Variations in CSR strategies along stress gradients in the herb layer of submediterranean forests (central Italy)

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Background and aims – Species grouping in plant functional types (PFTs) according to Grime's CSR theory has been found useful in understanding ecosystem functioning and processes and in quantifying variation along environmental gradients. However, little is known about the relationship between herbaceous plant strategies and stress gradients in submediterranean forest ecosystems. Our aim was to assess variations in CSR strategies along three stress gradients (related to the amount of photosynthetically active radiation, soil water deficit, and soil total nitrogen content) in the herb layer of submediterranean forests.

Material and methods – We collected floristic (species cover in the herb layer) and environmental data about topography, soil and light conditions in 48 sampling plots in a forest landscape of central Italy. We performed canonical redundancy analyses (RDAs) of species and PFT data sets, constrained by photosynthetically active radiation, soil water deficit and soil total nitrogen content. Cover trends of PFTs along the environmental gradients were graphically represented.

Key results – All the environmental factors considered did affect ecological strategies in the herb layer, but the variation of both species and PFT data sets were best explained by photosynthetically active radiation. Competitors were favoured by low/intermediate stress levels, with regard to soil water and light intensity. Competitive stress-tolerant ruderals peaked in moderate light stress intensity and in well-watered soils. Stress-tolerant competitors peaked in conditions of strong light and moderate dryness.

Conclusions – Spatial variations in environmental conditions and in the related stress gradients determine predictable variations in the functional composition of the herb layer. Therefore, it may be possible to use Grimes's PFTs for assessing environmental constraints and predicting whether a species with a specific strategy is likely to be positively or negatively affected by changes in environmental stress due, for instance, to climate change.

Key words – CSR theory, forest vegetation, life strategy, plant functional type, RDA, stress gradient.

INTRODUCTION

Since the classic studies of Whittaker (1956) and Bray & Curtis (1957), plant ecologists have sought to quantify the distribution of plant species along complex environmental gradients. Many papers have dealt with the relation between variation in forest species richness and gradients of environmental variables, such as nutrient levels, soil reaction, soil moisture and light intensity (e.g. Wilson & Keddy 1988, Pausas 1994, Pausas & Carreras 1995, Pausas & Austin 2001, Decocq 2002). However, exclusive focus on species richness can lead to misleading conclusions for conservation issues or ecological interpretation of plant communities (Campetella et

al. 2004). Instead, species grouping in plant functional types (PFTs) according to their life strategies and to the CSR theory (Grime 1974) has proven useful in understanding ecosystem properties, functioning and processes (Lepš et al. 1982, MacGillivray et al. 1995). CSR theory (Grime 2001) postulates the existence of three primary plant strategies (competitors, stress-tolerators, and ruderals). The defining characteristic of the competitor is the ability to rapidly monopolise resource capture by the spatially-dynamic foraging of roots and shoots. Stress-tolerators are distinguished by the capacity of their long-lived tissues to resist effects of environmental stress in conditions where growth is severely restricted by low rates of mineral nutrient, water or light supply. Ruder-

als are characterised by a short life-history and the tendency to rapidly invest captured resources in the production of offspring. In addition, the CSR model provides the existence of secondary strategies corresponding to the various tradeoffs in adaptation to competition, stress and disturbance (competitive ruderals, stress-tolerant ruderals, stress-tolerant competitors, CSR-strategists). Even though the ability of CSR theory to predict variation in species composition along environmental gradients, such as altitudinal and temperature ones, has been questioned (Oksanen & Ranta 1992, Austin & Gaywood 1994, van der Werf et al. 1998), it has nonetheless been demonstrated to be a useful tool for quantifying functional variations along succession gradients (Caccianiga et al. 2006). In spite of that, relationships between plant functional types (PFTs) based on Grime's CSR strategies and environmental variables have rarely been investigated in forest plant communities and never in submediterranean forest landscapes characterized by the alternation of summer drought stress and winter cold stress (Blasi 1994, Orsomando & Catorci 2000).

On these bases, the research aim was to assess variations in CSR strategies along three stress gradients (related to the amount of photosynthetically active radiation, soil water deficit, and soil total nitrogen content) in the herb layer of submediterranean forests. Hence, the specific research goals were: (1) to assess the variation in species and PFTs data sets explained by the three environmental variables, alone or in combination; (2) to understand the relationship between the analyzed CSR strategies and the stress due to low light intensity, high soil dryness, and low level of nitrogen content.

MATERIAL AND METHODS

Study area

The study area is a hilly and mountainous territory of central Italy (fig. 1), at altitudes ranging from 150 to 2,300 m a.s.l. (coordinates range 43°20'–42°50'N 12°26'–13°23'E). It is characterized by calcareous, marly-calcareous, marly-arenaceous, and arenaceous substrata and is included within a submediterranean context, at the border between Temperate and Mediterranean macroclimatic regions (Rivas-Martínez & Rivas-Saenz 1996–2009). Soil depth is very variable (ranging from 0.5 to 3 m), while pH values are quite homogeneous, mostly ranging from 6 to 7 (Giovagnotti et al. 2003, A.S.S.A.M. 2006). The forest landscape is composed of mixed woods (about 10,000 hectares) in which *Quercus ilex* L. subsp. *ilex*, *Quercus pubescens* Willd., *Ostrya carpinifolia* Scop., *Quercus cerris* L., *Castanea sativa* Mill. or *Fagus sylvatica* L. subsp. *sylvatica* play a dominant or a codominant role. These woods are managed as coppices with standards (mature trees retained through two or three coppicing rotation cycles) and cut down every 25–30 years.

Sampling design

To plan data collection, the study area was divided into homogeneous ecological units, according to Blasi et al. (2000), taking into account geology, bioclimatic belt, land form and aspect. To avoid a stress gradient due to temperature and because above 1,000 m a.s.l. the forest plant landscape changes dramatically, being mostly composed of *Fagus sylvatica*-dominated communities, only areas ranging from 500 to 950 m a.s.l. were considered. The a priori sites selection was based on the plant landscape geodatabase of Marches and Umbria Regions (Orsomando & Catorci 1999, 2000, Catorci et al. 2007, Pesaresi et al. 2007). Moreover, to avoid the effects of regenerative processes, only woods in the second half of the regenerative cycle were considered. Within each set of homogeneous ecological conditions, five sampling plots (for a total of 80) covering 400 m² each (20 m × 20 m) were chosen. In each of them floristic data were gathered.

The 80 relevés were submitted to cluster analysis on a sites × species matrix, using the complete linkage method, based on Bray-Curtis distance, after transformation of Braun-Blanquet classes according to van der Maarel's (1979) scale (see dendrogram in the electronic appendix 1). Within each of the sixteen groups of relevés identified by the preliminary multivariate analysis, a subsample (60%) of the relevés was randomly extracted. In each of these 48 plots photosynthetically active radiation (PAR) and soil data were eventually collected. Further analyses were performed using only these plots for which both species and environmental data were available.

Data collection

Original floristic and environmental data were collected by the authors in the period 2006–2007. Cover values of the species in the forest herb layer were visually estimated using Braun-Blanquet scale (Braun-Blanquet 1964). Field data on latitude (degrees and minutes), aspect (degrees from north) and slope (degrees) were also gathered.

Measurements of PAR in the understorey (μmol m^{-2} s^{-1}) were performed in June–July, at 50 cm above ground level (i.e. above the canopy of the herb layer), using a ceptom-
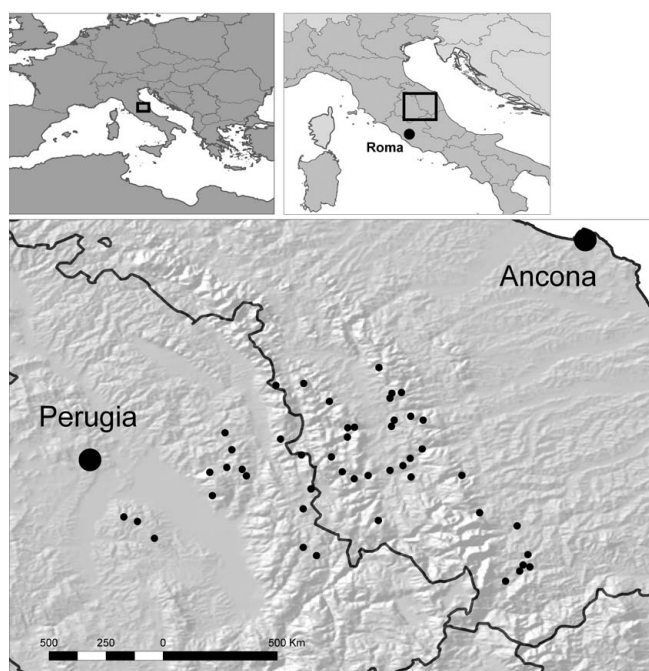
Figure 1 – Location of the study area. Black dots indicate relevé sites.

Table 1 – Classes of the environmental variables used for statistical analyses.

Environmental variable	Classes			
	1	2	3	4
Photosynthetically active radiation (μmol m^{-2} s^{-1})	0.0–25.0	25.1–50.0	50.1–75.0	> 75.0
Soil water deficit (mm yr^{-1})	> 240.0	240.0–140.1	140.0–40.1	40.0–0.0
Soil total nitrogen content (g Kg^{-1})	0.0–2.0	2.1–4.0	4.1–6.0	-

eter (Decagon Devices, Pullman, WA, USA). In each site, 20 measurements were made between 11.00 a.m. and 2.00 p.m. on cloudless days. Each soil sample (collected in five locations in each plot, at a depth ranging from 10 to 40 cm and thoroughly mixed) was analysed for total nitrogen content (g Kg^{-1}) and texture (skeleton, sand, clay and silt %) by the Marches Region agrochemical analysis and research laboratories, according to the methodological standards established by Italian ministerial decree 13/09/99. Soil depth (cm) was measured using a graduated pole.

Data about mean monthly temperature (°C) and mean monthly precipitation (mm) came from meteorological stations close to the relevé sites and at the same altitudes (Camerino, Macerata Province; Montemonaco, Ascoli Piceno Province; Assisi, Gualdo Tadino, Perugia and Rasiglia, Perugia Province). In each of the stations, data had been recorded for a period of thirty years.

Information about species life strategies (Grime 1974, 2001) were gathered from Grime et al. (1988), BiolFlor database (Klotz et al. 2002), or checked by field observations, on the basis of the criteria and examples provided by Grime et al. (1988) and Grime (2001).

Data analysis

Climatic data (mean monthly temperatures and mean monthly precipitation), latitude, aspect and slope angle served to estimate potential evapotranspiration; soil texture and soil depth data were used to calculate available water capacity and soil water reserve. All these data were processed using the software developed in Microsoft Office Excel 2000 by Armiraglio et al. (2003), in order to calculate soil water deficit (mm year^{-1}), namely the difference between potential and actual evapotranspiration in a given site. The methodological background of such data processing refers to Thornthwaite & Mather (1957), Bartorelli (1967), Pinna (1977), Constantinidis (1981), McRae (1991), Andreoli et al. (1994), Mariani (1994), Gupta (1995), and Pampaluna & Brenna (1996). Potential evapotranspiration is given by the not corrected evapotranspiration, calculated using Thornthwaite's formula, multiplied by two correction coefficients, k and As, depending, the former on latitude and month (day length), the latter on aspect and slope angle (amount of solar radiation hitting the topographic surface). Actual evapotranspiration is function of corrected evapotranspiration and soil water reserve, which depends, in turn, on available water capacity and cumulative water loss. This method allows an approximate estimation of water deficit, so that the resulting values cannot be used for punctual small-scale ecological studies; however they may be used for making comparisons among sites at larger scales within homogeneous macro-environmental conditions.

Species abundances were expressed in percent values using the average cover values of Braun-Blanquet classes. In each relevé, herb layer cover was calculated as the sum of species cover values. Cover values of species sharing the same ecological strategy (i.e. belonging to the same plant functional type or Grime's strategy) in each relevé were summed up. Five PFTs were considered: C – competitors, CR – competitive-ruderals, CS – stress-tolerant competitors, CSR – competitive stress-tolerant ruderals, and S – stress-tolerators.

Two canonical redundancy analyses (RDAs) of each community matrix (cover data of species and PFTs, respectively), constrained by soil water deficit, soil total nitrogen content, and PAR, were performed to compute the percentage of variation explained by the combination of the three explanatory variables. Prior to RDA, cover data matrices have been Hellinger-transformed to avoid considering double absence as a resemblance between sites (Legendre & Gallagher 2001). To assess the contribution of each environmental variable to the total variability of species and PFT data sets, the total variance was partitioned into fractions explained by each of the predictor variables by partial RDAs (Borcard et al. 1992, Borcard & Legendre 1994). Adjusted R-square values were calculated to produce unbiased estimates of the contributions of the independent variables to the explanation of the response variables (Peres-Neto et al. 2006). To test the significance of the adjusted R-squares (i.e. whether each independent fraction exhibits a significant influence on cover data), a permutation test with 1,000 permutations was applied, in accordance with Legendre & Legendre (1998).

To obtain a graphical representation of the cover trends of PFTs along the gradients, environmental variable values were categorized in classes (table 1) and the mean cover values of PFTs within each class were computed.

Cluster analysis was performed using the SYN-TAX 2000 package (Podani 2001); RDAs and variance partitioning were computed using *rda*, *varpart* and *decostand* functions in R software, version 2.13.0 (R Development Core Team 2011), and the *Vegan* package, version 1.17-9 (Oksanen et al. 2011).

RESULTS

The total explained variances for species and PFT data sets, constrained by soil water deficit, total nitrogen content, and PAR, were 21.1% and 46.9% (adjusted R-squares), respectively.

Table 2 – Results of redundancy analyses of herb species and PFT cover data (Hellinger transformed), constrained by soil water deficit, soil total nitrogen content and photosynthetically active radiation (PAR).
Scores (scaling 2) for explanatory variables, species, and PFTs are reported for the first two axes of each analysis. Only species more strictly linked to the environmental gradients are listed.

Species	Axis 1	Axis 2	Plant functional types	Axis 1	Axis 2
Scores for constraining variables			*Scores for constraining variables*		
Soil water deficit	-0.7120	-0.4272	Soil water deficit	0.8061	0.0922
Soil total nitrogen content	0.2387	-0.9495	Soil total nitrogen content	-0.0923	-0.8754
PAR	-0.9593	-0.0314	PAR	0.9318	-0.1215
Scores for species			*Scores for PFTs*		
Brachypodium rupestre (Host) Roem. & Schult.	-0.7396	0.0098	Competitive ruderals	-0.0046	0.0674
Buglossoides purpurocaerulea (L.) I.M.Johnst.	-0.1407	-0.0981	Competitive stress-tolerant ruderals	-0.5803	-0.0436
Carex digitata L.	0.1145	-0.1316	Competitors	-0.3052	0.0499
Cyclamen hederifolium Aiton	0.1867	-0.0059	Stress-tolerant competitors	0.9183	-0.0197
Cyclamen repandum Sm.	0.0075	-0.1233	Stress-tolerators	-0.0604	-0.1377
Festuca heterophylla Lam.	0.1698	0.1896			
Hepatica nobilis Schreb.	0.1744	-0.0560			
Lathyrus venetus (Mill.) Wohlf.	0.1667	0.0653			
Luzula forsteri (Sm.) DC.	0.1165	0.1170			
Melica uniflora Retz.	0.1645	0.0393			
Melittis melissophyllum L.	0.0324	-0.1710			
Primula vulgaris Huds.	0.1806	0.0310			
Pteridium aquilinum (L.) Kuhn	0.0239	0.1234			
Sanicula europaea L.	0.2268	-0.1000			
Teucrium chamaedrys L.	-0.1417	-0.0224			

With regard to species data set, *Brachypodium rupestre* (Host) Roem. & Schult. was linked to the most light conditions and to moderate-high soil dryness stress, while *Teucrium chamaedrys* L. and *Buglossoides purpurocaerulea* (L.) I.M.Johnst. were strictly associated to moderate-high light availability and dry soils, respectively; *Festuca heterophylla* Lam., *Luzula forsteri* (Lm.) DC., *Cyclamen hederifolium* Aiton, *Hepatica nobilis* Schreb., *Lathyrus venetus* (Mill.) Wohlf., *Melica uniflora* Retz., *Primula vulgaris* Huds. and *Sanicula europaea* L., were related to moist soils and shaded conditions; *Melittis melissophyllum* L., *Carex digitata* L. and *Cyclamen repandum* Sm. were particularly associated to nitrogen-rich soils (table 2, electronic appendix 2).

As regards PFT data set, stress-tolerant competitors (CS) were strictly related to high light intensity, and competitive stress-tolerant ruderals (CSR) to well-watered soils. Competitors (C), competitive-ruderals (CR), and stress-tolerators (S) were weakly linked to the considered environmental variables: C-strategists show some kind of preference for well-watered soils and medium-low PAR availability; CR-strategists, placed near axes origin of the ordination diagram, are not influenced by any of the considered stress; S-strategists are more linked to soil nitrogen content than to the other environmental variables (table 2, fig. 2).

The independent explained variance extracted from the species data set showed that PAR had the greatest effect (adj.-$R^2 = 0.0769$, $P = 0.001$), followed by soil total nitrogen con-
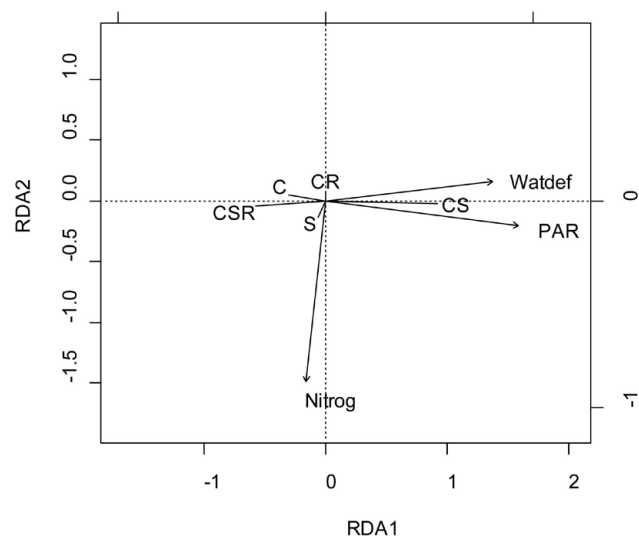
Figure 2 – Redundancy analysis ordination graph for life strategies data set, using environmental parameters (PAR – photosynthetically active radiation; Watdef – soil water deficit; Nitrog – soil total nitrogen content) as constraining variables (C – competitors, CR – competitive-ruderals, CS – stress-tolerant competitors, CSR – competitive stress-tolerant ruderals, S – stress-tolerators).

Table 3 – Partition of the total variation (adjusted R-squares) in species and PFTs composition. Importance of both single and joint effects of environmental variables are shown.
Significance of the adjusted R-squares was tested with 1,000 permutations (*** $P = 0.001$; *n.s.* not significant). The joint fractions and residuals could not be tested for significance. Negative values can be considered as null.

	Adj.-R^2 for species data set	Adj.-R^2 for PFT data set
Effect of single variables		
Soil water deficit	0.0359 ***	0.0592 ***
Soil total nitrogen content	0.0370 ***	0.0002 (*n.s.*)
PAR	0.0769 ***	0.1520 ***
Joint effect of variables		
Soil water deficit and total nitrogen content	-0.0021	-0.0026
PAR and soil total nitrogen content	0.0085	0.0128
Soil water deficit and PAR	0.0609	0.2657
Soil water deficit, total nitrogen content and PAR	-0.0066	-0.0186
Residuals	0.7895	0.5314

tent (adj.-R^2 = 0.0370, P = 0.001), and water deficit (adj.-R^2 = 0.0359, P = 0.001).

Variance extracted from the PFT data set for PAR had a greater importance (adj.-R^2 = 0.1520, P = 0.001) than soil water deficit (adj.-R^2 = 0.0592, P = 0.001), while no significant effect was shown by soil total nitrogen content (adj.-R^2 = 0.0002, P = 0.356). As indicated in table 3, PAR and water deficit showed the greatest shared variation for both species and PFT data sets (adj.-R^2 0.0609 and 0.2657, respectively).

As shown in figure 3A, the highest value for light in the understorey (> 75.0 µmol m^{-2} s^{-1}) determined high cover values of stress-tolerant competitors (about 66% of the total herb layer cover). As light intensity decreased (50.1–75.0 µmol m^{-2} s^{-1}), stress-tolerant competitors dropped and were replaced by competitors and by competitive stress-tolerant ruderals. A further PAR reduction (25.1–50.0 µmol m^{-2} s^{-1}) caused a decrease in competitor cover in favour of competitive stress-tolerant ruderals. At light intensities below 25.0 µmol m^{-2} s^{-1}, there was a 28% drop in the herb layer cover (mean value drops to 3.8%), involving above all competitive stress-tolerant ruderals and competitors, the latter reaching the lowest mean cover value (0.7%).

On the best-watered soils (water deficit < 40.0 mm yr^{-1}) competitive stress-tolerant ruderals were favoured (about 72% of the total herb layer cover) (fig. 3B). As water deficit increased (40.1–140.0 mm yr^{-1}), competitors peaked, while competitive stress-tolerant ruderals declined slightly; a great
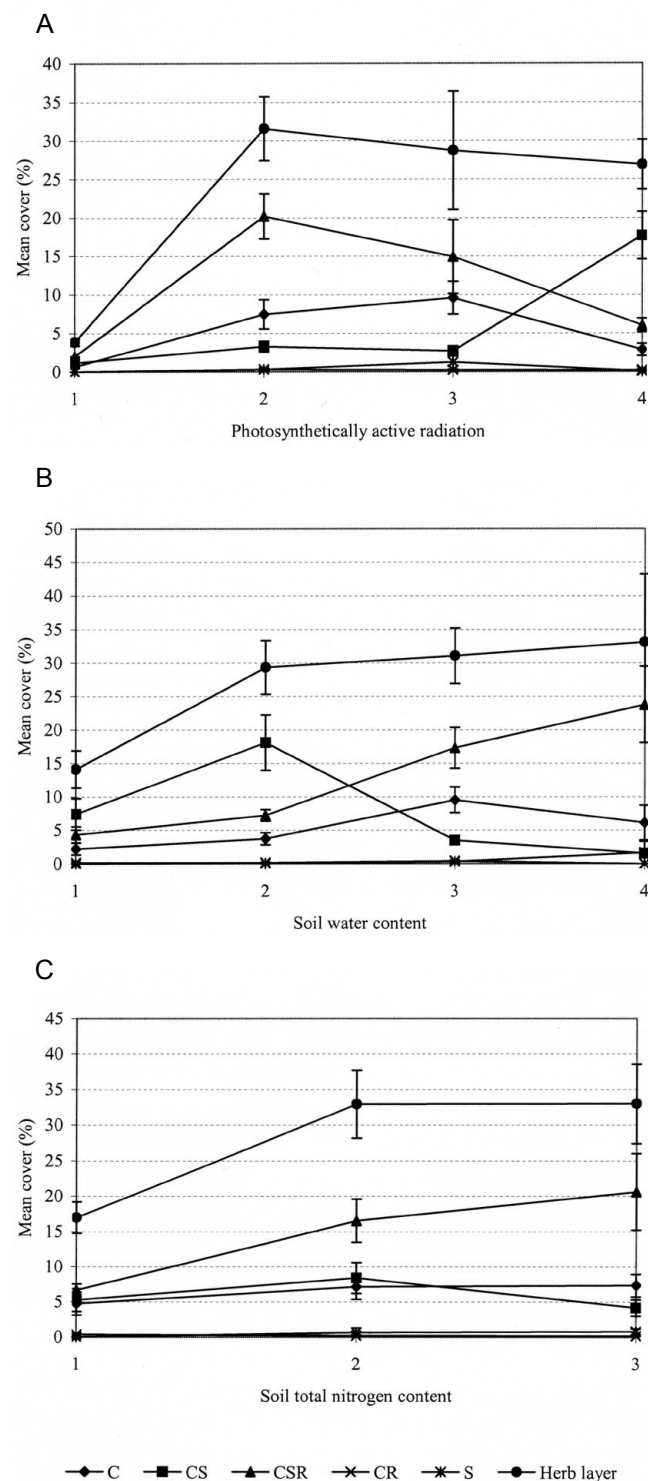
Figure 3 – Mean percentage cover of plant functional types (according to Grime's life strategies) and the total herb layer along photosynthetically active radiation (A), soil water content (B) and soil total nitrogen content (C) gradients. Standard error bars are shown. Environmental variables, whose classes follow an ascending order of light, water and nitrogen availability, are explained in table 1. C – competitors, CR – competitive-ruderals, CS – stress-tolerant competitors, CSR – competitive stress-tolerant ruderals, S – stress-tolerators.

part of them was replaced, within the range 240.0–140.1 mm yr^{-1}, by stress-tolerant competitors, which increased about 15% in cover. In the worst-watered soils (> 240.1 mm yr^{-1}) although the loss of stress-tolerant competitors accounted for about 70% of the herb layer cover decrease, they nonetheless prevailed over competitive stress-tolerant ruderals and competitors.

In the range 2–6 g Kg^{-1} of soil nitrogen content, competitive stress-tolerant ruderals were the most represented, showing a decreasing trend as nitrogen became lower, while stress-tolerant competitors increased (fig. 3C). Below 2 g Kg^{-1}, competitive stress-tolerant ruderals, competitors and stress-tolerant competitors showed a decreasing trend.

DISCUSSION

All the environmental factors considered did affect floristic composition and ecological strategies in the herb layer. Nevertheless, the variation of both species and PFT data sets were best explained by photosynthetically active radiation that, in turn, is strictly linked to slope aspect. The importance of aspect (north-facing vs. south-facing slopes) was confirmed by the highest shared variation shown by PAR and soil water deficit. Both these variables depend on site topographic features, which determine the total solar radiation amount per unit area and, consequently, evapotranspiration rate and soil water deficit. Light radiation, indeed, apart from being a resource, determines an evaporative water demand and the potential for drought stress (Pausas & Austin 2001).

From a floristic point of view, the main gradient of variation (table 2, electronic appendix 2) was related to low light availability, which favoured sciaphilous nemoral species (e.g. *Sanicula europaea* L., *Melica uniflora* Retz., *Lathyrus venetus* (Mill.) Wohlf. and *Hepatica nobilis* Schreb.) and high soil dryness, which favoured species spread also in pastures and forest edges (e.g. *Brachypodium rupestre* (Host) Roem. & Schult., *Teucrium chamaedrys* L. and *Buglossoides purpurocaerulea* (L.) I.M.Johnst.) (Catorci & Orsomando 2001).

About functional composition of the herb layer, our findings showed that moderate and high stress levels filter the most adaptive strategy, while the other strategies tend to decrease in abundance (fig. 3). Instead, the intermediate and low stress levels allow the co-existence of a higher number of strategies and are related to higher values of the herb layer cover.

Competitive species were favoured by low/intermediate stress conditions. In such conditions, competitors (e.g. *Bromus ramosus* Huds., *Festuca heterophylla* Lam., *Luzula sylvatica* (Huds.) Gaudin subsp. *sylvatica* and *Melica uniflora* Retz.) are favoured because of the presence of rhizomes or lateral shoots with long thin internodes and adventitious roots (Klotz et al. 2002). As stated by Grime (2001), these structures allow competitors to exploit environments with high resource levels. Indeed, in the study area nitrogen concentration increase is accompanied by competitive species cover increase. The decreasing trend of competitive species at the highest PAR value, instead, can be explained given that this environmental feature in the submediterranean forest landscape is related to south-facing slopes, which have high summer drought stress;

in this situation, water availability is the main limiting factor and thus the intensity of the overall environmental stress is not low. Moreover, competitors had their lowest value at low light intensities; indeed, as noted by Grime (2001), the ability to compete is likely to be of secondary importance to the capacity to tolerate shade conditions. In fact, in the study area, the positive effect of drought stress absence on competitor abundance in the north-facing slopes is reduced by the low light intensity, which becomes the limiting factor (fig. 3). Instead, competitive stress-tolerant ruderal species (e.g. *Lathyrus venetus* (Mill.) Wohlf., *Sanicula europaea* L. and *Viola reichenbachiana* Jord. ex Boreau) peaked in such ecological conditions, namely in moderate light stress intensity and in well-watered soils. As stated by Grime (2001), these species, having intermediate characteristics among those of the competitor, the stress-tolerator, and the ruderal species, are adapted to habitats in which the level of competition is restricted by moderate intensities of stress or disturbance. In the studied forest landscape all the above mentioned environmental features are those of north-facing slopes, covered by mixed woods with a dominance of *Ostrya carpinifolia* Scop., sometimes with *Fagus sylvatica* L. (in colder and more moist conditions) or *Quercus cerris* L. (with a higher level of light availability at the soil level) (Catorci et al. 2003, Vitanzi et al. 2009).

Stress-tolerant competitors (e.g. *Brachypodium rupestre* (Host) Roem. & Schult.) showed their peak in conditions of strong light and of moderate dryness, while they were not significantly affected by nitrogen variation. Species having this strategy grow in relatively undisturbed conditions, experiencing moderate intensities of stress, especially where the plant communities are established on shallow infertile soils in the semi-arid climatic conditions (Grime 2001). Van der Veken et al. (2004) argued that plant species with stress tolerating life strategies, such as stress-tolerant competitors, are more present in warmer conditions. This is consistent with our findings. Indeed, in the submediterranean forest landscape, such environmental features are characteristic of the south-facing slopes and are related to the most xerophilous plant communities, mostly dominated by *Quercus pubescens* Willd. and sometimes *Ostrya carpinifolia* Scop. (Agnelli et al. 2008).

No patterns were found about stress-tolerator and competitive-ruderal species, which always had very low cover percentages; this probably means that the studied forest communities are not characterized by highly stressful or disturbed conditions.

CONCLUSIONS

Our results showed that, in submediterranean forests, changes in environmental features, especially those linked to variation in topographic conditions, and in the related stress gradients determine shifts in the ecological strategies of the forest herb layer species, according to Grime's theory. As a consequence, it will be possible to use measurements of forest herb layer PFTs as an indirect method for the assessment of environmental constraints. However, the analysis of ecological strategies did not make it possible to develop predictive models of floristic shifting so far (Oksanen & Ranta 1992, Austin &

Gaywood 1994, Wilson & Lee 2000). Nevertheless, it will be possible to predict whether a species adopting a specific strategy is likely to be positively or negatively affected by change in stress level due, for instance, to climate change.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the following: (1) Dendrogram from a cluster analysis run on the matrix relevés × species, using the complete linkage method (pdf); and (2) Redundancy analysis ordination graph for species data set, using environmental parameters as constraining variables (pdf).

ACKNOWLEDGEMENTS

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