Vegetation Ecology and Conservation on Tuscan Ultramafic Soils

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I. Abstract

This article provides a review of studies concerning the floristics, vegetation description and ecology of the ultramafic (serpentine) soils of Tuscany, central Italy. After a concise history of geobotanical research on Tuscan ultramafic outcrops since the end of sixteenth century, the features of the flora are summarized. The most significant vegetation types are concisely described and their ecology discussed in the following section. The role of soil nickel toxicity in limiting vegetation development is reconsidered and appears less important than are drought and nutrient stress. Drought stress also has a special role during exceptionally dry summers, which can occasionally occur and significantly reduce vegetation structure by causing the local extinction of many late-successional species. Nutrient-addition experiments and permanent plot monitoring provided additional evidence supporting the drought and nutrient stress hypothesis. The last section of this article discusses the main threats to the conservation of the unique plant diversity of Tuscan ultramafic environments, the most significant of which are quarrying and pine plantations. Pine plantations, mostly established for soil amelioration and erosion control, determine not only the increase in vegetation cover and diversity but also a trend for serpentine endemic and rare species to disappear.

II. Introduction

Ultramafic outcrops in Italy are concentrated along the Alps and the Northern Apennines (Abbate et al., 1980). A large number of differently sized outcrops are located in Tuscany, central Italy, from the islands of Elba, Giglio and Gorgona, to the coastline, to the inland mountain chain of the Apennines (Fig. 1). The mainland outcrops are larger and more diverse. They are therefore considered more interesting from the botanical and ecological point of view than are the offshore islands. These outcrops are mostly formed by lherzolitic serpentinites, but gabbro and basalt are also widespread.

The first botanical investigations of ultramafic areas probably were in Tuscany, and it is here that the understanding of much of today's ultramafic plant ecology began. This was due in part to the long-established botanical studies at the University of Florence, where the first plant endemic to serpentine was identified and the phenomenon of metal hyperaccumulation first discovered.

In spite of the large number of studies, the only attempt at a comprehensive treatment was that of Vegnano Gambi (1992), which discussed ecophysiological problems related to soil metal toxicity and nickel hyperaccumulation. After centuries of geobotanical studies it appears timely to provide a comprehensive review of studies concerning the description and ecology of the vegetation of Tuscan ultramafics. This is the aim of the present article.

The first section of the article provides a historical synthesis of geobotanical studies. This is followed by a summary of the flora and a description of plant communities described for the Tuscan ultramafics in the second and third sections, respectively. The fourth section deals with the main factors related to vegetation ecology and dynamics. Section 5 summarizes recent work on nutrient-addition experiments and monitoring of permanent plots. Finally, problems related to conservation issues are discussed.

III. Notes on Historical Studies in Geobotany

The scientific literature on the flora of ultramafic outcrops of Tuscany dates back to the sixteenth century, when Andrea Cesalpino (1583) wrote about *Alyssum bertolonii,* "Quarta fruticosior, & brevior provenit in nudis saxosis, copiosa in Montacuto, juxta lapidem nigrum; quod multum Amianti nigri complectitur: in alia terra reperire non licet hanc herbam." Three centuries later the physician and botanist Gaspare Amidei from Volterra explored some ultramafic areas of Tuscany, collecting plants to make an herbarium, which is currently preserved at the Volterra Civic Library. He lectured on the ultramafic flora at the 3rd Congress of Italian Scientists (Amidei, 1841) and wrote an article in a local newspaper. He also wrote a still-unpublished manuscript on the subject (see Pichi Sermolli, 1948). Later, Teodor Caruel, author of the famous "Prodromo della Flora Toscana" (Caruel, 1860), made some interesting observations on the flora of Tuscan ultramafic soils. Caruel reported that several species were either preferential to or exclusive to ultramafic substrates. He also suggested that the soil features were the cause of the peculiar morphological features shown by many plants in these habitats (Caruel, 1867, 1871). In this period an international excursion was organized to Monte Ferrato, an ultramafic site near Prato, during the International Congress of Botany, held in Florence in 1874 (Atti del Congresso Internazionale Botanico, 1876).

In the first half of twentieth century other botanists from the University of Florence investigated the flora of Tuscan ultramafic areas. Pampanini (1912) published a floristic report on the small ultramafic outcrop of Montignoso; Adriano Fiori, the author of a well-known Flora of Italy (Fiori, 1923–1928), compared the flora of Monte Ferrato with that of the neighboring Calvana limestones (Fiori, 1914) and described the flora of the ultramafic outcrops in the
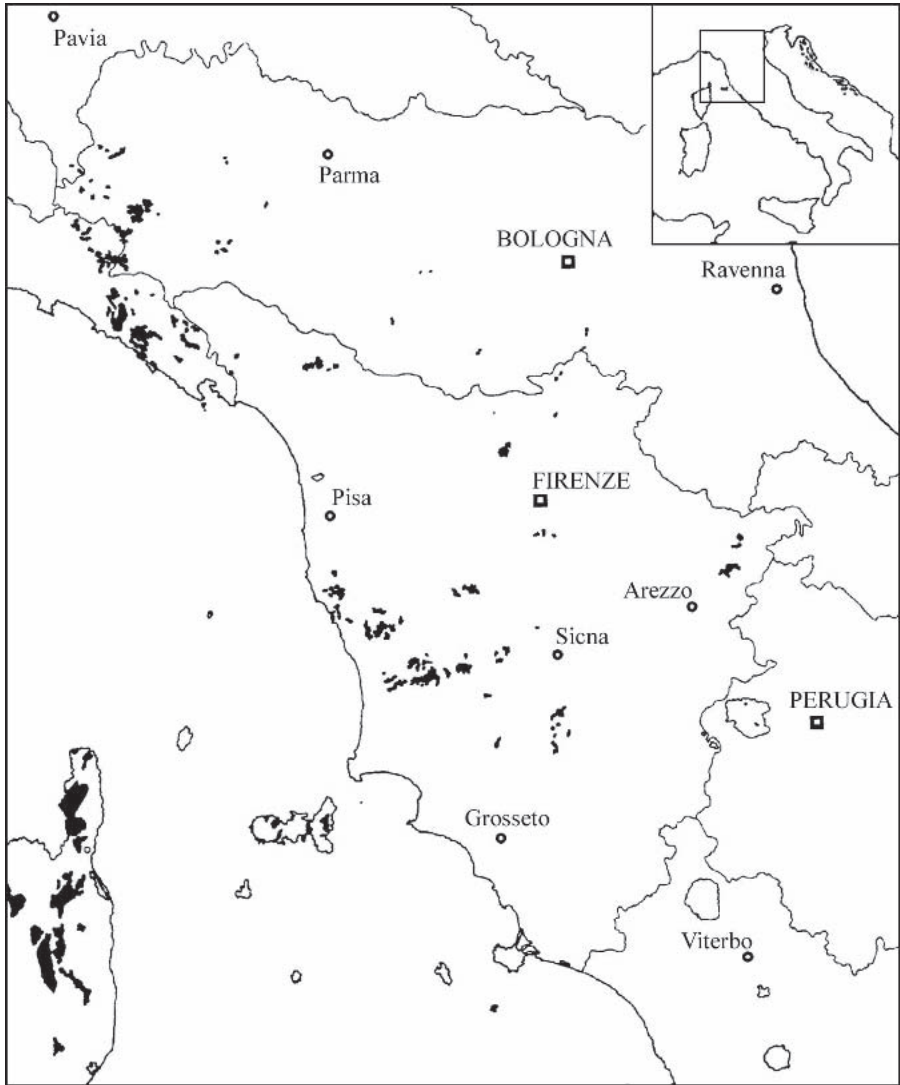
Fig. 1. Ultramafic outcrops of Tuscany, Italy, and surrounding areas.

Cecina Valley (Fiori, 1920). He also aimed to realize a "Flora of the Tuscan Serpentines" (Fiori, 1920), though he never succeeded. Some years later Albinia Messeri described the flora and vegetation of Monte Ferrato (Messeri, 1936); and Rodolfo Pichi Sermolli, the soil, flora and vegetation of the Upper Tiber Valley ultramafics (Pichi Sermolli, 1948). The article by Pichi Sermolli is still regarded as a classic of serpentine ecology. In 1940 Corti described the vegetation of ultramafics of Elba Island in a botanical excursion report; however, Elba has no serpentine endemics. During this period Sambo (1927, 1931) and Cengia Sambo (1937)

published floristic data on lichens and fungi of the Monte Ferrato. In 1934 the seventh international phytogeographical excursion was again on Monte Ferrato (Negri et al., 1934).

After World War II the plant ecology of Tuscan ultramafics was made known mainly by the work of Ornella Vergano Gambi and colleagues. The phenomenon of nickel hyperaccumulation by plants was discovered by Minguzzi and Vergnano (1948) in *Alyssum bertolonii,* the same plant species described as *lunaria quarta* by Andrea Cesalpino (1583). In the following years they carried out many studies on the ecophysiology of *A. bertolonii* and other serpentine plants in relation to soil metal content, with a special regard for nickel (for a review, see Vergnano Gambi, 1992). A few descriptive articles were also published on flora and vegetation during this period: floristic data on the Cecina Valley ultramafics (Vergnano, 1953) as well as short, descriptive reports on the bryophytes (Cortini Pedrotti, 1974), flora (Arrigoni, 1974) and vegetation (Corti, 1974) of Monte Ferrato. A phytosociological description of the garigues and grasslands of Monte Ferrato was published by Arrigoni et al. (1983). Some cytotaxonomical and chorological data of serpentine endemics were provided by Arrigoni et al. (1976, 1980). In two articles on element analysis in soils and plants, Sasse (1979a, 1979b) observed that the richest and closest vegetation types were related to soil with the lowest nickel content, but no data on vegetation were offered. A third international excursion was organized on Monte Ferrato during an OPTIMA meeting, held in Florence (Arrigoni et al., 1977).

In recent decades interest in geobotanical studies on Tuscan ultramafic areas has been renewed. New floristic data were compiled by Ansaldo et al. (1988) and Zocco Pisana and Tomei (1990) for the Livorno Hills and by Chiarucci et al. (1994) for the Siena province. Descriptive studies were published on the vegetation of the garigue plant communities growing over all outcrops (Chiarucci et al., 1995), on grasslands of the Upper Tiber Valley (Viciani et al., 2002) and on *Juniperus* scrub communities (Chiarucci et al., 1998b) growing over all outcrops. The vegetation dynamics at the Murlo site in Siena province were investigated by Chiarucci (1994). In recent years studies of the relationship between environment and vegetation have been carried out by researchers from the University of Siena. These studies specifically investigated the effects of pine plantations on natural plant communities (Chiarucci & De Dominicis, 1995; Chiarucci, 1996; Chiarucci et al., 1996) and the relationships between edaphic and physical properties of the site and vegetation structure and composition (Chiarucci et al., 1998a, 1998d, 2001). Manipulative studies, with nutrient additions to natural plant communities, have investigated the effects of nutrients on species diversity and productivity (Chiarucci et al., 1998a, 1999a, 1999b). Most recently, a checklist of all the plants reported from all the Tuscan ultramafics between 1841 and 1998 was published (Chiarucci & De Dominicis, 2001).

IV. Floristics

The checklist compiled by Chiarucci and De Dominicis (2001) consisted of 809 subgeneric taxa; i.e., 14.5% of the entire Italian flora. The families with the highest representation are listed in Table I. The relative importance of the families found in the Tuscan ultramafics is similar to that found on the ultramafics of northern Apennines (Ferrari et al., 1991). Analysis of the Raunkiaer life-form spectrum (Table II) shows that 40% of all flora consist of hemicryptophytes, roughly the same proportion as for the Tuscan and Italian floras (Pignatti, 1994). In comparison with the Northern Apennine ultramafics (Ferrari et al., 1991), there was a higher proportion of therophytes and a lower proportion of hemicryptophytes (Table II), possibly a reflection of the warmer and dryer climate of Tuscany (Chiarucci & De Dominicis, 2001).

Eleven serpentine endemic taxa are known from Tuscany (Table III). Among these, *Stipa etrusca* Moraldo and *Biscutella pichiana* Raff. ssp. *pichiana* were only recently described as

Table I

Richest families of the flora of ultramafic outcrops
in Tuscany

Family	Number of taxa	Percentage of the flora
Compositae	107	12.6
Graminaceae	99	11.6
Leguminosae	89	10.4
Caryophyllaceae	43	5.0
Rosaceae	42	4.9
Labiatae	38	4.5
Umbelliferae	28	3.3
Cruciferae	27	3.2
Orchidaceae	25	2.9
Cyperaceae	21	2.5
Liliaceae	21	2.5
Scrophulariaceae	20	2.3
Ranunculaceae	18	2.1

Source: Chiarucci & De Dominicis, 2001.

Table II

The life-form spectrum of the total flora recorded for Tuscan ultramafics, compared with
the life-form spectra of the Northern Apennine ultramafics (Ferrari et al., 1991),
the flora of Tuscany and the flora of Italy (Pignatti, 1994)

Life-form	Number of taxa	Percentage of the flora	Northern Apennine ultramafics (%)	Flora of Tuscany (%)	Flora of Italy (%)
Therophytes	222	27.4	17.7	30.7	25.1
Geophytes	98	12.2	10.3	14.1	12.1
Idrophytes	2	0.2	0.0	2.7	2.6
Hemicryptophytes	324	40.0	52.0	37.5	41.7
Chamaephytes	60	7.4	9.2	6.2	10.3
Phanerophytes	103	12.8	10.8	5.8	8.5
Total	809	100.0	100.0	100.0	100.0

autonomous taxa (Moraldo, 1986; Raffaelli & Fiesoli, 1993). Twelve taxa are considered lo-
cally serpentine preferential (Table III). Not much is known about the distribution of most of
these taxa; however, the single locality of *Stipa tirsa* Steven is known to be on the serpentine of
Upper Tiber Valley (Pichi Sermolli, 1948; Pignatti, 1982; Moraldo, 1986), where it is locally
endangered by pine afforestation (Chiarucci et al., 1996). Other interesting taxa found on Tuscan
serpentine are in need of more in-depth taxonomic investigations. Among these are a taxon of
Linum belonging to the *L.* gr. *alpinum,* an *Anthemis* close to *A. montana* L. (Chiarucci et al.,
1998d) and a *Sesleria* close to *S. insularis* Sommier (Chiarucci et al., 1998d; Rossi & Ubaldi,
1995). These taxa are likely to be restricted to ultramafic outcrops of Tuscany and are presently
known from only one (*Anthemis*) or two (*Linum* and *Sesleria*) sites.

Table III

Serpentine endemics and locally serpentine-preferential plants

Serpentine endemics
Alyssum bertolonii Desv.
Armeria denticulata (Bertol.) DC.
Asplenium cuneifolium Viv.
Biscutella pichiana Raff. ssp. *pichiana*
Centaurea aplolepa Moretti ssp. *carueliana* (Micheletti) Dostal
Euphorbia nicaeensis All. ssp. *prostrata* (Fiori) Arrigoni
Leucanthemum pachyphyllum Marchi et Illuminati
Minuartia laricifolia (L.) Sch. et Th. ssp. *ophiolithica* Pignatti
Stachys recta L. ssp. *serpentini* (Fiori) Arrigoni
Stipa etrusca Moraldo
Thymus acicularis W. et K. var. *ophioliticus* Lacaita

Locally serpentine-preferential plants
Artemisia saxatilis W. et K.
Euphorbia spinosa L. ssp. *spinosa*
Festuca inops De Not.
Festuca robustifolia Mgf.-Dbg.
Genista januensis Viv.
Iris lutescens Lam.
Notholaena marantae (L.) Domin ssp. *marantae*
Onosma echioides L.
Plantago holosteum Scop.
Silene paradoxa L.
Stipa tirsa Steven
Trinia glauca (L.) Dumort. ssp. *glauca*

V. Vegetation Structure and Composition

A. GARIGUES AND GRASSLANDS

Open vegetation types, mainly garigues and steppe grasslands, are the habitat of most serpentine endemics and rare species. Garigues, on shallow soils, were first described on Monte Ferrato by Messeri (1936) as "vegetation of stony grounds." Later Pichi Sermolli (1948) described this vegetation type, in the Upper Tiber Valley, as an "*Alyssum bertolonii* chamaephytic community." The relevés of these authors, sampled by the Raunkiaer method, were used by Ernst (1974) to describe the association *Alyssetum bertolonii* as belonging to the class *Violetaea calaminariae*. Arrigoni et al. (1983) remarked that Ernst's table gave no precise indication of the relevés taken from the original data, thus preventing lectotypification of the name (Art. 37 of the C.P.N.; Barkman et al., 1986), and that Ernst's unclear taxonomic interpretation of some critical species groups, such as *Festuca ovina* L. s.l., *Euphorbia nicaeensis* All. s.l., *Centaurea paniculata* L. s.l. and *Stachys recta* L. s.l. rendered it a useless syntaxon. These authors proceeded, therefore, to describe the same vegetation type from Monte Ferrato as *Armerio-Alyssetum bertolonii*. This association was later found on all of the main ultramafic outcrops in Tuscany, and two subassociations were recognized: *typicum,* in inland areas, and *euphorbietosum spinosae,* in areas closer to the coast and the southernmost areas (Chiarucci et al., 1995). Typical features of the garigue plant communities are: sparse plant cover (20–60%), low species richness, floristic homogeneity and the presence of several endemic and rare species (Chiarucci et al., 1995). Similar vegetation types, with floristic differences mostly due to endemic species, are

also known from the ultramafic areas of Liguria (Furrer & Hofmann, 1969; Nowak, 1987; Mariotti, 1994) and Emilia-Romagna (Pignatti & Pignatti, 1977).

On slightly more developed soil the chamaephytic vegetation of garigues may develop into steppe grasslands. Plant cover is higher, and the most abundant species are grasses, such as *Festuca inops, F. robustifolia, Bromus erectus, Koeleria splendens, Danthonia alpina,* and sedges, such as *Carex humilis*. These steppes have been reported in almost all of the Tuscan ultramafic areas, with differences in the dominant species and floristic composition, but they are more frequent in the inland sites: Monte Ferrato (Messeri, 1936; Arrigoni et al., 1983; Chiarucci et al., 1998c, 1998d) and the Upper Tiber Valley (Pichi Sermolli, 1948; Chiarucci et al., 1996, 1998d; Viciani et al., 2002). *Festuca robustifolia* and *F. inops* usually dominate in the less developed soils, whereas *Bromus erectus* and *Danthonia alpina* dominate in the more developed ones (Messeri, 1936; Pichi Sermolli, 1948; Chiarucci et al., 1998c, 1998d). In the Upper Tiber Valley Viciani et al. (2002) described these grasslands as a vegetation type exclusive to ultramafic substrates, namely the *Festuco robustifoliae–Caricetum humilis*. These grasslands may be dominated locally by *Stipa etrusca,* a recently described species endemic to Tuscan and Emilian ultramafics and to some volcanic soils of northern Latium (Moraldo, 1986). In some Upper Tiber Valley sites these grasslands are dominated by *Stipa tirsa (*Pichi Sermolli, 1948; Chiarucci et al., 1996; Viciani et al., 2002), a Euro-Siberian species found in only a few places in Italy. Pignatti (1982) reported the Upper Tiber Valley as its only Italian locality, while Moraldo (1986) stated that it grew in a few places in Italy but is abundant only in the Upper Tiber Valley ultramafic and a site in northern Italy. In some situations, with more organic matter or after burning, *Brachypodium rupestre* may form dense clumps within these grasslands, generally associated with very low species richness (Chiarucci et al., 1998c).

In the coastal areas, such as the Cecina Valley and Livorno Hills, similar grasslands can locally be found, where communities dominated by chamaephytic species, such as *Euphorbia spinosa,* are more abundant than true grasses (Chiarucci et al., 1995). Compared with the garigues, grasslands have fewer endemics and more central European species (Arrigoni et al., 1983; Chiarucci et al., 1995, 1998c, 1998d).

B. SCRUB AND WOODS

Unlike garigues, which are floristically very homogeneous on all outcrops, woody plant communities are more diverse, in relation to altitude and distance from the sea (Chiarucci et al., 1998d). Messeri (1936) provided the first complete description of woodland communities in the Monte Ferrato area. She described woodlands dominated by *Pinus pinaster, Quercus pubescens, Q. ilex* and *Q. cerris,* located in "stations with sufficiently deep soil." Well-structured woodlands, with a rich shrub layer of *Erica scoparia, Calluna vulgaris, Ulex europaeus, Genista pilosa* and other species, were, however, found mainly on gabbro. Pichi Sermolli (1948) reported *Juniperus oxycedrus* ssp. *oxycedrus* and *Erica scoparia* scrub communities and woodlands dominated by *Quercus pubescens* and *Q. cerris* and by *Fagus sylvatica* in the Upper Tiber Valley. On pure serpentinite, however, woodlands occur only in areas close to lithological contacts with limestone or other substrata. Pichi Sermolli (1948) observed that woodlands do not develop directly from typical ultramafic plant communities but by limited colonization of marginal areas by woody species from nearby sites. On soils originating from gabbro, scrub and woodlands similar to those growing on serpentinite are much more common. Chestnut woodlands were also reported from mixed soils originating from serpentinite, gabbro and diabase.

Chiarucci et al. (1998d) suggested that the scrub communities dominated by *Juniperus oxycedrus* ssp. *oxycedrus* may be the most developed vegetation stage on xeric slopes of the

Mediterranean ultramafic outcrops. These scrub communities may be sparse within garigues and grasslands or dense and with the presence of broad-leaved woodland species. The more typical aspect of this vegetation type has recently been described as a new association, named *Carici humilis–Juniperetum oxycedri* (Chiarucci et al., 1998b). The successional dynamics of these scrub communities toward closed maquis and woodland communities is prevented by nutrient deficiency and periodic reversions caused by stress factors such as extreme drought (Chiarucci et al., 1998d).

Where the environmental conditions are less harsh and drought stresses less frequent, the juniper communities can develop into broad-leaved maquis and woodland. Broad-leaved ever-green maquis, belonging to the *Viburno–Quercetum ilicis ericetosum,* have been reported on ultramafic soils, originating mainly from serpentinites, in the Livorno Hills (Marchiori & Tornadore Marchiori, 1977), the Murlo area (Chiarucci, 1994) and the Cecina Valley (Chiarucci et al., 1998d). Evergreen woods, with a structure determined by frequent cutting and a near absence of deciduous species, typically belong to this syntaxon on other soil types (Braun Blanquet, 1952). More developed and structured woodlands in the Murlo area have been ascribed to the *Viburno–Quercetum ilicis ornetosum* (Chiarucci, 1994). Because of their species composition, almost entirely evergreen species, these woodlands contrast with other *Quercus ilex* woodlands of this part of Tuscany, which have a mixture of evergreen and deciduous species (De Dominicis, 1973), being more similar to *Q. ilex* woodlands in coastal areas (Pignatti & Pignatti, 1968; De Dominicis & Barluzzi, 1983). Similar woodlands have also been reported for the Cecina Valley and the Livorno Hills (Chiarucci et al., 1998d).

C. CONIFER PLANTATIONS

Although natural woodlands can be found (Messeri, 1936; Pichi Sermolli, 1948; Chiarucci et al., 1998d), the most widespread woodlands on Tuscan ultramafics were conifer plantations. Because of their low productivity, ultramafic soils of Tuscany are frequently planted with coni-fers, mainly pines (*Pinus pinaster, P. pinea* and *P. nigra*). Pine woodlands originating from these plantations are typically low and scattered (Arrigoni et al., 1983; Chiarucci & De Dominicis, 1995), mainly due to soil nutritional deficiencies (Angelone et al., 1993; Vaselli et al., 1993). The effects of pine plantations on natural vegetation have only recently been investigated. In the shallow soils of Pievescola it was found that pine plantations strongly affect the natural plant communities, leading to an increase in total plant cover and species diversity, with a higher number of species showing intermediate abundance (Fig. 2). However, pine plantations caused the disappearance of some endemics and the spread of many alien species from sur-rounding areas (Chiarucci & De Dominicis, 1995; Chiarucci, 1996). The vegetation, originally a garigue with low ground cover, developed into a grassland dominated by *Bromus erectus, Festuca robustifolia* and *Danthonia alpina,* resembling some natural grasslands, with species diversity higher than that in garigues. Shrub species were also promoted by pine canopy, and successional dynamics toward a woodland community is likely. The disappearance of the less competitive species, typical of ultramafic soils, and the development of structured, species-rich grassland, less dependent on soil type, are closely related to the formation of an organic soil layer. Pine cover has a positive influence on soil genesis, providing protection against erosion and supplying organic matter that binds soil particles. Chiarucci (1996) hypothesized that an increase in nutrient input, mainly nitrogen, under tree cover may also be due to the intercepting action of the tree canopies with respect to dry deposition (see, e.g., Van Breemen & Van Dijk, 1988). Similar changes were observed in the pinewood understory of Monte Ferrato (Chiarucci et al., 1998c) and the Upper Tiber Valley (Chiarucci et al., 1996, 2001).
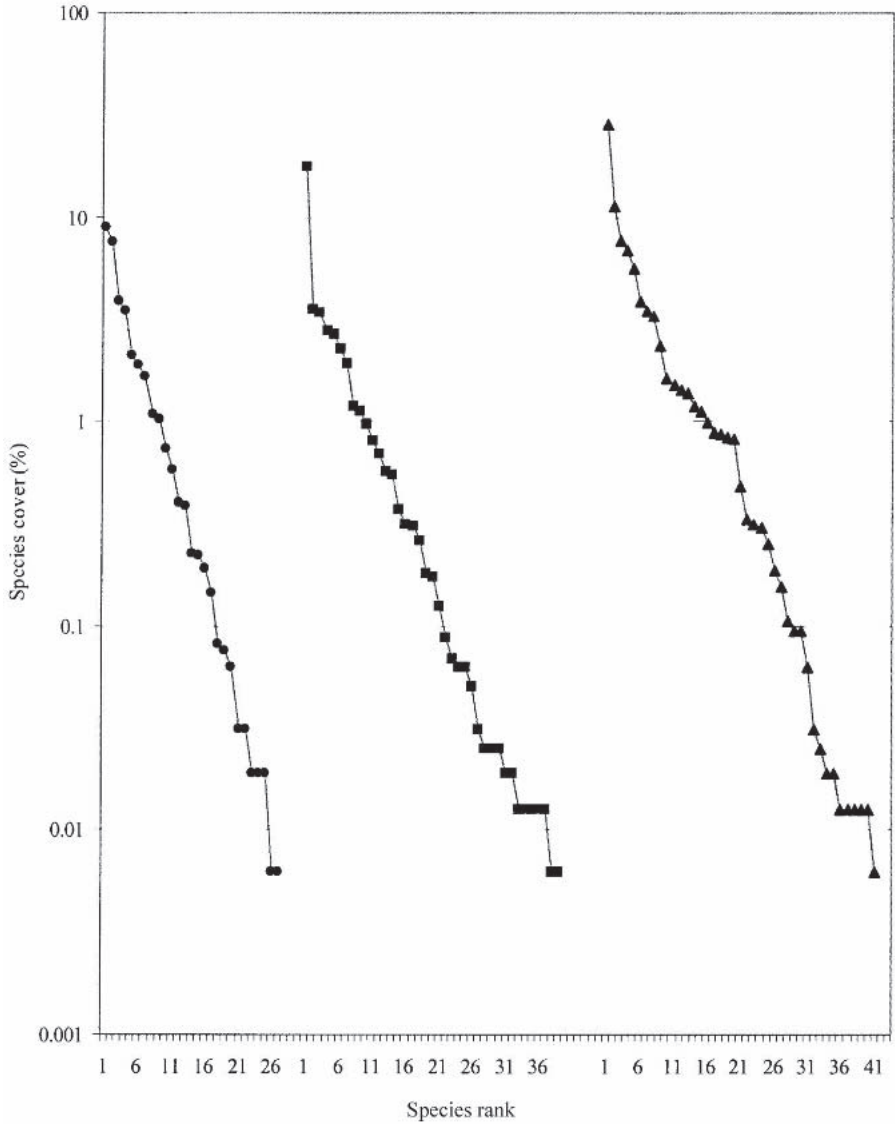
Fig. 2. Relative distributions of species abundance in natural garigue vegetation (left curve, circles), in sparse pine plantations (center curve, squares) and dense pine plantations (right curve, triangles).

VI. Environmental Factors Associated with Vegetation Dynamics

Recent articles (Chiarucci et al., 1998c, 1998d, 2001) indicate that the exchangeable fraction of metals is higher in the soil under the more developed and structured communities, both in natural (maquis and woodland) and anthropogenic (pine plantation) habitats, suggesting that soil metal content is not the most important limiting factor for the vegetation. For example, the
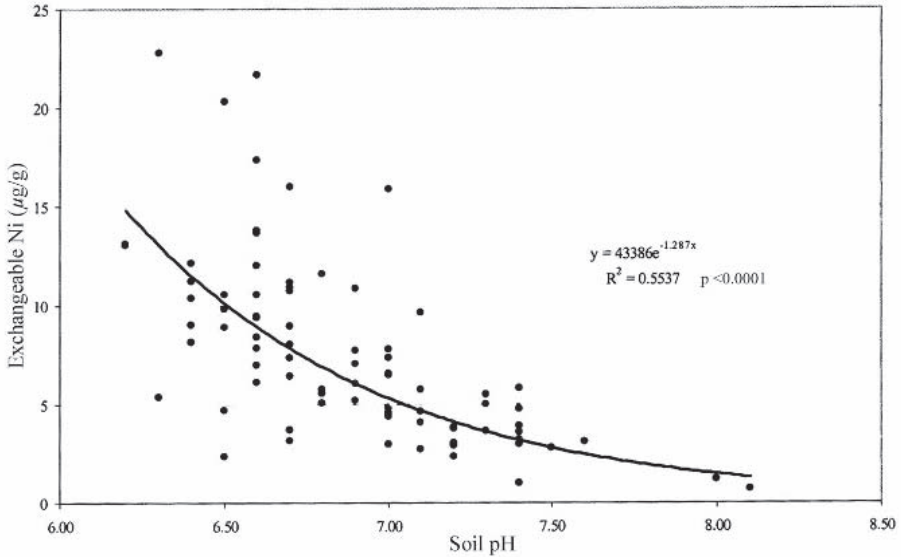
The chart shows data with the equation:

$$y = 43386e^{-1.287x}$$
$$R^2 = 0.5537 \quad p < 0.0001$$

with axes Exchangeable Ni (μg/g) on the vertical axis and Soil pH on the horizontal axis.

Fig. 3. Exchangeable nickel concentration in the soil (μg g^{-1}) as a function of soil pH. Data from 80 plots in different ultramafic areas of Tuscany sampled by Chiarucci et al. (1998d).

soluble fraction of chromium is generally too small to affect vegetation (Pandolfini & Pancaro, 1992; Chiarucci et al., 1998c, 1998d, 2001). The increased availability of metals in the soil under the more developed vegetation types may be a direct consequence of the lower pH in these areas (Robinson et al., 1996), as shown in Figure 3. Closed woody vegetation is likely to lower the soil pH, as locally moister conditions increase humic decay acidifying the soil. This in turn induces a higher availability of metals.

Recent pedological (Angelone et al., 1991, 1993) and vegetation (Chiarucci et al., 1998c, 1998d, 2001) studies contradict the long-held assumption that metal content is the most impor- tant limiting factor in Tuscan ultramafic soils. In contrast to previous studies, the importance of the metal fraction available to plants rather than the total metal concentrations was emphasized. Other authors have made similar observations in well-studied serpentine sites. Carter et al. (1987) reported that nickel was not the cause of the low fertility of serpentine soils in the Keen of Hamar, Shetland Islands. Kruckeberg (1992) did not find any evidence that cobalt, chro- mium, 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 toxicity likely to reduce plant growth. Proctor and Nagy's (1992) review suggested that many assump- tions about the role of 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 limiting factors for the vegetation of Tuscan ultramafic soils appears to be drought stress due to topographical position. Water stress, together with soil nutritional deficiencies, constantly limit vegetation development. In both Mediterranean and inland sites, the annual solar radiation was found to be significantly higher in juniper scrub communities, a relatively undisturbed vegetation type where the serpentine endemics grow, than in sites with a proper woodland vegetation (Chiarucci et al., 1998c, 1998d). Juniper scrub communities, when sufficiently dense, can be colonized by many forest species; i.e., evergreen
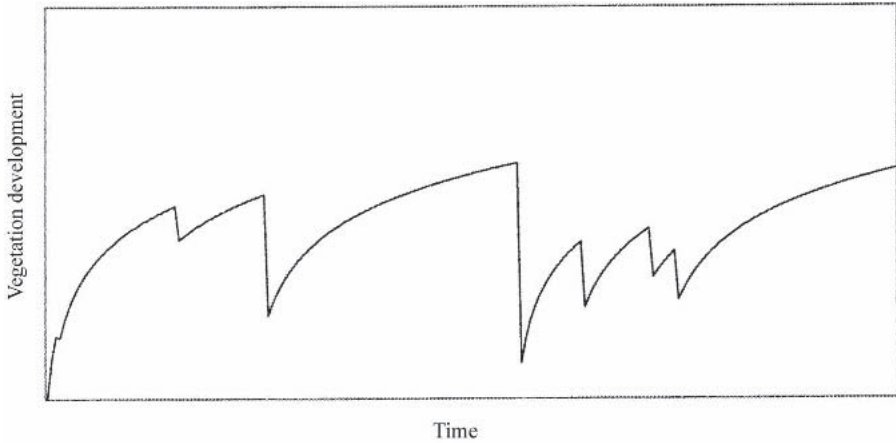
Fig. 4. Scheme of the "pulsating dynamics model" proposed by Chiarucci et al. (1998d), according to which vegetation development is occasionally interrupted by exceptional drought stresses.

species such as *Quercus ilex, Phillyrea latifolia, Arbutus unedo* and *Rhamnus alaternus* in Mediterranean sites (Chiarucci et al., 1998d) and deciduous species such as *Fraxinus ornus* and *Quercus pubescens* in inland sites (Messeri, 1936; Pichi Sermolli, 1948; Chiarucci et al., 1998c, 1998d). This development of more structured woody communities improves soil structure and fertility, thus allowing better plant growth through positive feedback. Natural dynamics toward more developed vegetation types would lead to the disappearance of the endemic species, linked to the less evolved soils, and the spread of the more competitive forest species. However, occasional periodic droughts and other exceptional stresses (e.g., fire) may kill off forest plant species, creating gaps in the juniper canopies, which can be colonized by xerophile and heliophile plants, such as the serpentine endemics, interrupting vegetation dynamics and promoting soil erosion. This "pulsating dynamics model" (Fig. 4) is likely to represent the driving force (Grime, 1990; Van der Maarel, 1996) behind the permanence of pioneer vegetation types, in which *Alyssum bertolonii* and the other serpentine endemic and rare species may persist within a patchy landscape dominated by juniper scrub communities (Chiarucci et al., 1998d).

In addition, the garigues were found to be located on soils with the lowest concentrations of potentially toxic metals and in sites with a wide range of physical conditions (Chiarucci et al., 1998d). The apparent lack of correlation between environmental limiting factors and garigues suggests that their commonness has been partially favored by human disturbance through destruction of more developed vegetation types, such as the juniper scrub communities and the evergreen maquis. For the serpentine soils of the Keen of Hamar, where rainfall is distributed throughout the year, Carter et al. (1987) suggested that a summer drought of seven or more consecutive days, which happen on average once every three to five years, may exhaust the soil water reserve. This dry period is considered one of the most significant causes of retarded plant colonization and vegetation succession. In Tuscany, located in the middle of the Mediterranean area, summer droughts may be much longer and are likely to have significant effects on vegetation dynamics. Permanent plots have been set up to test this hypothesis (periodic drought stress). The exceptional drought of summer 1998 has already provided some support for this hypothesis. A dieback of many xerophile shrubs, such as *Cistus salvifolius* and *C. monspeliensis,*
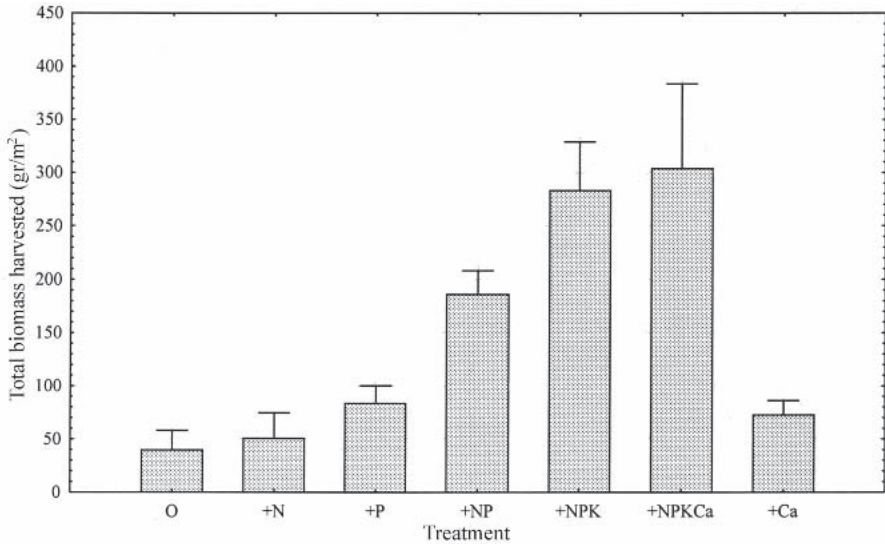
Fig. 5. Total biomass harvested per 1m² plot (geometric mean ± standard deviation) after two years of nutrient addition in the Murlo area by Chiarucci et al. (1999a).

as well as of branches of taller shrubs, such as *Erica scoparia, Juniperus oxycedrus* ssp. *oxycedrus* and *Arbutus unedo,* was observed (Chiarucci, unpubl. data).

VII. Fertilization Experiments and Monitoring of Permanent Plots

The evidence that soil metal toxicity is not the most important limiting factor for the vegetation of Tuscan ultramafics has been reenforced by recent nutrient-addition experiments (Chiarucci et al., 1998a, 1999a, 1999b). The addition of small amounts of nitrogen, phosphorus and potassium to a garigue plant community induced a significant increase in ground cover (Chiarucci et al., 1998a) and biomass production (Chiarucci et al., 1999a) after two years (Fig. 5). A higher nutrient availability has also been reported to alleviate the effects of drought (Grime, 1990). Proctor and 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; the addition of calcium, alone or with nitrogen, phosphorus and potassium (NPK), led to a nonsignificant increase (Fig. 5) of cover and biomass, compared with the control plots and the NPK-added plots (Chiarucci et al., 1999a). This is likely to be due to the fact that in these soils the Mg/Ca quotient is relatively low, averaging from 1.5 to 3.0 (Chiarucci et al., 1999a). The addition of fertilizer favored the growth of species already present within the plots, rather than colonization by other species, as observed in other ultramafic areas following nutrient addition; e.g., California (Huenneke et al., 1990). In fact, in an analysis of three years of cover data of fertilized plots, Chiarucci et al. (1998a) showed that nutrient addition significantly improved the cover of the species already present without any significant colonization. The data from the fertilization experiment by Chiarucci et al (1998a, 1999a) were employed to study the use of *Alyssum bertolonii* for
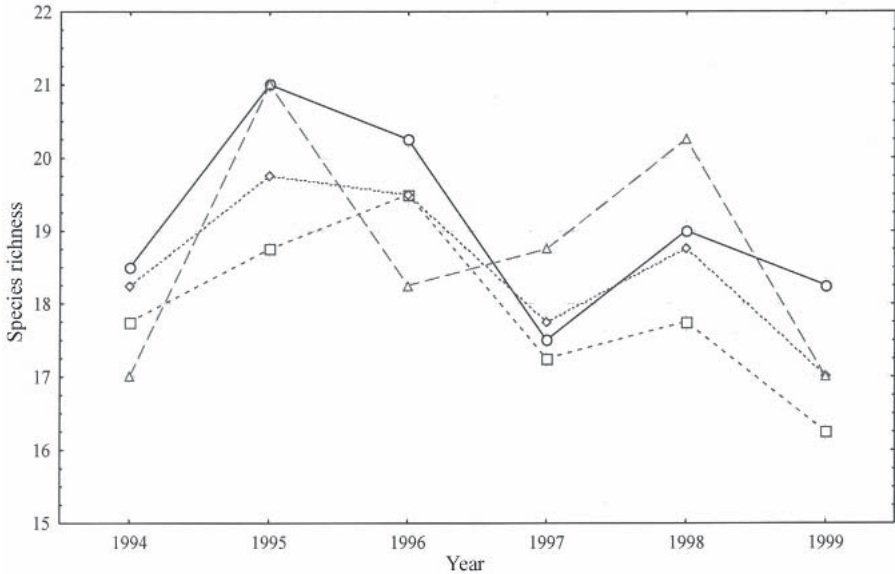
Fig. 6. Five years of data on species richness per 4m² plots (mean value of four plots) in the nutrient-addition experiment at Pievescola, Italy. Nutrients were added in the autumn of 1994 and of 1995, and species richness was sampled every spring. Species richness was linked more to climatic variation than to fertilization (Chiarucci, unpubl. data). *Key:* circles = control plots; squares = plots fertilized with potassium; diamonds = plots fertilized with nitrogen; triangles = plots fertilized with phosphorus.

extracting nickel from serpentine soils, with phytoming and phytoremediation aims (Robinson et al., 1997; Brooks et al., 1998, 2002).

In another experiment performed with single nutrient treatments of nitrogen, phosphorus and potassium, Chiarucci (unpubl. data) found that phosphorus was the main limiting factor for this Tuscan ultramafic vegetation. Treatments were performed for two years, during which time total plant cover continued to increase: from about 20% before nutrient addition to more than 45% two years after the cessation of treatments. Species richness in this study was found to be related more to interannual climatic variations than to nutrient addition (Fig. 6), confirming the importance of drought in the structuring of serpentine plant communities. Increase of plant cover in the years after the cessation of nutrient addition similar to those found in this study have also been reported for other serpentine sites, such as the Keen of Hamar (Carter et al., 1988; Slingsby, 1991).

VIII. Conservation

The main threats to the conservation of ultramafic environments of Tuscany are quarrying, conifer plantations and eutrophication. Since ultramafic rocks, especially serpentinites, represent inert materials important in certain industrial processes, they are often quarried. Ultramafic rocks are also used as building material: Monte Ferrato serpentinite is a prestigious marble, known as "verde e nero di Prato" (green and black marble of Prato), widely used in decorative elements in Tuscan buildings and monuments. Although a few large quarries are still active, quarrying was once more widespread, and smaller quarries are presently worked only

sporadically or have been abandoned. The problem was recognized in the 1970s, in a motion proposed at the second OPTIMA Congress in 1977 (Anonymous, 1979).

The greatest threat to biodiversity conservation in Tuscan ultramafics, however, is presently soil eutrophication due to the increased nutrient content of rainfall and the effects of tree cover in afforestation. Vegetation changes similar to those reported by Chiarucci & De Dominicis (1995), Chiarucci (1996) and Chiarucci et al. (1996), have been described by Carter et al. (1987) at Keen of Hamar as a consequence of eutrophication from winter feeding of stock. Rare species totally disappeared, and closed grassland dominated by *Agrostis* spp. and *Festuca* spp. developed. The cessation of nutrient input did not lead to disappearance of the grassland and reversion to original vegetation, which was achieved only by mechanical removal of the established vegetation and the soil that had developed (Slingsby, 1991).

The survival of the typical ultramafic vegetation of Tuscany is seriously threatened in areas with intense afforestation. Artificial removal of the pines would probably not sufficiently modify the established vegetation because of the organic matter accumulated and the structure of vegetation that developed. In many sites, to enable serpentine plants to spread again it is probably necessary to remove the organic layer of soil together with the pines (Chiarucci & De Dominicis, 1995). Indeed, conservation of the endemic ultramafic vegetation of Tuscany calls for a general examination of the interests connected with pinewood forestry and biodiversity conservation. If we wish to conserve this typical vegetation, ultramafic areas must not be planted for soil protection or timber production, and some areas should be rehabilitated to the original vegetation types.

In conclusion, it should be noted that changes are under way. Parts of the ultramafic habitat of Tuscany are presently protected as nature reserves, and some projects are undergoing restoration of degraded habitat: In the Upper Tiber Valley a project funded by the EU Life program was recently promoted to restore a *Stipa tirsa* grassland in which pines had been planted in preceding decades (see Chiarucci et al., 2001).

IX. Acknowledgments

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