Community dynamics of serpentine vegetation in relation to nutrient addition and climatic variability

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Abstract

To investigate the effects of nutrients and climate on community composition and structure of serpentine vegetation in Tuscany, Italy, a fertilization experiments was carried out over a period of six years. Response curves of vegetation to the addition of nitrogen, phosphorous and potassium were analyzed by a permutation-based approach. Phosphorus addition induced a significant increase in vegetation cover, and the observed changes in total plant cover persisted years after the cessation of fertilization. Plant species richness showed marked fluctuations during the experiment, but these were not related to any treatment. Although six years did not allow a robust test of the relations between climate and vegetation, some interesting observations were obtained. Total vegetation cover, a surrogate measure for community biomass, was positively related to the amount of rainfall in the whole period of the growing season, an often observed relationship in Mediterranean-type ecosystems. Species richness was positively related to the mean temperature of spring, and negatively related to mean spring temperature indicating that a warm and xeric spring season may induce local extinction of some species. Species of the community responded differently in relation to climate and phosphorus addition. Many species were positively influenced by phosphorus addition; however, in some annual species the effect disappeared with the cessation of fertilization, whereas in some perennial species it persisted in the following years.

Introduction

Ultramafic (serpentine) soils generally host distinctive vegetation, which is often stunted and interspersed with bare patches. These features have been attributed to the chemical and physical properties of serpentine soils. Plant growth is limited by many factors, including low nutrient levels, calcium deficiency, magnesium toxicity, high concentrations of potentially toxic elements, such as chromium, nickel and cobalt, and soil xericity (Brooks, 1987; Baker *et al.*, 1992; Roberts & Proctor, 1992). However, the factors controlling serpentine flora and vegetation differ from site to site (Proctor & Nagy, 1992). In general, the vegetation of serpentine soils is peculiar and well differentiated with respect to the surrounding areas. An high proportion of species is normally endemic to serpentine soils and some of these present special physiological adaptation to grow in the unfavorable conditions of serpentine soils (Brooks, 1987).

Ultramafic rocks outcrop in many parts of Tuscany, Italy. The most typical vegetation on these soils is a garigue (*Armerio-Alyssetum bertoloni*), characterized by scarce plant cover, low species richness and a high proportion of endemic species, among which the well-known nickel-hyperaccumulator *Alyssum bertolonii* (Arrigoni *et al.*, 1983; Vergnano Gambi, 1992; Chiarucci *et al.*, 1995). Recent studies suggested that soil metals are not the most important limiting factor for serpentine vegetation of Tuscany. Chiarucci & De Dominicis (1995) and Chiarucci (1996) showed how pine plantation promotes species richness and plant cover in the understorey. A higher exchangeable metal content was found in the soil under the pine plantations as well as under the naturally more structured vegetation types (Chiarucci & De Dominicis, 1995; Chiarucci *et al.*, 1998b; Chiarucci *et al.*, 1998c). Fertilization experiments (Chiarucci *et al.*, 1998a; Chiarucci *et al.*, 1999a) shown that vegetation response posi-

tively to nutrient addition, with an increase in productivity and species richness, suggesting that nutritional stresses represent the most important limiting factor for the existence of many species and plant productivity. Carter *et al.* (1988) showed that, on the serpentine soils of the Keen of Hamar, Shetland Islands, the increase in cover caused by nutrient addition is maintained for many years after the cessation of fertilization.

The present paper is part of a research program on the vegetation ecology and conservation of the serpentine soils of Tuscany. The specific questions asked in our study are: (1) do the addition of small amounts of major nutrients, such as nitrogen, phosphorus and potassium, alter community structure and diversity? (2) Are the eventual changes in community structure and diversity limited to the time span of fertilization or do they persist? (3) Do the inter-annual differences of climate alter the community structure and diversity?

Materials and methods

Site description

The fertilization experiment was carried in an ultramafic outcrop located about ten km west of Siena (Lat. 43°19'06" N, Long. 11°06'33" E), in the upper Elsa Valley, near the village of Pievescola (Fig. 1). The Climate is sub-Mediterranean, with summer drought and 13.5°C of mean annual temperature. January is the coldest month with an average temperature of 2.3° C; August is the hottest with 21.5° C. Annual rainfall averages 791.2 mm. July is the driest month with an average rainfall of 35 mm, and November is the wettest with 119 mm (Barazzuoli, 1993).

The site selected for the experiment was a slope with a vegetation cover formed by a serpentine garigue (Chiarucci *et al.*, 1995) characterized by *Alyssum montanum*, a non-exclusive serpentine plant. Although the lack of *Alyssum bertolonii*, species composition was similar to that of the typical *Armerio-Alyssetum bertoloni* association. Other sites with *Alyssum bertolonii* were also fertilized (Robinson *et al.*, 1997; Chiarucci *et al.*, 1998a; Chiarucci *et al.*, 1999a)

Experimental design, treatments and data collection

Sixteen 2x2m plots were randomly chosen in early spring 1994. In May 1994, all vascular plants growing in
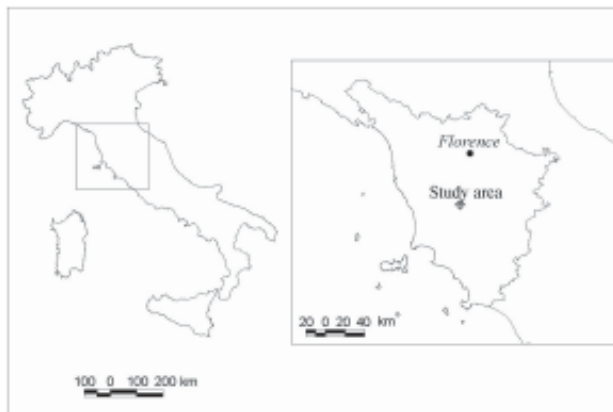

Figure 1. Geographic location of the study area.

each plot were recorded and their cover accurately estimated by the point-quadrats method (see Moore & Chapman, 1986), with a density of 441 points/plot.

To test the relative importance of nitrogen, phosphorus and potassium on plant community diversity and structure, a fertilization experiment of was conducted, according to a completely randomized scheme, with four replicates per treatment. The treatments were: *i)* control (referred to as 0); *ii)* fertilized with nitrogen (5 g m^{-2}, corresponding to 50 Kg ha^{-2}) as NH_4NO_3 (N); *iii)* fertilized with phosphorus (5 g/m^2) as $NaH_2PO_4 * H_2O$ (P); *iv)* fertilized with potassium (5 g/m^2) as KCl (K). The plots were fertilized in autumn 1994 (October 21st) and one year later (October 21st 1995). Species presence and cover were recorded, with the method used in 1994, also in the month of May each following year from 1995 to 1999.

Climatic data were obtained from the closest climatic station (Siena Poggio al Vento), located at about 10 Km from the study site. Climatic data were summarized for the following periods, according to the growing period and to the sampling date, which always was between May 28th and June 6th: summer (June-August of the previous year with respect to sampling date), autumn (September - November), winter (December - February), Spring (March-May). Additionally, we also calculated the data for the whole year before sampling (June of the previous year - May of the same year of sampling). For each period we calculated average temperature, total rainfall and the ratio between total rainfall and average temperature.

Data analysis

Five variables were used to analyze the changes in community structure and diversity: species richness (S), total plant cover (C), Shannon index of diversity (H'), Pielou index of evenness (E) and Simpson index of dominance (D). For each variable, a response curve as function of years was determined in each plot.

Standard parametric tests on response curves from randomization experiments involve some nuisance assumptions to be verified (Grizzle & Allen, 1969). Zerbe & Walker (1977) and Zerbe (1979) developed a permutation test on response curves based on an additive effect model and free from such assumptions. The randomized design involves *g* treatments and *n* experimental units, randomly assigned to treatment; if n_k denotes the number of units assigned to treatment *k*, then there are $M = n! / (n_1! \, n_2! ... n_g!)$ possible assignments. Zerbe (1979) showed that the response curve over *T* periods of the *i-th* experimental unit randomly assigned to treatment *k*, turns out to be a collection of random variables, say $\{Y_{ik}(t), t=1,...,T\}$, where

$$Y_{ik}(t) = m(t) + t_k(t) + e_{ik}(t) , \quad t = 1,...,T \qquad (1)$$

and $e_{ik}(t)$ represents the residual component. A structure of type (1) is difficult to use with standard parametric techniques, in that the residuals $e_{ik}(t)$ have mean 0 but are neither independent nor omoscedastic (see e.g. Rao, 1973, p. 504).

To test the hypothesis H_0 of no treatment effect, as well as to identify specific differences, H_0 may be decomposed as the intersection of the hypotheses H_{kh} of no differences between treatments *k* and *h* ($h > k = 1, ..., g$). Obviously, H_0 is true if any H_{kh} is true, i.e. any single

hypothesis H_{kh} has to be assessed. Zerbe & Walker (1977) proposed a ANOVA-like test statistic, say F_{kh} which constitutes an index of the differences between response curves of treatment k and those of treatment h. If (1) holds, F_{kh} tends to be small when H_{kh} is true and be large in case of differences between treatments k and h. The theoretical distribution of F_{kh} under H_{kh} is difficult to obtain owing to the lack of suitable properties for the residuals. However, the p-values of any F_{kh}, say p_{kh}, it can be straightforwardly obtained from the M permutations of the data. Moreover, to assess the overall hypothesis H_0, Westfall & Young (1993) suggested the use of the minimum p-value, say p^*. The analytical determination of the p^* distribution is prohibitive owing to the dependence among the collection of the p_{jh}'s. Once again, the significance of p^* may be determined by the M permutations of the data. For example, under the balanced assignment $n_k = n/g(k = 1,...,g)$, the F_{kh}'s are identically distributed so that the overall significance may be computed as the proportion of the maxima of the F_{kh} statistics computed on the M permutations of data greater than the maximum of the same statistics on the real data.

This experiment gave rise to $n = 16$ curves (4 for each treatment) for each variable. The purpose of the statistical analysis was to assess of the equality of treatment effects over the time. To this purpose, for each variables the response curves were compared at the beginning of the experiment (1994) and over the intervals of time 1994-95, 1994-96, 1994-97, 1994-98, 1994-99. Thus, for any variable and any time interval, the p-values of the 6 paired comparisons and the overall p-values were exactly computed on the basis of all the possible $M = 16! / (4!)^4 = 63,063,000$ assignments of the 16 plots to the 4 treatments, which were generates by the algorithm proposed by Baker (1977).

To investigate vegetation-climate relations, only the data from the control plots were used, to avoid any influence due to the treatments. The correlation coefficient was calculated for the mean annual values of the vegetation variables with respect to the climatic variables above described.

Results

Climatic variables

Mean annual rainfall and mean annual temperature at the climatic station of Poggio al Vento, in the period 1951-1980, were 791.2 mm and 13.5°C respectively (Barazzuoli 1993). The study period (1994-1999), although too short to make significant comparisons, was relatively warmer (mean 13.9 °C) and drier (mean 767 mm) compared to the mean on a 30 years basis. Annual rainfall and temperature varied largely between the years of the experiment: annual rainfall ranged from 479.5 to 930.8 mm (Fig. 2a), whereas mean annual temperature ranged from 13.4 to 14.4 °C (Fig. 2b); the ratio between rainfall and temperature ranged from 34.1 to 67.8 mm/°C (Fig. 2c). Important differences also existed for the four seasonal periods considered, in particular as far as concerns the total rainfall and the rainfall/temperature ratio. An important decrease of rainfall and rainfall/temperature ratio was observed in the last year of observation.
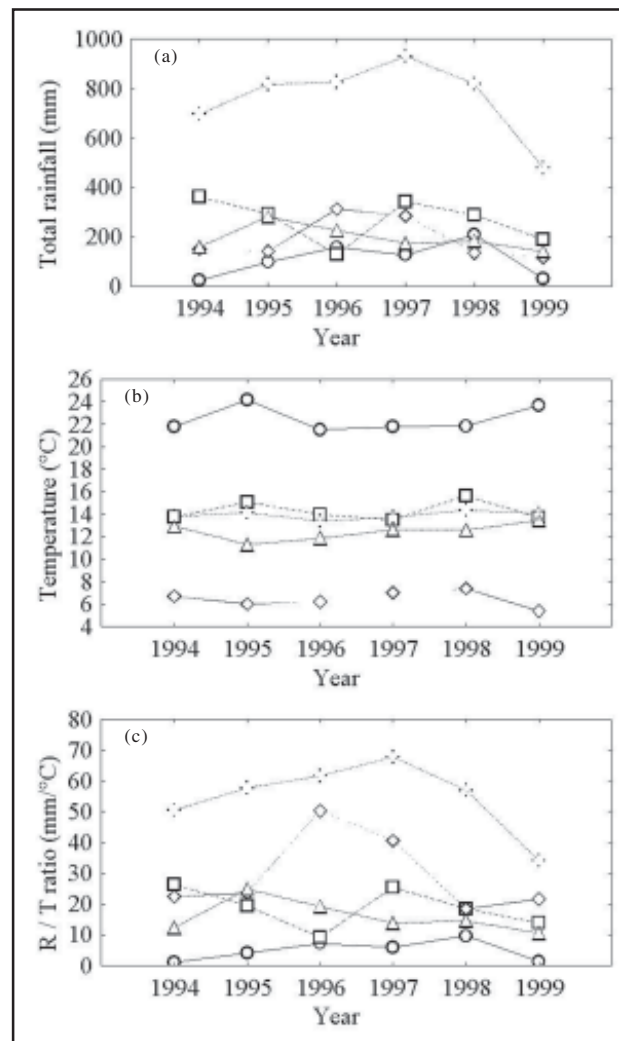

Figure 2. Pattern of climatic data at the Poggio al Vento climatic station over the 6 years of the experiment. a) total amount of rainfall; b) mean temperature; c) ratio between total amount of rainfall and mean temperature. Circles: summer data; squares: autumn data; diamond: winter data; triangles: spring data; crosses: annual data.

Vegetation cover and diversity

According to the results of the permutation test applied to all the variables (table 1), only the response curve of total plant cover significantly differed in the six years. The significance of the differences among the response curves of total plant cover increased starting from the second year, *i.e.* the first following fertilization, as indicated by the p-values.

Table 1. Results of the permutation tests reporting significant differences revealed by each variable. The global p-values for the significance of the difference resulting for each variable are reported. Bold characters evidenced significant p-levels.

	1994	1995	1996	1997	1998	1999
Total plant cover	0.9713	**0.0039**	**0.0020**	**0.0011**	**0.0010**	**0.0009**
Species richness	0.7005	0.8493	0.8751	0.7720	0.7803	0.2561
Evenness (E')	0.4090	0.3929	0.3934	0.4370	0.5187	0.3782
Diversity (H')	0.3814	0.3836	0.2774	0.1506	0.2390	0.2800
Dominance (D)	0.6603	0.5685	0.6250	0.7711	0.6683	0.6925

Before fertilization, total plant cover was extremely low for all the plots (mean 19.3%; s.d. 2.8; range 14.3 - 24.5%). As indicated by the permutation test (table 2), the pattern of the total plant cover of the P-fertilized plots (Figure 3) significantly differed from all the other, whereas differences between the other treatments were never significant. Total plant cover increased immediately after fertilization with phosphorous (years 1995 and 1996) and continued to increase in the period following the cessation of fertilization. The permutation test (table 2) indicated that the significance of the difference between the total plant cover of the P-fertilized plots and all the others increased with time, indicating an increasing effect of phosphorus. The patterns of the control plots, as well as of the N- and K-fertilized plots had some fluctuations in the different years (Figure 3), but the differences were not statistically significant.

Before fertilization, species richness averaged 17.9 (s.d. 1.8; range 15 – 22). The permutation test (table 1) indicated that the response curves of species richness in the four treatments were not significantly different (Figure 4). However, marked fluctuations in species richness were evident in the different years. Almost all the life-form groups were affected by similar fluctuations in number of species. Species richness per each year was significantly correlated to the number of hemicryptophytes ($r = 0.577$, $p < 0.001$), geophytes ($r = 0.361$, $p < 0.001$), therophytes ($r = 0.65$, $p < 0.001$) and phanerophytes ($r =$

0.675, $p < 0.001$); the latter group was almost exclusively represented by seedlings of trees. The number of chamaephytes was not significantly correlated to species richness, indicating that this group of species had very scarce inter-annual fluctuations.
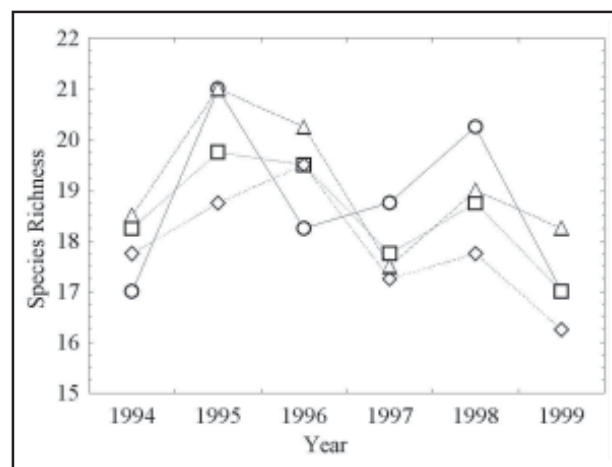

Figure 4. Effects of fertilization treatments (control, N, P, K) on species richness over the 6 years of the experiment. Triangles and interrupted line: control plots (0); diamonds and dotted line: plots fertilized with nitrogen (N); circles and continuous line: plots fertilized with phosphorus (P); squares and broken line: plots fertilized with potassium (K).

The response curves of the Shannon index of diversity H' (Fig 5a), the Pielou index of evenness E (Fig. 5b) and the Simpson index of dominance D (Fig. 5c) showed, for the four treatments and the six years fluctuating patterns, analogous to that showed by species richness, but according to the permutation test the response curves of these indices did not show any significant difference for the four treatments in the six years. These indices, in the four treatments and the six years, showed that these plant communities were characterized by a relatively high diversity (Shannon diversity index H' 1.74 - 2.79), a relatively high evenness (Pielou evenness index E 0.63 - 0.90) and an extremely low dominance (Simpson dominance index D 0.08 - 0.25). Species richness, H' and E were significantly correlated one to each other, whereas D was negatively related to species richness, H' and E ($p < 0.01$ for all relations).

Relationships between vegetation and climate

Although performed only with six years of data, the correlation analysis revealed some interesting relations. In particular, mean total plant cover in each year was positively related to the total amount of rainfall in the year before sampling ($r = 0.927$, $p = 0.008$), as well as to the rainfall/temperature ratio in the year before sampling ($r = 0.906$, $p = 0.013$). This positive relation clearly indicated that total plant cover is promoted by the amount of the rainfall, in this xeric habitat. The mean number of species per plot in each year was negatively correlated to mean spring temperature ($r = -0.852$, $p = 0.031$) and positively correlated to the spring rainfall ($r = 0.898$, $p = 0.015$) and to the spring rainfall/temperature ratio ($r = 0.897$, $p = 0.015$), suggesting that xericity during the spring period might reduce the probability of success of established plants, which are mostly annuals.

Table 2. Results of the permutation tests reporting the *p*-values for the 6 pairwise comparison between treatments for the variable *total ground cover*.

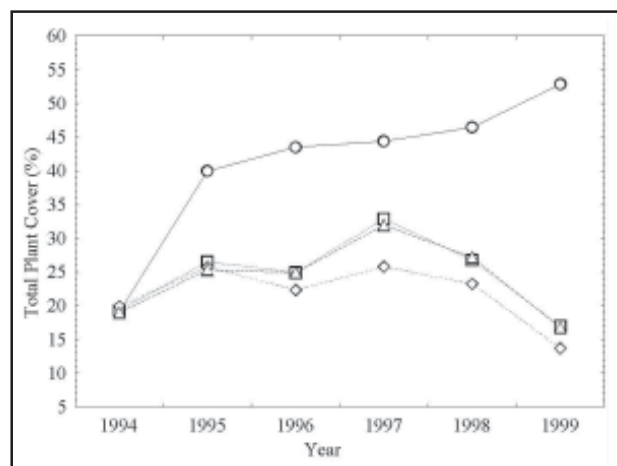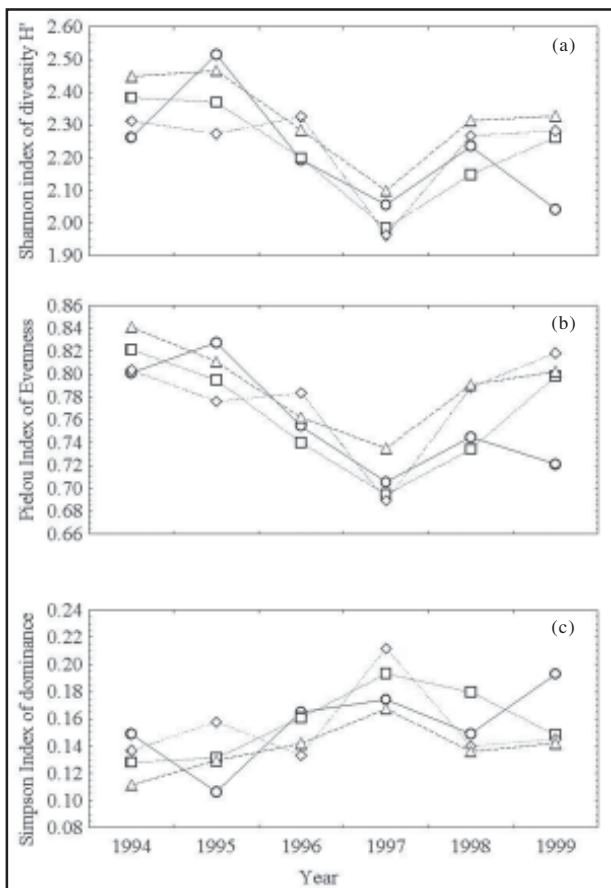|	94	95	96	97	98	99
Control *vs* N	0.999	0.998	0.999	1.000	1.000	1.000
Control *vs* K	0.971	0.999	0.956	0.717	0.710	0.811
Control *vs* P	1.000	**0.004**	**0.003**	**0.004**	**0.003**	**0.002**
K *vs* N	0.989	0.999	0.955	0.633	0.664	0.782
K *vs* P	1.000	**0.008**	**0.003**	**0.005**	**0.003**	**0.002**
N *vs* P	0.976	**0.005**	**0.002**	**0.001**	**0.001**	**0.001**

Figure 3. Effects of fertilization treatments (control, N, P, K) on total plant vegetation cover over the 6 years of the experiment. Triangles and interrupted line: control plots (0); diamonds and dotted line: plots fertilized with nitrogen (N); circles and continuous line: plots fertilized with phosphorus (P); squares and broken line: plots fertilized with potassium (K).

Figure 5. Effects of fertilization treatments (control, N, P, K) on Shannon Index of diversity H' (a), Pielou index of Evenness E (b) and Simpson index of dominance D (c). Triangles and interrupted line: control plots (0); diamonds and dotted line: plots fertilized with nitrogen (N); circles and continuous line: plots fertilized with phosphorus (P); squares and broken line: plots fertilized with potassium (K).

Patterns of the most frequent species

Different species responses can be observed in relation to time since and type of fertilization (Figure 6a-r). Many species were positively influenced by the addition of phosphorus; however in some species the increase in cover ceased with the cessation of fertilization (*Sedum album*, *Herniaria glabra*, Figure 6a-b), whereas in some others it persisted also in the following three years (*Sedum rupestre*, *Armeria denticulata*, Figure 6c-d). In both *Sedum* species we observed a reduction of the purpurescence, reported when they grow on serpentine soils. Two annuals forbs, *Cerastium ligusticum* and *Echium vulgare* (Figure 6e-f), increased their cover right after P-fertilization in the first year but they reduced it in the following years; however, cover increased again in the last year of observation, 6 year after fertilization. This cover increase in the P-fertilized plots in the last year of the experiment was observed also in other annual species (*Brachypodium dystachion*, *Aira elegantissima*, *Psilurus incurvus*, Figure 6g-i) which had not responded positively right after the addition of phosphorus. Other species showed different patterns of positive (Figure 6l-m) or negative (Figure 6n-o) relations to the total amount of rainfall (Figure 2a) or to the rainfall temperature ratio (Figure 2c). Other species showed no clear patterns.

Discussion

Effects of fertilization

Total vegetation cover strongly varied between fertilization and years, but never reached very high values (from 11.8 to 66.1%), which demonstrated the scarce productivity of this vegetation type. In 35 1 m^2 plots sampled in a similar serpentine vegetation and submitted to seven fertilization treatments, Chiarucci et al. (1999a) found that total biomass harvested per plot was highly correlated with the total vegetation cover (r = 0.957; P < 0.001). In addition, Chiarucci et al. (1999b) observed that the DCA scores of these plots obtained using cover and biomass data showed a good correlation, meaning that the DCA plot scattering obtained with these two measures of abundance was consistent. On the other hand, significant differences were observed if relative abundance distribution of species were analyzed, because of different properties of cover and biomass measures (Chiarucci et al. 1999b). These indications suggested that, despite some differences in fine structural features of the communities, changes in cover should indicate analogous changes in total community biomass within this community type.

Phosphorus addition significantly improved the productivity of this vegetation type, as already reported by many authors and different serpentine outcrops (see Carter et al., 1988; Proctor, 1992). Phosphorus was already found a key element for inducing higher productivity on serpentine vegetation of Tuscany (Chiarucci et al., 1998a; Chiarucci et al., 1999a; Robinson et al., 1997); these studies, however, were performed over a shorter period and with high amounts of phosphorus applied compared to the present survey (10 gm^{-2} *vs* 5 gm^{-2}). The present study confirms the role of phosphorus as key factor for serpentine vegetation, demonstrating how low amounts of phosphorus induce marked changes in vegetation cover and that the changes can still be observed six years after the fertilization. Proctor (1992) reported that in a fertilization experiment, performed in 1965-1968 by Ferreira & Wormell (1971), the addition of major nutrients (NPK) and calcium modified a herb rich *Calluna* heat into a *Festuca* grassland and that the changes were still present in 1982, many years after the cessation of fertilization, confirming the permanence of the vegetation changes induced by phosphorus fertilization. Total vegetation cover was even higher in 1982 compared to the original data by (Ferreira & Wormell 1971). In addition, a reduction of the purpurescence was observed in both *Sedum* species and this is likely to confirm phosphorus deficiency as the cause of this typical serpentinomorphoses, reported for different sites (Menez de Sequeira & Pinto da Silva, 1992; Pichi Sermolli, 1948; Tatic & Veljovic, 1992).

Our fertilization treatments did not show any significant effects on species richness and indices of species diversity. However, a slight increase in species richness after fertilization was reported by Chiarucci et al. (1998a) for serpentine vegetation of Tuscany; these authors fertilized garigue vegetation similar to that of this study, but characterized by the presence of the nickel hyperaccumulator species *Alyssum bertolonii*. Nevertheless, af-
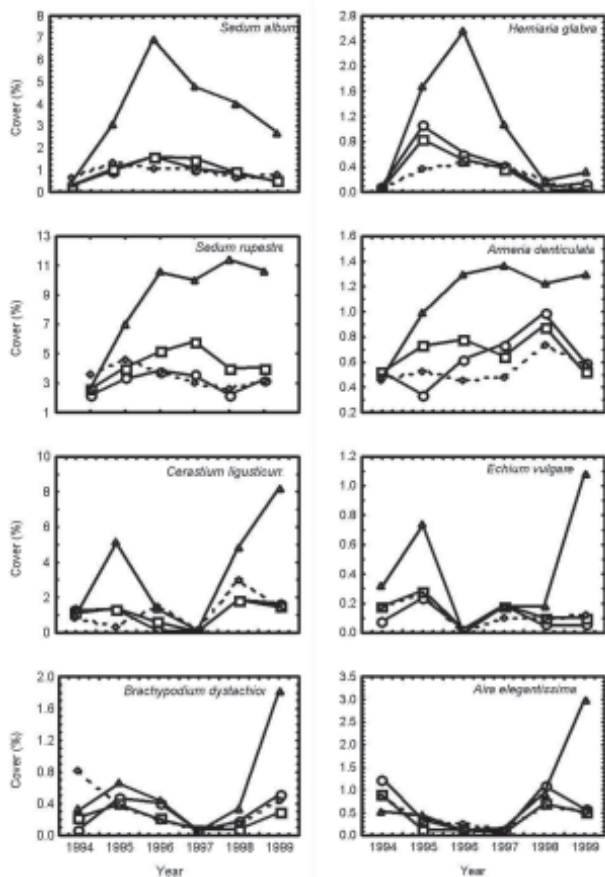
Figure 6. Mean cover values for the 16 most abundant species in the period 1994-1999. Circles and continuous line: control plots (0); squares and broken line: plots fertilized with nitrogen (N); diamonds and dotted line: plots fertilized with potassium (K); triangles and interrupted line: plots fertilized with phosphorus (P).

Figure 6 (cont.). Mean cover values for the 16 most abundant species in the period 1994-1999. Circles and continuous line: control plots (0); squares and broken line: plots fertilized with nitrogen (N); diamonds and dotted line: plots fertilized with potassium (K); triangles and interrupted line: plots fertilized with phosphorus (P).
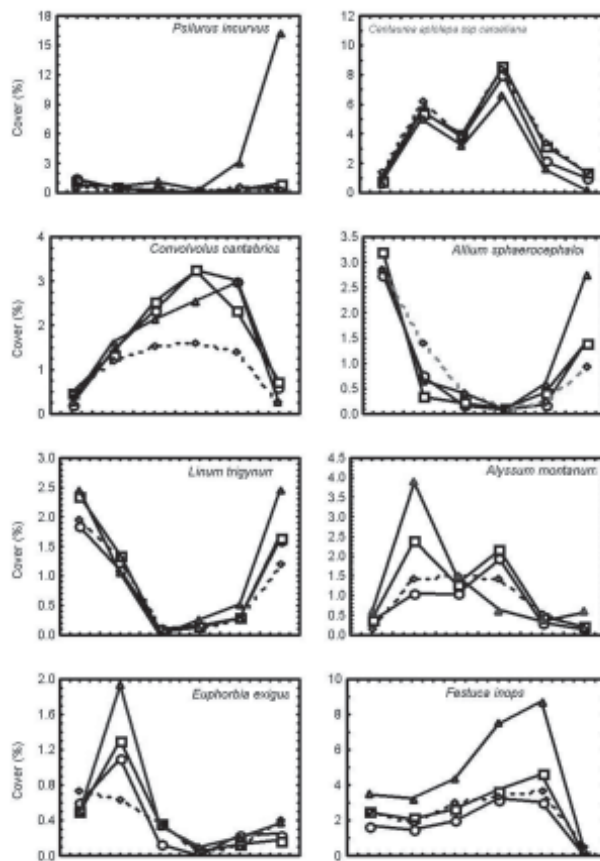
ter a period of 6 years, we did not observe any significant change in species composition and/or invasion by alien species: only species-richness fluctuations were observed, without any connection with treatments. It should be remarked, however, that the fertilization treatment applied by Chiarucci et al. (1998a) was more conspicuous compared to treatments used in the present work and this could have induced some changes in species richness. Other nutrient addition experiments on serpentine soil in Rhum and Keen of Hamar, Scotland, showed an increase in total ground cover and species richness, together with changes in species composition (Ferreira & Wormell, 1971; Looney & Proctor, 1989; Proctor & Nagy 1992; Slingsby 1991). Huenneke et al. (1990) reported a decrease in species richness and an invasion of alien species after soil enrichment with nitrogen and phosphorus in California serpentine grasslands. In summary, the effects of fertilization on species richness and species composition are likely to be variable in different serpentine grasslands and not so clear as those on cover and productivity. The effects of fertilization on species richness are likely to be dependent on the local species assemblage and the species pool capable to colonize serpentine habitat. A significant role might also been played by a local lack of plant propagules which may need of several years to allow the colonization of species from external sources.

Effects of climate

The main climatic effect on the serpentine plant communities was an positive relation of total vegetation cover and, thus, productivity (Chiarucci et al., 1999b), to the amount of rainfall of the whole period before sampling. This relation, although based only on six years of data is rather obvious in a xeric habitat such as the serpentine soil of Tuscany (Chiarucci et al., 1998c), were water supply is certainly a very important limiting factor. Chiarucci et al. (1998b; 1998c) observed how the xericity, due to slope exposure and acclivity, was a significant factor in controlling species composition and abundance. The variability of total plant cover observed as well as the changes of species abundances in the different years indicates marked fluctuations of community structure and diversity. As known for other types of vegetation (Grime 1990, Van der Maarel 1996), drought stresses may be the driving force for serpentine vegetation of Tuscany, reducing the cover of dominant plants and creating new niches in space and time to be occupied by different species.

The observed effects of climatic variables on species richness and diversity were lower than those on cover, but species richness and species diversity were likely to be negatively influenced by spring temperature, suggesting that warmer spring might cause local extinction of some species. The most abundant species (*Sedum rupe-*

stre, *S. album*, *Cerastium ligusticum*, *Centaurea aplolepa* ssp. *carueliana*, *Festuca inops*, *Convolvolus cantabrica*) showed different temporal responses, but their interpretation is rather difficult due to the relatively short duration of the experiment. Several studies reported that annual grasslands of regions with a Mediterranean-type climate positively respond to the total amount of precipitation as well as to the timing of rainfall (Grizzle & Allen, 1969; Murphy, 1970; Pitt & Heady, 1978; Hobbs & Mooney, 1991a, 1991b). Climatic effects on - mostly annual - plant communities were also reported for California serpentine grasslands (Hobbs & Mooney, 1991a; Armstrong & Huenneke, 1992). Hobbs and Mooney (1991a) found a relationship between the abundance of some species and annual rainfall amounts. However, longer series of data (Hobbs & Mooney, 1995) did not confirm the relationships found in experiments with a shorter time period. Therefore, interpretation of the climatic effects on species richness and species abundance remains difficult.

Inter-annual variations of total vegetation cover, species richness and species diversity indices demonstrated that these community characteristics strongly depend on the year of sampling mostly because the dominance of annual species. Therefore, comparison between sampling years should be performed with caution. The use of indices of species diversity, evenness and dominance, provided very few additional information with respect to the simple measure of total plant cover and species richness.

Conclusion

Fertilization experiment in serpentine vegetation showed that limited amount of phosphorus can strongly enhance total plant cover and thus community productivity without inducing significant changes in species richness and composition. Although these communities are mostly composed by annual species, the changes induced by the addition of phosphorus may persist for many years after the cessation fertilization. However only few species are able to maintain an higher abundance in the year following fertilization (*Sedum rupestre*,

Armeria denticulata), while some others show a decrease of abundance after an initial increase (*Sedum album* and *Herniaria glabra*) and some other species show an increase of cover some years after the cessation of fertilization (*Echium vulgare*, *Aira elegantissima*). Climatic effects on plant community structure reflect the positive relation known for Mediterranean habitats between rainfall and productivity. Species richness was found to be negatively related to spring temperature and positively related to spring rainfall suggesting that a mild and humid spring season may promote species establishment in these xeric habitat.

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