	.	II	0.17	.	.	.	.	III	0.75
Genista januensis	.	.	V	0.30	IV	0.17	II	0.12	II	0.05
Spartium junceum	.	.	II	0.13	II	0.43	I	0.05	II	0.01
Rubus ulmifolius	.	.	I	0.08	IV	0.16	.	.	V	8.33
Cistus salvifolius	.	.	.	.	III	0.13	.	.	.	.
Inula viscosa	.	.	.	.	I	0.07	.	.	.	.
Rhamnus alaternus	.	.	.	.	II	0.29	II	0.08	.	.
Asparagus acutifolius	.	.	.	.	II	0.13	I	0.02	.	.
Pinus pinaster	.	.	.	.	III	1.76	III	1.58	.	.
Juniperus communis	.	.	.	.	I	0.09	III	0.08	II	0.50
Ruscus aculeatus	.	.	.	.	I	0.03	.	.	II	0.75
Prunus spinosa	.	.	.	.	.	.	.	.	IV	8.28
Cornus mas	.	.	.	.	.	.	.	.	III	0.33
Prunus avium	.	.	.	.	.	.	.	.	III	0.23
Rosa arvensis	.	.	.	.	.	.	.	.	III	0.30
Clematis vitalba	.	.	.	.	.	.	.	.	II	0.25
Coronilla emerus	.	.	.	.	.	.	.	.	II	0.50
Cytisus sessilifolius	.	.	.	.	.	.	.	.	II	0.38
Lonicera caprifolium	.	.	.	.	.	.	.	.	II	0.63

Cluster/Group	A/1		A/2		B/3		B/4		B/5	
	F	C	F	C	F	C	F	C	F	C
Ostrya carpinifolia	.	.	.	.	.	.	.	.	II	0.50
Sorbus domestica	.	.	.	.	.	.	.	.	II	0.20
Ulmus minor	.	.	.	.	.	.	.	.	II	0.10
Field layer										
Cerastium ligusticum	III	0.04	.	.	.	.	.	.	.	.
Centaurium pulchellum	II	0.01	.	.	.	.	.	.	.	.
Filago germanica	II	+	.	.	.	.	.	.	.	.
Arenaria serpyllifolia	I	0.01	.	.	.	.	.	.	.	.
Asterolinon linum-stellatum	I	+	.	.	.	.	.	.	.	.
Fumana procumbens	I	0.07	.	.	.	.	.	.	.	.
Jasione montana	I	+	.	.	.	.	.	.	.	.
Stipa tirsa	I	+	.	.	.	.	.	.	.	.
Vulpia ciliata	I	+	.	.	.	.	.	.	.	.
Aira elegans	IV	0.01	I	+	.	.	.	.	.	.
Anthyllis vulneraria subsp. *praepropera*	IV	0.15	I	0.01	.	.	.	.	.	.
Armeria denticulata	IV	0.46	I	+	.	.	.	.	.	.
Sedum album	III	0.06	I	+	.	.	.	.	.	.
Echium vulgare	III	+	III	0.01	.	.	.	.	.	.
Hypochoeris achyrophorus	I	+	I	+	.	.	.	.	.	.
Minuartia laricifolia* subsp. *ophiolithica	I	0.01	I	0.01	.	.	.	.	.	.
Plantago holosteum	III	0.77	V	0.37	.	.	.	.	.	.
Centaurea cf. *jacea*	I	0.01	IV	0.06	.	.	.	.	.	.
Hypericum perforatum	.	.	III	0.01	.	.	.	.	.	.
Asplenium cuneifolium	.	.	II	+	.	.	.	.	.	.
Aira caryophyllea	.	.	I	+	.	.	.	.	.	.
Asplenium adiantum-nigrum* var. *serpentini	.	.	I	0.01	.	.	.	.	.	.
Centaurium erythraea	.	.	I	+	.	.	.	.	.	.
Ceterach officinarum	.	.	I	+	.	.	.	.	.	.
Geranium robertianum	.	.	I	+	.	.	.	.	.	.
Polygala nicaeensis	.	.	I	+	.	.	.	.	.	.
Anthericum liliago	.	.	.	.	II	0.01	.	.	.	.
Inula viscosa	.	.	.	.	II	0.29	.	.	.	.
Plantago lanceolata	.	.	.	.	II	0.01	.	.	.	.
Leucanthemum pachyphyllum	.	.	.	.	I	0.21	.	.	.	.
Gymnadenia cf. *conopsea*	.	.	.	.	I	+	.	.	.	.
Quercus ilex	.	.	.	.	I	+	.	.	.	.
Hieracium pilosella	.	.	.	.	.	.	IV	0.01	.	.
Euphorbia nicaeensis* subsp. *prostrata	.	.	.	.	.	.	II	0.02	.	.
Linum tenuifolium	.	.	.	.	.	.	I	+	.	.
Cistus incanus	.	.	.	.	.	.	I	0.17	.	.
Silene paradoxa	III	0.07	IV	0.07	I	+			.	.
Dianthus sylvestris subsp. *longicaulis*	V	0.05	IV	0.10	.	.	I	0.01	.	.
Herniaria glabra	V	0.09	.	.	.	.	I	+	.	.
Artemisia alba	IV	1.29	V	1.40	.	.	II	0.67	.	.
Sedum rupestre	V	0.59	III	0.03	.	.	II	0.01	.	.
Cheilanthes marantae	III	0.19	I	0.02	.	.	I	+	.	.
Cistus salvifolius	II	0.51	I	0.83	.	.	I	+	.	.
Linum trigynum	V	0.02	V	0.01	.	.	IV	0.01	.	.
Stipa etrusca	III	12.24	V	1.63	I	0.03	I	0.02	.	.
Alyssum bertolonii	V	0.34	V	0.43	I	0.03	II	0.01	.	.
Cuscuta epithymum	III	0.01	III	0.01	I	+	I	+	.	.
Helichrysum italicum	IV	0.56	V	1.43	III	0.25	V	0.28	.	.
Stachys recta* subsp. *serpentini	III	0.01	III	0.15	III	0.04	II	0.01	.	.

Cluster/Group	A/1		A/2		B/3		B/4		B/5	
	F	C	F	C	F	C	F	C	F	C
Sanguisorba minor subsp. *muricata*	IV	0.47	V	0.19	III	0.04	II	0.08	.	.
Trinia glauca* subsp. *glauca	III	0.03	V	0.04	II	0.06	III	0.04	.	.
Thymus striatus* var. *ophioliticus	V	2.64	V	2.03	II	0.02	V	0.77	.	.
Reichardia picroides	III	0.01	II	0.02	III	0.01	III	0.02	.	.
Danthonia alpina	III	0.45	II	9.23	III	1.93	V	31.00	.	.
Potentilla hirta	III	0.30	I	0.01	IV	0.03	IV	0.04	.	.
Hieracium piloselloides	II	0.01	I	+	III	0.05	IV	0.02	.	.
Convolvulus cantabrica	I	0.01	.	.	I	+	I	0.02	.	.
Genista januensis	II	0.08	.	.	I	0.11	IV	0.13	.	.
Aster linosyris	I	+	.	.	I	0.01	II	0.02	.	.
Centaurea aplolepa* subsp. *carueliana	III	0.93	.	.	III	0.03	V	0.69	.	.
Allium sphaerocephalon	III	0.02	.	.	.	.	III	0.01	.	.
Scorzonera austriaca	I	0.01	.	.	III	0.03	IV	0.12	.	.
Centaurea rupestris subsp. *rupestris*	I	0.03	.	.	III	0.54	V	3.13	.	.
Knautia arvensis	.	.	IV	0.50	III	0.34	I	0.13	.	.
Hippocrepis comosa	.	.	IV	0.06	I	0.01	III	0.05	.	.
Lotus corniculatus	.	.	I	+	.	.	I	+	.	.
Carlina corymbosa	.	.	III	0.03	V	0.11	IV	0.11	.	.
Briza media	.	.	.	.	I	0.01	I	+	.	.
Holoschoenus australis	.	.	.	.	I	7.14	I	0.17	.	.
Festuca inops	V	7.19	V	1.63	III	0.21	IV	2.08	II	0.03
Bromus erectus	III	0.79	V	27.80	III	8.00	V	28.67	II	0.03
Galium corrudifolium	III	0.04	V	0.12	V	0.12	V	0.07	III	0.26
Festuca robustifolia	II	1.46	I	+	IV	5.10	V	9.08	II	0.01
Carex humilis	I	0.36	I	0.33	III	0.19	IV	0.50	II	3.00
Vincetoxicum hirundinaria	I	+	I	0.03	IV	0.07	V	0.28	II	+
Melica ciliata	I	0.03	III	0.38	.	.	.	.	II	+
Dorycnium hirsutum	II	0.01	IV	0.25	.	.	.	.	II	0.03
Silene vulgaris	I	+	.	.	.	.	.	.	III	0.03
Quercus pubescens	I	+	.	.	II	+	II	+	II	0.01
Crepis leontodontoides	.	.	I	+	.	.	.	.	II	0.03
Phleum bertolonii	.	.	I	+	.	.	.	.	II	0.01
Viola alba subsp. *dehnhardtii*	.	.	I	+	.	.	.	.	IV	0.40
Carex flacca	.	.	II	0.13	I	0.21	.	.	III	0.63
Brachypodium rupestre	.	.	I	0.83	V	62.14	II	1.00	V	8.63
Filipendula vulgaris	.	.	.	.	I	0.01	.	.	II	0.01
Stachys officinalis	.	.	.	.	I	0.01	.	.	II	0.50
Tanacetum corymbosum	.	.	.	.	I	0.01	.	.	III	0.02
Agrostis gigantea	.	.	.	.	.	.	II	0.12	II	0.03
Clinopodium vulgare	.	.	.	.	.	.	.	.	IV	0.03
Carex divulsa	.	.	.	.	.	.	.	.	III	0.28
Cephalanthera rubra	.	.	.	.	.	.	.	.	III	0.01
Arabis hirsuta	.	.	.	.	.	.	.	.	II	0.01
Cruciata glabra	.	.	.	.	.	.	.	.	II	0.50
Dactylis hispanica	.	.	.	.	.	.	.	.	II	0.03
Dorycnium pentaphyllum	.	.	.	.	.	.	.	.	II	0.03
Festuca heterophylla	.	.	.	.	.	.	.	.	II	0.38
Hedera helix	.	.	.	.	.	.	.	.	II	0.05
Inula conyza	.	.	.	.	.	.	.	.	II	0.01
Lathyrus latifolius	.	.	.	.	.	.	.	.	II	0.08
Lonicera caprifolium	.	.	.	.	.	.	.	.	II	0.05
Peucedanum cervaria	.	.	.	.	.	.	.	.	II	0.02
Torilis arvensis	.	.	.	.	.	.	.	.	II	0.01

Table 7. Soil and environmental data (mean ± s.e.) for the six groups identified by cluster analysis in the inland data-set. When analyses were applied to log-transformed data the standard error range is given in brackets. Different letters indicate significant differences between groups of plots. Duncan multiple-range test at $P < 0.05$.

Cluster/Group	A/1	A/2	B/3	B/4	B/5
n	7	6	7	6	4
Rockiness (%)	14.0 ± 6.8	8.5 ± 2.7	5.0 ± 1.2	9.2 ± 2.9	0.3 ± 0.3
Stoniness (%)	42.1 ± 8.0	16.7 ± 8.2	1.3 ± 0.3	4.3 ± 1.8	25.0 ± 21.7
Insolation	2140 ± 110 ab	2344 ± 56 a	1907 ± 153 b	2235 ± 50 ab	2031 ± 158 b
LOI	10.8 a (9.6–12.0)	13.5 a (12.4–14.7)	21.3 b (20.3–22.4)	18.6 b (17.6–19.6)	21.3 b (20.7–21.9)
pH	7.1 ± 0.1 a	6.9 ± 0.1 a	6.5 ± 0.1 b	6.5 ± 0.1 b	6.7 ± 0.1 b
Ca	667 a (421–1058)	631 a (523–762)	827 a (744–919)	1611 a (1014–2560)	1668 a (1222–2276)
Mg	1460 ab (931–2288)	1170 a (1035–1323)	1651 ab (1422–1918)	4193 b (2624–6699)	1620 ab (1328–1976)
Mg/Ca	2.2 ± 0.1 ab	1.9 ± 0.2 bc	2.0 ± 0.2 a	2.7 ± 0.3 ab	1.3 ± 0.5 c
Cu	0.2 a (0.2–0.3)	0.3 a (0.2–0.3)	0.3 ab (0.3–0.4)	0.3 ab (0.3–0.4)	0.4 b (0.4–0.5)
Fe	1.7 a (1.6–1.8)	2.9 b (2.4–3.4)	3.0 b (2.8–3.3)	2.4 ab (2.0–3.0)	3.5 b (3.0–4.2)
K	76 a (44–132)	49 a (40–61)	62 a (56–69)	175 a (100–306)	169 a (133–214)
Mn	2.1 a (1.6–2.6)	4.4 b (3.2–5.9)	7.1 b (5.7–8.9)	7.2 ab (5.0–10.3)	10.8 b (6.3–18.1)
Ni	2.6 a (2.3–2.9)	4.5 ab (3.5–5.7)	10.4 c (8.6–12.5)	13.7 c (11.6–16.1)	7.5 ab (5.1–10.9)

Cluster B contained markedly different vegetation types. Group 3 consisted of plots in grassland dominated by *Brachypodium rupestre* under a relatively dense pine (*Pinus pinaster*) canopy (20% of cover on average). The strong dominance of *Brachypodium rupestre* (mean cover 62%) reduced species richness in the field layer. Group 4 was formed by less strongly dominated grasslands under a lower pine cover (14% of cover on average). These evolve from garigues similar to those of group 1 because of the pine canopy, which protects against erosion and is responsible for an increase in nutrient input (CHIARUCCI & DE DOMINICIS 1995, CHIARUCCI 1996, CHIARUCCI et al. 1998) and probably they also evolve into the grasslands of Group 3. The plots of Groups 3 and 4 were sampled exclusively on Mt. Ferrato. The plots of Group 5, sampled in the Upper Tiber Valley, were recorded in the most evolved vegetation, i.e. woodlands dominated by *Quercus pubescens* and *Fraxinus ornus*. These communities were not common and, as observed by PICHI SERMOLLI (1948), were almost exclusively associated with less xeric conditions, such as slope-bottoms, or close to the ultramafic/non-ultramafic lithological ecotone.

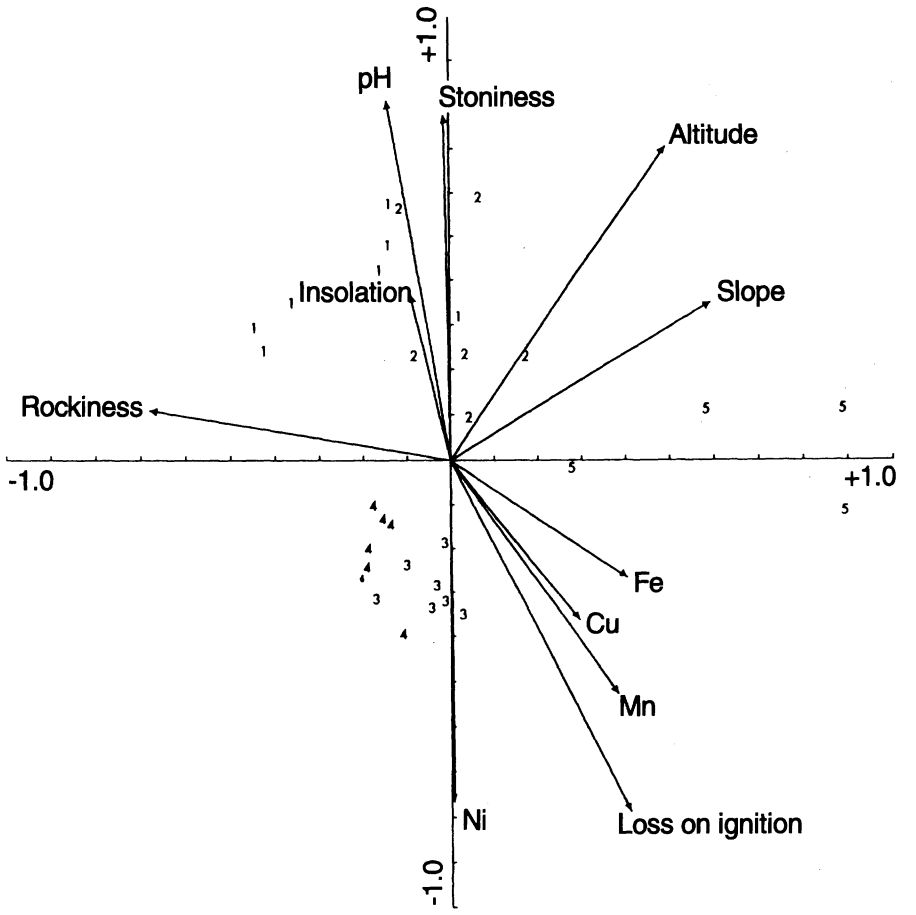

Fig. 3. CCA ordination diagram of the environmental variables and 30 plots of the inland data-set. The numbers refer to the group of plots (see text). The environmental variables Ca, K, Mg and Na are not shown, because of their short length.

Soil and physical environment

The main soil features of the vegetation groups of inland areas (Tab. 7) showed a picture similar to that reported for the Mediterranean areas. The plot groups in the inland data-set did not represent a natural succession, as those of the Mediterranean data-set, but included anthropogenically induced vegetation, such as the pine-dominated communities. Despite all this, pH, organic matter content, and metal availability were correlated with vegetation cover and structure, implying that the soil under garigue and scrub vegetation may be transformed by the growth of forests, such as invading pine trees.

Gradient analysis

The CCA ordering of plots and environmental variables is shown in Fig. 3. The cumulative percentage of variance accounted by the first two axes was 35.4% (19.1% and 16.3%) of the species data and 48.9% (26.3% and 22.6%) of the species-environment relationships (Fig. 3). The eigenvalue of the first canonical axis was highly significant ($P < 0.01$). The first axis,

Table 8. Intraset correlations of environmental variables with the first two axes of CCA ordination in the inland data-set. Statistically significant correlation are marked in bold.

Variable	Correlation coefficients Axis 1	Axis 2
Altitude	0.464	**0.697**
Slope	**0.574**	0.361
Insolation	-0.095	0.351
Rockiness	**-0.673**	0.077
Stoniness	-0.047	**0.746**
LOI	0.428	**-0.743**
pH	-0.167	**0.775**
Ca	–	–
Cu	0.300	-0.343
e	0.412	-0.245
K	–	–
Mg	–	–
Mn	0.392	**-0.495**
Na	–	–
Ni	0.028	**-0.742**

which differentiated the woods of Group 5 with respect to other vegetation groups, was correlated positively with slope and negatively with rockiness. The second axis, which differentiated (a) Groups 3 and 4, (b) Group 5 and (c) Groups 1 and 2, was positively correlated with altitude, stoniness and pH, and negatively with organic matter, Mn and Ni content of the soil (Tab. 8).

DISCUSSION

The results indicate that the exchangeable fraction of soil metals was higher under the more evolved and structured communities, in both natural and anthropogenic environments, suggesting that soil metal content is not the most important limiting factor for the vegetation of Tuscan ultramafic soils. The soluble fraction of chromium was, in any case, too small to affect the vegetation (BROOKS 1987, PANDOLFINI & PANCARO 1992, ROBINSON et al. 1996). The increased availability of metals in the soil under the more evolved vegetation types may be a direct consequence of the lower pH. ROBINSON et al. (1996) showed that metal solubility in New Zealand serpentines increased exponentially as the pH of the extracting solution was lowered. The effect of closed woody vegetation on soil may be to lower the pH by humic decay under moist conditions and therefore induce a higher availability of metals. The hypothesis that metal content is not the most important limiting factor causing the infertility of Tuscan serpentine soils was recently advanced in pedological (ANGELONE et al. 1991, 1993) and vegetation (CHIARUCCI & DE DOMINICIS 1995, CHIARUCCI 1996, CHIARUCCI et al. 1998) studies. The results of these studies were at variance with previous reports, and these authors emphasised the importance of the metal fraction available to plants as opposed to total metal concentrations.

Many other authors claim that soil metal toxicity is not the most important limiting factor for serpentine vegetation. CARTER et al. (1987) did not find any evidence that nickel was the cause of the serpentine infertility in the keen of Hamar, Shetland Islands. KRUCKEBERG (1992) did not find any evidence that cobalt, chromium, iron and nickel affect plant growth in the ultramafic soils of western North America. In New Zealand, LEE (1992) observed that only in some southern ultramafics is nickel likely to reduce plant growth. In a review, PROCTOR & NAGY (1992) stated that many assumptions about causal roles for nickel in causing the unusual serpentine vegetation are unfounded and in-depth studies have often disproved the importance of this element.

One of the most important factors controlling the vegetation of Tuscan ultramafic soils appears to be drought stress due to topographical position. In both Mediterranean and inland sites, the insolation of juniper scrub communities, a relatively undisturbed vegetation type where the serpentine endemics are found, was significantly higher than that of the sites with a woodland vegetation cover. The index used in the present survey indicates the hours per year of overhead sunlight to give the radiation the site actually receives in one year, given

its aspect, slope, and latitude, but the differences between sites might also be more important if considering summer drought. Water stress, together with soil nutritional deficiencies, constantly limits vegetation development. Periodic drought and other exceptional stresses may kill off the forest species, interrupting vegetation dynamics and thereby causing reversion to stunted and open plant communities and promoting soil erosion. For the serpentine soils of the Keen of Hamar, Shetland Islands, where rainfall is abundant throughout the year, CARTER et al. (1987) suggested that summer droughts of seven or more consecutive days, which happen on average once every 3–5 years, may exhaust the water reserves of the soil. This leads to the development of xerophilous, mainly annual, plant communities even in the humid oceanic climatic zone.

There is now also strong evidence that nutrient availability is another important factor limiting plant growth and hence vegetation development in Tuscan ultramafic soils. The lower pH under woody plant communities not only increases the availability of plant nutrients such as K, Zn, Cu, Fe, but also facilitates their uptake. The N and P available (not measured) under maquis and woodland vegetation types are greater because of the higher organic matter content. Some recent studies showed that the addition of small amounts of nitrogen, phosphorus and potassium to garigue vegetation induced a strong increase in ground cover and biomass (CHIARUCCI et al., unpubl. data). Higher nutrient availability has also been reported to alleviate the effects of drought (GRIME & CURTIS 1976). PROCTOR & NAGY (1992) considered the low nutrient content of the soil a "key feature" in causing serpentine infertility in many areas. On the other hand, Ca-deficiency or the Mg/Ca ratio, considered very important limiting factors for serpentine vegetation (BROOKS 1987, BAKER et al. 1992, ROBERTS & PROCTOR 1992), did not appear as very important in these ultramafic soils. In fact the addition of calcium, alone or with nitrogen, phosphorus and potassium (NPK), led to a non-significant increase of cover and biomass with respect to controls and NPK alone (CHIARUCCI et al. unpubl. data). This was probably due to the fact that in these soils the Mg/Ca quotient is relatively low, averaging 1.5 to 3.0.

The development of more-structured woody communities positively improves soil structure and fertility, allowing a better plant growth by positive feedback. The natural dynamics towards more evolved vegetation types lead to the disappearance of the endemic species, linked to the less evolved soils, and the spread of the more competitive forest species. This implies that the persistence of garigue and open scrub vegetation, in which the serpentine endemics grow (PICHI SERMOLLI 1948, PIGNATTI 1982, ARRIGONI et al. 1983, CHIARUCCI et al. 1995), might require periodic disturbance or a factor that limits vegetation dynamics. Although specific data are not available, it can be inferred that forest fires are not rare, especially in the Mediterranean sites, but normally do not result in reversion to garigue vegetation. Likewise, anthropogenic disturbance over the last 3000–5000 years would have been insufficient for the evolution of serpentine endemic species such as the endemic nickel hyperaccumulator *Alyssum bertolonii*. Unlike the open juniper scrubs, the garigues of the *Armerio-Alyssetum bertolonii* association are not always located in areas with less favourable ecological conditions, such as xeric slopes. In addition, soils under the garigue plant communities show the lowest concentrations of potentially toxic metals. The lack of correlation between environmental limiting factors and garigue vegetation suggests that the spread of garigues has been partially favoured by human activity through destruction of more evolved vegetation types, such as the juniper scrub communities and the evergreen maquis.

According to this picture, the *Juniperus oxycedrus* subsp. *oxycedrus* scrub communities are the most natural vegetation type on xeric slopes and their successional dynamics, towards closed and structured woodland communities, is prevented by nutrient deficiency and periodic reversion due to special stress factors such as drought. As is known for other environments (GRIME 1990, VAN DER MAAREL 1996), these droughts may be the driving force for the serpentine vegetation of Tuscany, creating gaps for new species to occupy. Xerophilous and heliophilous plants, such as the serpentine endemic *Alyssum bertolonii*, find optimal ecological conditions in open patches between shrubs. During evolutionary time, soil metals might have induced a selective pressure on plant populations growing in these patches, where the low-nutrient content of the soil and the drought stress cannot alleviate metal toxicity, allowing the selection of specialised taxa. True forest communities, on the other hand, can only be found in more favourable topographic conditions, where water stress is lower, exceptional droughts are less frequent and soil can accumulate. Long-term monitoring of permanent plots can test this hypothesis.

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