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Understory vegetation as a useful predictor of natural regeneration and canopy dynamics in *Pinus sylvestris* forests in Italy

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Abstract

The relations between understory vegetation, canopy characteristics and natural regeneration have been studied in natural Scots pine forests growing in sub-Mediterranean conditions in Italy. Multivariate ordination techniques (detrended correspondence analysis, DCA, and detrended canonical correspondence analysis, DCCA) have been applied to extract vegetation gradients. The first four DCA axes accounted for 41% of the total variation in vegetation data and DCA ordination patterns have been interpreted by the variability of forest stands, ranging from pioneer pine communities to closed pine stands mixed with hardwood species. Characteristic indicator values (CIVs), computed by understory species abundance using the Ellenberg's species scores, have been tentatively used as estimators of environmental variability. Relating vegetation gradients extracted by DCA to CIVs allowed further interpretation of the multivariate ordination patterns. Geographic and edaphic factors had only a minor effect on plant communities in the present study. The competition exerted in mixed stands by hardwood species seems to be the main limiting factor for Scots pine recruitment in the study area. Multivariate synthetic variable and CIVs were found to predict a large proportion of variation in Scots pine recruitment. The application of CIVs for predicting ecological meaningful conditions and their use as a tool for management decisions is discussed.

Keywords: Scots pine, understory vegetation, recruitment, characteristic indicator values, ordination techniques.

Résumé

Les relations entre la végétation basse, les caractéristiques de la canopée et la régénération naturelle ont été étudiées dans les forêts naturelles à pin sylvestre sous climat sub-méditerranéen en Italie. Des techniques d'ordination multivariées (analyse de correspondance détendancée, DCA, et analyse de correspondance canonique détendancée, DCCA) ont été appliquées pour extraire des gradients de végétation. Les quatre premiers axes de la DCA rendent compte de 41 % de la variation totale des données de la végétation et les patrons d'ordination de la DCA ont été interprétés par la variabilité des parcelles forestières qui vont de communautés pionnières à des parcelles fermées où les pins sont mêlés à des espèces à bois dur. Les valeurs indicatrices caractéristiques (CIVs) calculées par abondance d'espèces de sous-bois à l'aide des échelles de notation d'espèces d'Ellenberg, ont été utilisées, à titre d'essai, comme estimateurs de la variabilité environnementale. Relier les gradients de végétation extraits par la DCA aux CIVs a permis d'interpréter plus avant les patrons d'ordination multivariés. Les facteurs géographiques et édaphiques n'ont qu'un effet mineur sur les communautés végétales dans cette étude. La compétition exercée dans les parcelles mixtes par les espèces à bois dur semble être le principal facteur limitant le recrutement de pins sylvestres dans la zone d'étude. Des variables synthétiques multivariées et les CIVs prédisent une grande proportion de la variation du recrutement de pins sylvestres. L'application de CIVs à la prédiction de conditions écologiques significatives et leur utilisation comme outil de décision pour la gestion sont discutées.

INTRODUCTION

Patterns of distribution of plant species in the understory layer of forests have been considered to reflect differences in ecological conditions, affecting the natural regeneration of canopy species and influencing long-term forest dynamics (WHITTAKER, 1967). On the other hand, the natural regeneration of forest communities is a complex process driven by several factors, depending on ecological, demographic, historical and stochastic events (SILVERTOWN, 1987).

For a long time attempts have been made to establish relationships between understory vegetation and forest stands characteristics (CAJANDER, 1926). FENAROLI (1933) correlated growing patterns of spruce and pine forests in the Alps with their flora. Quantitative understory vegetation analysis can highlight environmental gradients in forest ecosystems (GOLDEN, 1979) and it is potentially useful for monitoring the effects of management practices (KENT & COKER, 1992). Indeed, the quantitative analysis of understorey vegetation plays an important role in the site classification systems of Finnish forests (ILVESSALO & ILVESSALO, 1975; NIEPPOLA & CARLETON, 1991; NIEPPOLA, 1993*a*; LAHTI, 1995) and the evaluation of forest phytosociological types was proposed as an important tool for taking silvicultural decisions in Italy (MAGINI, 1953; HOFMANN, 1982). Application of vegetation science to forestry has been extensively discussed by MIKOLA (1982).

Several methods can be used to interpret vegetation changes, relating them to ecosystem and landscape variations (WHITTAKER, 1967, 1978; ORLOCI, 1978; JONGMAN *et al.*, 1987; LEGENDRE & FORTIN, 1989). Multivariate techniques, such as principal component analysis, detrended correspondence analysis (DCA) (HILL & GAUCH, 1980) and detrended canonical correspondence analysis (DCCA) (TER BRAAK, 1986, 1988) have been applied as ordination techniques for the analysis of vegetation (TER BRAAK & PRENTICE, 1988). Methods have also been proposed to describe environmental changes quantitatively in terms of vegetation characteristics: by attributing ecological values to plant species (ELLENBERG, 1988; ELLENBERG *et al.*, 1991), understory vegetation may be used as an environmental indicator (PERSSON, 1981). The reliability of CIVs in predicting meaningful environmental variation has been demonstrated in several European countries including Italy (CELESTI GRAPOW *et al.*, 1993; see also DIEKMANN, 1995 and citation therein).

The objective of this work was to interpret the relationships between understory vegetation, stand characteristics, recruitment processes, and environmental variables in natural Scots pine stands (*Pinus sylvestris* L.) growing in sub-Mediterranean conditions in Italy. DCA and DCCA have been applied to extract vegetation and environmental gradients, and ELLENBERG's characteristic indicator values (CIVs) (ELLENBERG, 1988) have been used as estimators of environmental variability.

In the study area Scots pine forms pioneer communities on eroded hillsides and abandoned fields, or it is mixed with hardwood species in closed forest stands. As additional aim, we tried answering the following question: are the mixed stands evolving from Scots pine pioneer communities, or is the natural regeneration in these stands balanced between the different species? To this purpose, the forest recruitment process has been compared between different stand types – previously identified by ordination techniques – and multiple regression models for predicting Scots pine regeneration have been evaluated, using stand structural characteristics, CIVs and multivariate vegetation parameters as independent variables.

MATERIALS AND METHODS

The study area

The study was performed in the province of Parma (northern Italy, Lat. 44° 27′ - 44° 38′ N, Long. 10° 08′ - 10° 17′ E, Alt. 350-750 m. a.s.l.). In the region the mean annual temperature varies between 7.5 and 11°C and annual precipitation is between 900 and 1200 mm, with peaks in spring and autumn. Dominant bedrocks are allochtonous deposits of thinly bedded sandstone shales and clay (flysh) or Pliocenic clays. Soils show sub-alkaline reaction and are often prone to erosion. In the study area Scots pine grows at the southern limit of its natural range, with relic populations (small nuclei) spread across a wide area (AGOSTINI, 1955; JEDLOWSKI & MINERBI, 1967; BORGHETTI & FRAZZI, 1986), establishing mainly within sub-Mediterranean mixed oak woods (*Quercion pubescenti-petraeae*) or in xerothermic mixed broad-leaved woods on limestone (*Orno-ostryon*) (UBALDI, 1980). The most abundant species in the canopy layer are *Quercus pubescens, Fraxinus ornus* and *Ostrya carpinifolia.* Other common species are *Corylus avellana, Acer opulifolium, Acer campestris, Prunus avium, Sorbus torminalis, Sorbus domestica* and rarely *Quercus cerris* and *Fagus sylvatica.* Shrubs are often represented by *Crataegus monogyna, Juniperus communis, Prunus spinosa, Viburnum lantana,* and rarely by *Salix pentandra* and *Spartium junceum.*

Sampling procedures

After a detailed survey of the natural Scots pine vegetation nuclei growing in the area (BORGHETTI & FRAZZI, 1986), 18 major forest stands spanning different ecological conditions were identified, covering nearly all the Scots pine populations growing in the area. In each stand one circular plot (plot surface = 1256 m^2) was located at random. In each plot: i) total and single species density (trees/ha) and basal area (m^2/ha) were determined; ii) the cover of plant species was estimated by the "point quadrat method", using a 2 m-long frame with 50 pins (CAUSTON, 1988). A 10 × 10 m area was positioned in the centre of the plot, and 5 two-metre sections were marked on each side to determine a regular grid made up by 25 quadrats. One quadrat and one out of the four quadrat sides were chosen at random: the frame of pins was positioned along this side; iii) a tree recruitment index (R_i) (MAGINI, 1967) was computed separately for each tree species as the product of seedling density (n/m^2) and the mean height (cm) of all seedlings. Arbitrarily, we have defined "seedlings" as all plants that were less than 1.5 m high. A canopy (total) recruitment index was computed for each plot by summing R_i across all tree species.

In 10 out of the previous 18 forest stands, further structural analyses were carried out within 40 × 10 m rectangular transects: the crown cover of all trees was measured and attributed to one of the three canopy layers: i) the upper, extending from maximum stand height (H_{max}) to 2/3 H_{max}; ii) the middle, from 2/3 H_{max}; iii) the lower, from 1/3 H_{max} to the ground. In all cases tree seedlings ($H < 1.5$ m) were assigned to the lower canopy layer.

Data analysis

Characteristic indicator values (CIVs) for light, temperature, moisture, soil nitrogen content, soil reaction and continentality were calculated for each plot using the species scores proposed by ELLENBERG (1988). Following PERSSON (1981), CIVs were computed by understory species abundance.

Detrended correspondence analysis (DCA) (HILL & GAUCH, 1980) of cover data was applied to investigate vegetation gradients. Cover values of each species were previously transformed to $\ln (y_i + 1)$, where y_i is the species cover. Correlations between DCA axes, CIVs, recruitment data and structural stand characteristics were assessed by SPEARMAN rank correlation analysis (JONGMAN *et al.*, 1987). Detrended canonical correspondence analysis (DCCA) was carried out on the same data set using the following variables as predictors, evaluated for each plot studied: i) total tree species density and total basal area; ii) single tree species basal area; iii) altitude; iv) prevailing aspect, evaluated at the microtopographic level (two categories: North and South); v) pedological substratum (two categories: flysh and clays). Partial DCCA was performed to evaluate the effect of single tree species on understory vegetation. Significance of the DCCA ordination axes was verified by Monte Carlo permutation test ($\alpha = 0.05$).

Recruitment indices and structural data of different stand types, which turned out to be grouped by DCA, were compared by KRUSKALL-WALLIS non-parametric ANOVA. Spearman rank correlations and multiple (stepwise) regression analyses were also carried out between tree recruitment indices, stand structural characteristics, CIVs and floristic (multivariate) parameters.

Statistics were carried out using the CANOCO (TER BRAAK, 1988) and the SAS (SAS Institute Inc., 1988) packages.

RESULTS

In the understory layer, 59 plant species were recorded: 32 (54.2%) herbs, 7 (11.9%) grasses, 15 (25.4%) shrubs and 5 (8.5%) trees. For the complete list of species see table I.

DCA axes 1 to 4 accounted for 41 per cent of total variance in vegetation data (table II). DCA axis 1 showed significant negative correlations with stand density, average height of trees, total and Scots pine basal area, *Ostrya carpinifolia* basal area and canopy cover. Both total and Scots pine recruitment indices were positively correlated with DCA axis 1; DCA axis 4 also showed a significant positive correlation with total recruitment index and significant negative correlations with *Quercus pubescens* and *Ostrya carpinifolia* canopy cover. DCA axis 1 was positively correlated with light and reaction CIVs, and negatively correlated with nitrogen CIVs; DCA axis 2 showed a positive correlation with water and nitrogen CIVs (table II).

The first four axes of the DCCA analysis carried out accounted for 87.6 per cent of the total variance in the vegetation data. A high correlation ($r > 0.9$) was found between DCCA axes (site scores) that included linear combinations of structural and environmental variables and DCCA axes that were weighted averages of the species scores. Thus, the considered "site" DCCA predictors accounted fairly well for variability in vegetation data. Total basal area, rather than stand density, seems to have the most dramatic effect on the understory vegetation (table III*a* and III*b*). The overall effects of the environmental predictors on the species' ordination turned out to be significant by Monte Carlo permutation test (P = 0.02 and P = 0.04 for the first eigenvalue and the sum of all canonical eigenvalues, respectively). Partial DCCA (table III*b*) with single variables as environmental predictors, and all others as cova-

TABLE I. – *List of the species recorded in the studied plots and their life forms according to* RAUNKIAER *(1937): (H) = hemicryptophytes; (Ch) = cryptophytes; (G) = geophytes; (P) = phanerophytes; (NP) = nanophanerophytes. Nomenclature:* PIGNATTI *(1982).*

1 *Acer opulifolium* (P)
2 *Achillea millefolium* (H)
3 *Alliaria petiolata* (H)
4 *Anthyllis vulneraria* (H)
5 *Arabis hirsuta* (H)
6 *Aristolochia rotunda* (G)
7 *Brachipodium pinnatum* (H)
8 *Bromus erectus* (H)
9 *Calamagrostis arundinacea* (H)
10 *Calamintha nepeta* (Ch)
11 *Carduus nutans* (H)
12 *Carex flacca* (G)
13 *Cistus salvifolius* (NP)
14 *Clematis vitalba* (P)
15 *Cornus sanguinea* (P)
16 *Coronilla emerus* (NP)
17 *Cotinus coggyria* (NP)
18 *Crataegus monogyna* (P)
19 *Cytisus sessilifolius* (P)
20 *Dactylis glomerata* (H)
21 *Daphne laureola* (P)
22 *Deschampia flexuosa* (H)
23 *Dorycnium hirsutum* (Ch)
24 *Euphorbia cyparissias* (H)
25 *Festuca ovina* subsp. *laevis* (H)
26 *Foeniculum vulgare* (H)
27 *Fragaria vesca* (H)
28 *Fraxinus ornus* (P)
29 *Galium odoratum* (G)
30 *Galium lucidum* (H)
31 *Hedysarum coronarium* (H)
32 *Helichrysum italicum* (Ch)
33 *Hepatica nobilis* (G)
34 *Heracleum spondilium* (H)
35 *Hieracium sylvaticum* (H)
36 *Hieracium cymosum* (H)
37 *Inula conyza* (H)
38 *Lathyrus latifolius* (H)
39 *Listera ovata* (G)
40 *Lonicera etrusca* (P)
41 *Lonicera xylosteum* (P)
42 *Lotus corniculatus* (H)
43 *Onobrychis viciifolia* (H)
44 *Ostrya carpinifolia* (P)
45 *Pimpinella major* (H)
46 *Pinus sylvestris (P)*
47 *Plantago media* (H)
48 *Polytrichum juniperinum* (M)
49 *Potentilla erecta* (H)
50 *Primula vulgaris* (H)
51 *Quercus pubescens* (P)
52 *Rosa canina* (NP)
53 *Rubus sp.p.* (NP)
54 *Senecio erraticus* (H)
55 *Stachys salviifolia* (H)
56 *Thymus longicaulis* (Ch)
57 *Trifolium pratense* (H)
58 *Viburnum lantana* (P)
59 *Vicia cracca* (H)

riables, demonstrated that single tree species did not exert, when considered one at a time, significant effects on understory vegetation.

Along the first DCA axis (fig. 1) a discrimination can be attempted between four groups of stands; i) pine stands growing on eroded slopes (stands 2 and 5); ii) pine stands colonizing abandoned fields (stands 1 and 6); iii) pure Scots pine stands (stands 4, 8, 9 and 14); iv) mixed stands of pine and hardwood species growing under the pine canopy (stands 3, 7, 10-13, 15-18). No easy interpretable scattering of multivariate stand means is observed along DCA axis 2. Groups i), ii) and iii) are not discriminated by DCCA (fig. 2). No different ordination patterns were obtained when presence/ absence data, instead of abundance data, were used in multivariate analyses.

Significant differences between stand types identified by DCA (eroded slopes stands, abandoned fields stands, pure Scots pine stands, mixed stands) were observed for Scots pine recruitment index and pine basal area, tree density and total basal area, *Ostrya carpinofolia* basal area, canopy cover of the upper stand layer, light and nitrogen CIVs (table IV).

TABLE II. – *Eigenvalues and percent of variance explained by DCA axes, Spearman rank correlation coefficients between multivariate axes scores and environmental data, stand structural and canopy cover data, recruitment indices of the different species, characteristic indicator values (CIVs). Ps* = Pinus sylvestris; *Qp* = Quercus pubescens; *Oc* = Ostrya carpinifolia; *Fo* = Fraxinus ornus. H_{av} = *average height of trees;* H_{max} = *maximum height of trees;* D_{av} = *average diameter of trees; G = basal area.* * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	DCA			
	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.81	0.65	0.60	0.41
Var. expl. (%)	14.6	10.7	10.3	5.3
Environmental data				
Altitude	-0.27	0.27	0.14	-0.10
Aspect	0.18	-0.16	0.22	-0.21
Substratum	-0.27	-0.11	0.16	-0.24
Stand structural data				
Tree density	-0.71*	0.08	0.27	-0.08
H_{av}	-0.74*	0.00	-0.06	-0.24
H_{max}	-0.56	0.56	0.23	0.10
D_{av}	-0.69*	0.26	0.24	-0.35
G Total	-0.83**	0.06	0.12	-0.14
G Ps	-0.78**	0.03	0.08	-0.22
G Qp	-0.08	-0.13	-0.04	0.02
G Oc	-0.75*	-0.01	0.16	-0.10
G Fo	-0.11	-0.23	0.22	-0.23
Canopy cover data				
Total	-0.60	0.07	-0.12	-0.39
Ps	-0.11	0.34	-0.13	-0.05
Qp	-0.46	-0.11	-0.28	-0.80**
Oc	-0.87**	-0.13	0.14	-0.74**
Fo	-0.38	-0.26	0.27	-0.49
Recruitment index				
Total	0.65*	0.12	0.10	0.61*
Ps	0.62*	0.30	-0.14	0.52
Qp	0.15	0.36	0.37	0.27
Oc.	0.12	0.11	-0.22	0.02
Fo	-0.04	-0.27	0.41	-0.14
other species	-0.25	-0.04	0.31	0.18
CIVs				
Light	0.62**	-0.22	-0.13	0.11
Temperature	0.10	-0.19	0.02	0.47
Continentality	-0.26	-0.45	-0.07	0.42
Water	-0.44	0.67**	0.11	-0.14
Reaction	0.53*	-0.11	0.29	-0.11
Nitrogen	-0.56*	0.47*	0.18	0.01

The recruitment index estimated for Scots pine was negatively correlated with stand density, basal area of both Scots pine and *Ostrya carpinifolia* and crown cover area of hardwood species (mainly *Ostrya carpinifolia* and *Quercus pubescens*) in the lower canopy layers (table V). Scots pine seedling density, rather than seedling height,

TABLE III. – *(a) Weighted correlation matrix between DCCA ordination axes and variables used as environmental predictors. Axes 1-4 in columns represent site scores on axes which are linear combinations of environmental variables, whereas Spec Axes 1-4 in rows represent site scores on axes that are derived from species scores: species-environment correlations between the above axes are reported. (b) Eigenvalues for the first DCCA axis, their significance obtained by Monte-Carlo permutation test and intra-set correlation between the first DCCA axis and the environmental variable. Covariables refer to environmental predictors whose effects were partialled out in partial DCCA. Number of covariables refers to the variables reported in the first column.*

(a)

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**G Tot**	**Elev**	**Dens**	**Subst**	**Exp**
Spec Axis 1	0.977								
Spec Axis 2	0.000	0.972							
Spec Axis 3	0.000	0.000	0.969						
Spec Axis 4	0.000	0.000	0.000	0.926					
Eigenvalues	0.720	0.597	0.413	0.373					
G Tot	-0.866	0.041	0.166	0.005	1				
Elevation	-0.137	0.424	-0.196	-0.208	0.102	1			
Density	-0.084	-0.389	-0.517	0.007	-0.125	-0.024	1		
Substratum	0.202	-0.548	-0.400	-0.244	-0.073	0.159	0.451	1	
Exposition	-0.420	-0.246	-0.561	0.017	0.062	0.046	0.158	0.109	1

(b)

N	Variable	Covariables	Eigenvalues	Probability	Correlation
1	Density	2,3,4,5	0.3928	0.47	-0.084
		2,3,4,6,7,8,9	0.4407	0.36	-
2	Elevation	1,3,4,5	0.3860	0.45	-0.137
		1,3,4,6,7,8,9	0.3805	0.48	-
3	Substratum	1,2,4,5	0.3427	0.70	0.202
		1,2,4,6,7,8,9	0.4187	0.23	-
4	Exposition	1,2,3,5	0.4167	0.33	-0.420
		1,2,3,6,7,8,9	0.4266	0.33	-
5	G Tot	1,2,3,4	0.6142	0.01**	-0.866
6	G *P.s.*	1,2,3,4,7,8,9	0.4252	0.27	-0.746
		7,8,9	0.4115	0.38	-
7	G *Q.p.*	1,2,3,4,6,8,9	0.3801	0.40	-0.163
		6,8,9	0.4346	0.31	-
8	G *O.c.*	1,2,3,4,6,7,9	0.3773	0.51	-0.199
		6,7,9	0.4087	0.37	-
9	G *F.o.*	1,2,3,4,6,7,8	0.3074	0.77	-0.661
		6,7,8	0.2555	0.96	-

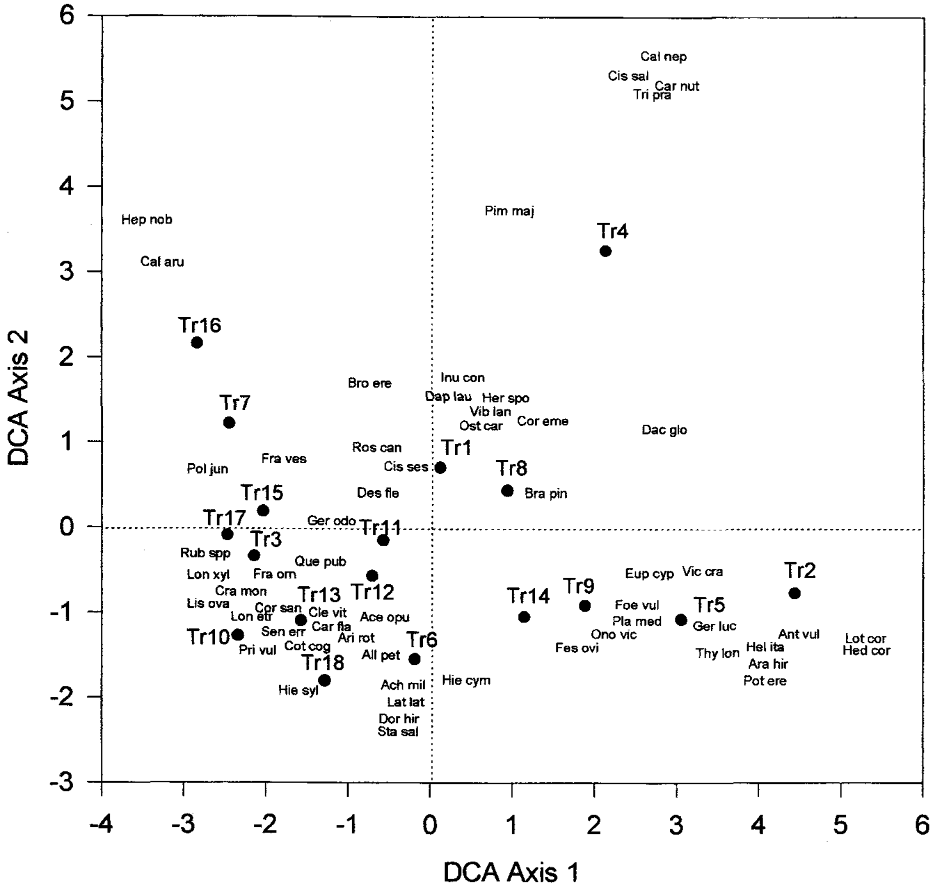

FIG. 1. – Ordination diagram for detrended correspondence analysis (DCA). Labels (reporting the first three letters of genus and species names) refer to the species reported in table I. Black dots indicate multivariate stands centroids. Stands belonging to the same structural type are: 2 and 5 = stands growing on eroded slopes; 1 and 6 = stands growing on abandoned fields; 4, 8, 9 and 14 = pure Scots pine stands; 3, 7, 10, 11, 12, 13, 15, 16, 17 and 18 = mixed stands with hardwood species.

was found to be negatively correlated with stand density. On the contrary, recruitment indices of hardwood species were unaffected by stand density, although a significant negative correlation between stand density and total R_i was found. R_i was not found to change significantly with altitude, aspect or soil characteristics. Scots pine recruitment index was positively correlated with the temperature CIVs, whereas a negative correlation was found between the average height of pine seedlings and nitrogen CIVs (table V).

Significant relationships were found, by multiple stepwise regression analysis, between the Scots pine recruitment index and the hardwood species canopy cover

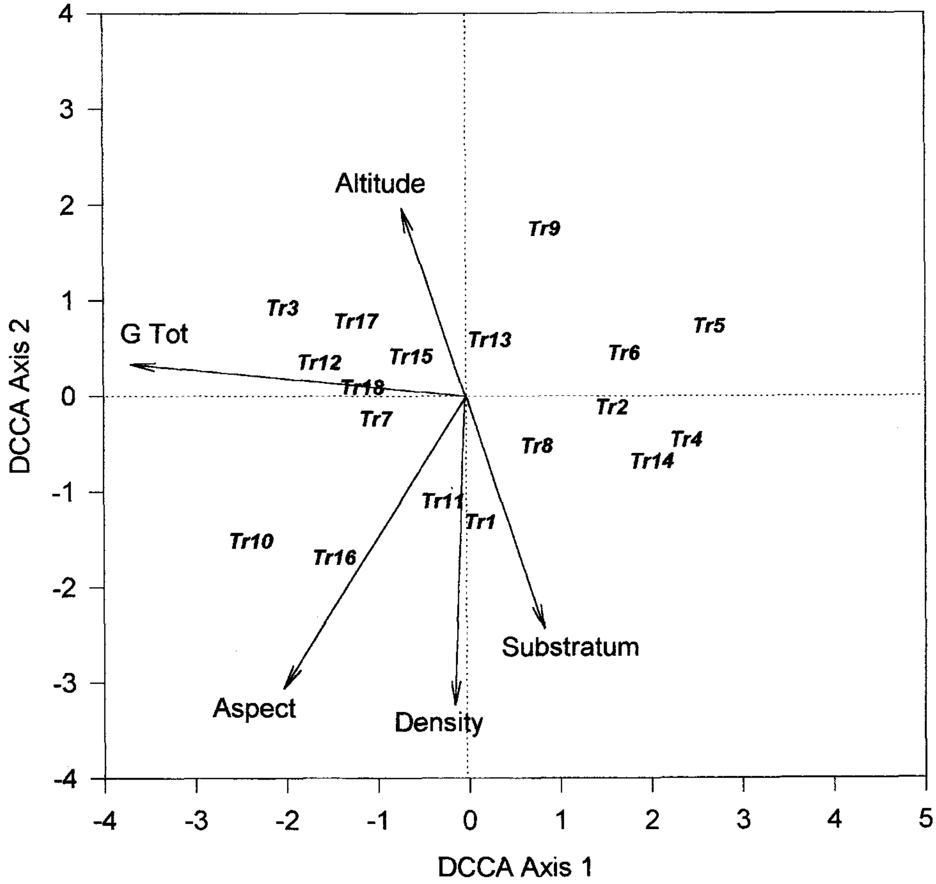

FIG. 2. – Ordination diagram from detrended canonical correspondence analysis (DCCA). Species scores are omitted. Labels indicate multivariate stands centroids. Predictor variables (whole stand basal area (G Tot), stand density, altitude, aspect and pedological substratum) are represented by lines originating from the center of the diagram and pointing in the direction of maximum variation. The length of lines is proportional to the importance of each predictor variable.

(table VI). The best model ($R^2 = 0.955$) was obtained using *Quercus pubescens, Fraxinus ornus* and “other species” total canopy cover as predictor variables. Considering both the single hardwood species and the single canopy layer effects, a significant negative relationship between Scots pine recruitment index and *Quercus pubescens* and *Fraxinus ornus* crown cover in the lower canopy layer was observed (table VI).

Multivariate synthetic variables (DCA and DCCA axes scores) and temperature and nitrogen CIVs were found to predict a large proportion of the variation of Scots pine recruitment index (table VII).

TABLE IV. – *Mean recruitment indices, stand structural and canopy cover data, and CIVs for the four stand types defined by DCA analysis. Kruskall-Wallis (K-W H) comparison between the four stand types is reported; P = probability of K-W H. Symbols are the same as for table II.*

	Units	Eroded slopes	Aband. fields	Pure pine stands	Mixed stands	K-W *H*	*P*
Recruitment indices							
R_i Ps	n m^{-2} cm	7.80	13.06	22.11	0.00	7.919	0.0477*
R_i Qp	n m^{-2} cm	2.90	12.77	2.37	2.83	2.545	0.4671
R_i Oc	n m^{-2} cm	1.21	16.34	3.25	1.43	4.358	0.2253
R_i Fo	n m^{-2} cm	11.36	1.60	0.67	3.60	0.648	0.8853
R_i others	n m^{-2} cm	1.69	1.25	0.13	2.37	5.068	0.1669
R_i Tot	n m^{-2} cm	4.99	9.01	5.71	2.05	3.836	0.2797
Stand structural data							
Tree density	ha^{-1}	1705	1687	1546	3357	9.921	0.0193*
H av	m	5.25	6.60	5.70	13.13	6.242	0.1004
H max	m	7.75	10.75	11.00	14.58	4.532	0.2095
D av	cm	11.25	13.05	13.07	28.37	6.091	0.1073
G tot	m^2 ha^{-1}	8.60	15.05	12.47	28.18	13.359	0.0039**
G Ps	m^2 ha^{-1}	4.90	11.00	8.03	19.60	10.385	0.0156*
G Qp	m^2 ha^{-1}	1.40	3.40	1.53	2.22	3.275	0.3511
G Oc	m^2 ha^{-1}	0.15	0.40	0.05	4.59	13.700	0.0033**
G Fo	m^2 ha^{-1}	0.70	0.10	0.18	0.44	1.126	0.7708
Canopy cover data							
Upper Layer	m^2	73	34	94	138	4.581	0.0205*
Middle Layer	m^2	123	121	203	274	3.700	0.2947
Lower Layer	m^2	75	112	117	128	2.631	0.4512
Overall	m^2	272	268	415	542	7.432	0.0592
CIVs							
Light	-	7.29	6.38	6.72	5.82	9.732	0.0210*
Temperature	-	5.59	5.53	5.83	5.80	1.398	0.7058
Continentality	-	3.55	3.35	3.85	3.95	1.850	0.6040
Water	-	3.67	4.14	4.14	4.31	4.371	0.2240
Reaction	-	7.42	7.50	7.58	6.83	6.356	0.0955
Nitrogen	-	2.68	3.74	3.91	4.49	7.759	0.0451*

DISCUSSION

Ordination patterns by multivariate analyses

Both direct and indirect gradient analyses (TER BRAAK & PRENTICE, 1988) were applied in this study to explore vegetation-environment relationships. Detrended correspondence analysis (DCA) is considered to capture the essential and ecologically meaningful variation in vegetation data (HILL & GAUCH, 1980; TER BRAAK, 1988).

TABLE V. – *Spearman rank correlation coefficients between recruitment index of the different species, stand structural and canopy cover data at different layers, characteristic indicator values (CIVs). Upper = upper canopy layer; Middle = middle canopy layer; Lower = lower canopy layer; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Symbols are the same as for table II.*

	Recruitment Index						*Scots pine seedlings*	
	Total R_i	*Pinus sylvestris*	*Quercus pubescens*	*Ostrya carpinifolia*	*Fraxinus ornus*	Other species	Height	Density
Stand structural data								
Tree dens.	-0.696*	-0.938***	-0.175	-0.601	0.381	0.361	-0.510	-0.635*
H_{av}	-0.534	-0.566	-0.285	-0.298	0.119	0.547	-0.176	-0.530
H_{max}	-0.189	-0.012	-0.030	0.024	-0.264	0.283	-0.437	-0.142
D_{av}	-0.406	-0.607	-0.309	-0.334	0.506	0.595	-0.468	-0.295
G Tot	-0.478	-0.533	-0.333	-0.164	0.306	0.435	-0.322	-0.365
G Ps	-0.527	-0.644*	-0.345	-0.291	0.400	0.496	-0.237	-0.459
G Qp	-0.128	-0.068	0.360	0.331	-0.116	-0.340	0.447	-0.292
G Oc	-0.500	-0.753**	-0.079	-0.107	0.349	0.574	-0.165	-0.478
G Fo	-0.220	-0.302	0.265	-0.507	0.056	-0.564	-0.198	-0.282
Canopy cover data								
Ps Upper	-0.381	-0.386	-0.369	-0.668*	0.350	-0.067	-0.504	-0.264
Ps Middle	0.236	0.141	-0.163	0.218	0.075	-0.128	-0.115	0.503
Ps Lower	0.474	0.769**	0.091	0.472	-0.479	-0.689*	0.390	0.498
Total	0.030	0.030	-0.296	-0.085	0.068	-0.263	-0.449	0.352
Qp Upper	-0.126	0.022	0.126	-0.231	-0.538	-0.113	0.014	-0.232
Qp Middle	-0.175	-0.337	0.006	0.279	0.256	-0.055	0.407	-0.169
Qp Lower	-0.781**	-0.644*	-0.539	-0.218	0.187	0.141	-0.261	-0.692*
Total	-0.587	-0.472	-0.187	0.006	-0.125	-0.030	-0.012	-0.591
Oc Upper	-0.454	-0.611	-0.201	-0.082	0.123	0.067	-0.344	-0.247
Oc Middle	-0.796**	-0.818**	-0.255	-0.213	-0.015	0.350	-0.298	-0.741**
Oc Lower	-0.626*	-0.830**	-0.121	-0.378	0.235	0.584	-0.292	-0.634
Total	-0.723**	-0.830**	-0.158	-0.219	0.147	0.350	-0.310	-0.678*
Fo Upper	0.043	-0.183	0.043	-0.420	0.481	-0.227	-0.164	0.035
Fo Middle	-0.446	-0.543	0.226	-0.577	0.066	-0.229	-0.363	-0.537
Fo Lower	-0.206	-0.671*	-0.075	-0.608	0.458	0.189	-0.263	-0.051
Total	-0.484	-0.838**	-0.104	-0.670*	0.436	0.055	-0.480	-0.356
Oth Upper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Oth Middle	-0.008	-0.218	-0.371	0.182	0.102	0.455	0.242	0.157
Oth Lower	-0.437	-0.350	-0.881**	-0.207	0.344	0.233	0.076	-0.249
Total	-0.437	-0.350	-0.881**	-0.207	0.344	0.233	0.076	-0.249
Tot Upper	-0.393	-0.546	-0.224	-0.547	0.256	0.055	-0.431	-0.258
Tot Middle	0.030	-0.165	-0.018	0.006	0.137	-0.079	-0.255	0.245
Tot Lower	-0.466	-0.116	-0.733*	-0.012	-0.231	-0.079	-0.109	-0.239
Overall	-0.466	-0.582	-0.418	-0.389	0.168	0.042	-0.589	-0.151
CIVs								
Light	0.187	0.214	0.236	-0.273	-0.237	-0.496	0.194	0.062
Temp.	0.814**	0.892**	0.212	0.509	-0.090	-0.307	0.378	0.801**
Continent.	-0.357	-0.325	-0.600	-0.553	0.143	-0.079	0.006	-0.220
Water	-0.248	-0.202	0.066	-0.024	-0.068	0.276	-0.583	-0.182
Reaction	0.442	0.312	0.151	0.273	0.468	-0.276	0.212	0.434
Nitrogen	-0.321	-0.165	-0.090	0.158	-0.250	0.141	-0.644*	-0.151

TABLE VI. – *Multiple (stepwise) regression analysis between Scots pine recruitment index (R_i Ps) and hardwood species cover at different canopy layers. R^2 = determination coefficient of the regression model; SEE = standard error of the estimate; β = standardized regression coefficient; Coefficient = non-standardized regression coefficient ; Multiple R^2 = determination coefficient obtained including the current variable in the model. Symbols of species are the same as for table II.*

Lower Canopy Layer

Model	R^2	SEE	F (2,7)	p-level
R_i *Ps* = 37.930 -0.696*(Qp Lower) - 1.053*(Fo Lower)	0.7969	7.5551	13.735	0.004

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		37.930			0.000
Qp Lower	-0.752	-0.696	0.499	7.964	0.026
Fr Lower	-0.548	-1.053	0.797	10.274	0.015

Middle Canopy Layer

Model	R^2	SEE	F (2,7)	p-level
R_i *Ps* = 30.795 -0.446*(Qp Middle) - 0.118*(Oc Middle)	0.5356	11.4243	4.038	0.068

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		30.795	0.008		
Qp Middle	-0.555	-0.446	0.450	6.534	0.085
Oc Middle	-0.315	-0.118	0.536	1.298	0.292

Upper Canopy Layer

Model	R^2	SEE	F (2,7)	p-level
R_i *Ps* = 13.546 -0.290*(Oc Upper)	0.1485	14.4710	1.396	0.271

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		30.795			0.030
Oc Upper	-0.385	-0.290	0.149	1.396	0.271

Overall Canopy Layer

Model	R^2	SEE	F (3,6)	p-level
R_i *Ps* = 46.564 - 0.340*(Qp Tot) - 0.421*(Fr Tot) - 0.150*(Oth.Tot)	0.9553	3.8285	42.743	0.0002

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		46.546			0.000
Qp Total	-0.739	-0.340	0.646	14.568	0.009
Fr Total	-0.494	-0.421	0.845	8.980	0.024
Oth Total	-0.347	-0.150	0.955	14.843	0.008

TABLE VII. – *Multiple (stepwise) regression analysis between Scots pine recruitment index (R_i Ps), DCA and DCCA axes scores, characteristic indicator values (CIVs). Symbols of species are the same as for table II.*

Floristic parameters (DCA and DCCA axes scores)

Model	R^2	SEE	F (2,7)	p-level
$R_i\ Ps$ = 8.051 + 0.070*(DCA 2) + 0.029*(DCA 1)	0.7169	8.9205	8.8623	0.01207

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		8.051			0.030
DCA 2	0.729	0.070	0.517	8.560	0.008
DCA 1	0.447	0.029	0.717	4.944	0.062

$R_i\ Ps$ = 8.051 + 0.070*(DCCA 1) + 0.029*(DCCA 4)	0.8071	7.3635	14.643	0.003

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		10.396			0.004
DCCA 1	0.770	6.111	0.585	11.277	0.012
DCCA 4	-0.471	-5.185	0.807	8.059	0.025

Characteristic Indicator Values

Model	R^2	SEE	F (2,7)	p-level
$R_i\ Ps$ = 216.625 - 35.662*(Temp.) - 8.189*(Nitrogen)	0.5978	10.632	5.2022	0.04126

Predictor	β	Coefficient	Multiple R^2	F	p-level
Intercept		-216.625			0.020
Temp	0.733	35.662	0.431	6.058	0.043
Nitro	0.415	8.189	0.598	2.904	0.132

In our study the total variation explained by DCA was rather small: this may be expected due to the large micro-environmental variability and the small-scale variations of ground vegetation in the forest community (see MASLOV, 1989; KUULUVAINEN *et al.*, 1993). Noteworthy proportions of unexplained variation in vegetation data were observed in similar studies (NIEPPOLA & CARLETON, 1991).

Nonetheless, DCA ordination axes may be interpreted by forest stand variability and environmental gradients. Indeed, ordination of multivariate stand scores along the first DCA axis reflects differences in forest stand structure, ranging from mixed and closed forests to edgy and shrubby forest communities (fig. 1). The hypothesis can be advanced that the first DCA axis mainly represents a light gradient. Ranking of species along DCA axis 1 agrees with this interpretation: *Hedysarum coronarium, Anthyllis vulneraria* and *Helicrysum italicum*, which are species mostly occurring in open, dry and poor habitats, showed the highest DCA scores on axis 1; on the contrary, *Hepatica nobilis*, *Lonicera xylosteum* and *Polytrichum juniperinum*, mostly occurring in shaded and moist habitats, were characterised by the lowest scores on DCA axis 1.

The lack of correlation between DCA axes, altitude, aspect and substratum suggests that geographic variables account for a minor proportion of understory composition and do not represent *per se* the main factor affecting vegetation dynamics in the studied forest stands. DCCA carried out using only geographic variables as predictors were not significant when stand structural variables were partialled out, supporting the hypothesis that the main effect driving understory community composition may be represented by stand structural factors. On the other hand, we cannot exclude that the gradients of the geographic variables considered might have been too small in the area covered by this investigation to generate significant changes in the understory composition.

As it was revealed from partial DCCA, in mixed stands no species did exert, singularly, a significant effect on understory vegetation (table V). Thus, none of the tree species may be considered as a prominent canopy species, driving the forest microenvironmental conditions in mixed stands.

Stand structure and pine recruitment

Stand density, composition, and canopy structure were found to account for some of the differences in Scots pine recruitment processes between the studied stands. In particular, the cover exerted by hardwood species in the lower and middle canopy layers seems to limit strongly the natural regeneration of a light-demanding species like *Pinus sylvestris* (AGOSTINI, 1955; BERNETTI, 1995).

Pine regenerates better in relatively open stands, forest margins and canopy gaps, where light and temperature-demanding understory vegetation was found to prevail (positive correlation between pine recruitment index and temperature CIV). The negative correlation between pine regeneration and nitrogen CIV seems to be in accordance with the observation that mixed and closed stands, where more organic matter tends to accumulate in the soil, are less favourable to Scots pine recruitment.

Investigations of factors influencing Scots pine recruitment, using stand structural parameters as predictor variables in stepwise regression analysis, suggest both a strong early-staged competition between hardwoods and Scots pine, as well as differential colonization of tree species at different microsites. However, since negative correlations were found between the Scots pine recruitment index and hardwood canopy cover at the lower level (but not *vice versa*) (table V), the former hypothesis seems more likely. Moreover, no significant differences between stands were observed in any hardwood species recruitment index, supporting the latter hypothesis. Therefore, a tentative hypothesis could be advanced that the studied stands represent different stages along a successional gradient (primary on eroded slopes, secondary on abandoned fields) rather than different ecosystems bearing different plant communities.

Understory vegetation has been used as predictor of forest productivity and site characteristics in northern Scots pine forest (NIEPPOLA & CARLETON, 1991; NIEPPOLA, 1993*a*; NIEPPOLA, 1993*b*; LATHI, 1995). Less information is available, to our knowledge, on the relationship between understory vegetation, natural regeneration and canopy dynamics of *Pinus sylvestris* forests. The large variation in pine recruitment index accounted for by multivariate synthetic variables (table VII) indicates that the vegetation gradients extracted by ordination techniques reflect factors which affect – directly or indirectly – the Scots pine recruitment as well. Thus, the understory plant community may provide useful hints for predicting Scots pine recruitment in the study area.

Characteristic indicator values

Ellenberg's characteristic indicator values (CIVs) have been claimed to be a useful and attractive tool in the interpretation of the patterns emerging from vegetation data (Persson, 1981; Roo-Zielinska & Solon, 1990). Single-species indicator values have been reported for both broad- and narrow-ranged central European species (Ellenberg, 1988). The consistency of CIVs for moisture, and the robustness of the Ellenberg's calibration method, have been assessed by Ter Braak & Gremmen (1987). After an extensive study in mature Scots pine stands in Southern Finland, Nieppola (1993*b*) suggests that Ellenberg's method may be useful for predicting forest site productivity.

In this study, the suitability of CIVs, based on understory species cover, has been evaluated as a simple method for predicting environmental factors and interpreting natural regeneration and canopy dynamics in sub-Mediterranean forest communities. The observed variation of CIVs seems to reflect true ecological patterns in the studied forest stands. For instance, significant differences in light and soil nitrogen content CIVs were observed between open and closed forests. The increase of nitrogen CIV in closed stands may be interpreted as dependent on the larger litterfall, thicker organic layers, well-structured soils and higher site fertility, while the decrease of light CIV reflects larger values of canopy cover. It is worth recognising, following the work by Diekmann (1995), that CIVs based on species cover may be less accurate than CIVs based on species frequencies, which are independent on the specific plant growth form.

In this investigation, multiple regression models including floristic data (CIVs and multivariate scores) have predicted Scots pine recruitment fairly well. Further analyses based on larger surveys are needed in order to confirm the above evidence. Nonetheless, our data provided useful hint of the feasibility of the use of CIVs as predictors of Scots pine recruitment in sub-mediterranean stands for reafforestation/management effort.

The use of CIVs for predicting ecologically meaningful conditions has some advantages with respect to stand structural parameters or floristic composition. First, they could allow ecological comparisons between plant communities even though they share a few species; second, they could summarise in a few parameters most of the factors influencing the species recruitment and the forest persistence, providing a helpful predictive tool for management choices; third, once the reliability is demonstrated by exploratory investigations in the study area, and by calibration against independent data, they can be useful for monitoring ecological changes (*vs.* changes in the community composition) over time in both small forest plots and larger forests.

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