Journal of Vegetation Science 18: 743-750, 2007
© IAVS; Opulus Press Uppsala.

Geographical and ecological differentiation in Greek *Fagus* forest vegetation

Tsiripidis, Ioannis[1*]; Bergmeier, Erwin[2] & Dimopoulos, Panayotis[3]

[1]*Department of Botany, School of Biology, Aristotle University of Thessaloniki, GR-54124 Greece;*
[2]*Department of Vegetation and Phytodiversity Analysis, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, DE-37073 Göttingen, Germany; E-mail erwin.bergmeier@bio.uni-goettingen.de;*
[3]*Department of Environmental and Natural Resources Management, University of Ioannina, Seferi 2, GR-30100 Agrinio, Greece; E-mail pdimopul@cc.uoi.gr;* [*]*Corresponding author; Fax +30 2310998295; E-mail tsiripid@bio.auth.gr*

Abstract

Question: Which are the gradients of floristic differentiation in Greek beech (*Fagus sylvatica*) forests? Which is the role of geographical and ecological factors in this differentiation?

Location: Beech forests of the plant geographical regions Northeast, North Central and East Central Greece.

Methods: A total of 1404 published and unpublished phytosociological relevés were used in the analyses. TWINSPAN and DCA were applied to classify and ordinate the relevés. Altitude, Indicator Values of relevés and their X and Y coordinates were used in *a posteriori* interpretation of the ordination axes. Kendall's correlation coefficients were calculated between DCA relevé scores and explanatory variables. Multiple linear regression was used to partition the variation explained by the first two DCA axes, between the geographical and the ecological variables.

Results: Classification resulted in 14 vegetation units defined by species composition. Two types of gradients, ecological and geographical, were revealed by the DCA of all relevés. The partition of the variation accounted for by the first and second DCA axis was attributed mainly to ecological and geographical variables, respectively.

Conclusions: Beech forests of northeast and Central Greece show phytogeographical differences, while ecologically similar vegetation units occur in both regions. A west-east gradient is revealed in Greek beech forest vegetation. The extent of the study area, its position along regional gradients and the comprehensiveness of the data set that is analysed determine the types of the gradients which can be revealed in a vegetation study.

Keywords: Balkan; Beech; Classification; Gradient analysis; Phytosociology.

Nomenclature: For names of mountains: Strid & Tan (1997). For names of plant taxa: Tutin et al. (1968-1993); Greuter et al. (1984-1989); Strid (1986); Strid & Tan (1991, 1997, 2002).

Abbreviations: DCA = Detrended Correspondence Analysis; IV = Indicator Value.

Introduction

A complex pattern of ecological and geographical factors is evident in many surveys of European *Fagus sylvatica* forest communities, especially when relatively large study areas are concerned (e.g. Horvat et al. 1974; Moravec 1985; Török et al. 1989; Dierschke 1990, 1998; Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001; Willner 2002; Tzonev et al. 2006). As reflected by the different concepts in beech forest syntaxonomy the relative importance of the ecological and phytogeographical factors in the floristic differentiation of beech forests has been a matter of discussion throughout Europe. According to the ecological approach (e.g. Willner 2002; Tzonev et al. 2006) mesophytic, thermophytic and acidophytic beech forests are distinguished, while the syntaxonomic approach by Dierschke (1998), Dzwonko & Loster (2000) and Bergmeier & Dimopoulos (2001) emphasizes the geographical differentiation, with chiefly differences in the macroclimate and species pool of the different regions (Bergmeier & Dimopoulos 2001; Knollová & Chytrý 2004). The former approach takes substrate and microclimatic differentiation as well as disturbance regimes into account (Horvat et al. 1974; Knollová & Chytrý 2004). The latter approach reflects partly a large-scale ecological differentiation, and partly differences in evolutionary and migration history. Obviously, the gradients revealed in a vegetation study depend on the size of the study area as well as on the vegetation type under investigation (Kuželová & Chytrý 2004; Fortin & Dale 2005).

The patchy occurrence of beech forest in Greece (Horvat et al. 1974; Bergmeier 1990), its diversity at the species and the community level, its wide ecological amplitude even close to the southeastern boundary of this community type (Bergmeier & Dimopoulos 2001), and the complex floristic gradients in Greece (Strid 1997) provide an excellent opportunity to explore the role of ecological and geographical gradients in the floristic differentiation of vegetation.

Views and hypotheses on the role of the ecological and geographical factors in the differentiation of beech forest vegetation in the southern Balkan are partly complementary and partly contradictory.

This appears from (1) the old classifications of Balkan beech forests in geographically framed alliances (e.g. Horvat et al. 1974), (2) the strong north-south gradient in the southwestern Balkan (including Central Greece) revealed by Dzwonko & Loster (2000), and (3) the complex-pattern classification by Bergmeier & Dimopoulos (2001) which strengthened the primarily geographical differentiation, and the dominance of the ecological over the geographical differentiation as found in Bulgarian beech forests (Tzonev et al. 2006) The topic is likely to be of interest for general biogeography and for applied fields such as silviculture and conservation biology.

The objectives of the present study are: (1) to explore the floristic differentiation within the beech forests of Central (C) and Northeast (NE) Greece by applying multivariate analysis on the basis of TWINSPAN and DCA, and (2) to assess the relative importance of geographical and ecological factors in this differentiation.

Material and Methods

Study area

Most beech forests in Greece occur in the mountains of the phytogeographical regions Northeast (NE), North Central (NC) and Northern Pindos (Strid & Tan 1997). The southernmost occurrences are in Southern Pindos and East Central (EC) Greece. The study area includes the beech forests of Northeast (Vouna Evrou, West and East Rodopi, Falakro, Vrontous, Pangeo, Cholomon, Chortiatis), North Central (Voras, Pieria, Olimbos, Kato Olimbos) and East Central Greece (Mavrovouni, Pilio and Ossa) (Fig. 1). The lowest altitude of the relevés in this study is 180 m a.s.l. (the lowest altitude of beech forest in Greece; Moulopoulos 1965) and the highest is 1920 m. Within the study areas, beech forests are found on a variety of substrates, including schist, gneiss, granite, marble, granodiorite, monzonite, phyllite, quartzite-sandstone, limestone, volcanic tuff and ophiolite.

Relevés

In all studies vegetation was sampled according to the Braun-Blanquet approach (Braun-Blanquet 1964). A database with relevés from beech forests of C (EC and NC) and NE Greece was created in TURBOVEG version 1.99 (Hennekens & Schaminée 2001). The relevés from the following sources were used to build the data base:

Raus (1980): 41 relevés;	Smiris (1980): 96;
Gerasimidis (1985): 20;	Smiris (1985): 6;
Volpers (1989): 5;	Adamis (1989): 82;
Bergmeier (1990): 94;	Theodoropoulos (1991): 52;
Karagiannakidou (1993): 25;	Habeck & Reif (1994): 61;
Schreiber (1998): 73;	Reif & Löblich-Ille (1999): 206;
Tsiripidis (2001): 584.	

Furthermore 13 relevés of Gamisans & Hebrard (1980) and 6 of Zoller et al. (1977) from the Rodopi mountain range, and 52 unpublished relevés of I. Tsiripidis from Mt. Falakro were added to the database.

From the above relevés we omitted those with a canopy cover of beech ≤ 10 %. In total 1404 relevés comprised the final data set.

Species misidentifications were corrected according to distribution and taxonomic information from Flora Hellenica (Strid & Tan 1997, 2002) and the Mountain Flora of Greece (Strid 1986; Strid & Tan 1991), as well as by checking herbarium material and floristic inventories (e.g. Tsiripidis & Athanasiadis 2003). In a few cases subspecies were aggregated to species and some species to species groups. *Fagus sylvatica* ssp. *sylvatica* and ssp. *orientalis* were merged into *F. sylvatica* s.l. because of the difficulty to define their distribution limits in NE Greece and in order to avoid distortion of the numerical analyses.

Where abundance values had been specified for different strata (herb, shrub, tree), these were recalculated to one value for each taxon in each relevé. In order to reduce noise, taxa occurring in seven or less relevés were excluded from the analyses. In total 340 taxa remained in the relevé set.

Explanatory variables

Species indicator values (Ellenberg et al. 1992; Pignatti et al. 2005) for temperature, moisture, reaction and nitrogen were used for the estimation of the ecological variables of the relevés. The indicator values (IV) of taxa were taken from the list covering Italy (Pignatti et al. 2005), as well as from the extended list distributed by Pignatti during the 16th Workshop of the European Vegetation Survey in 2006.

As 50 out of 340 species of the relevé set were not included in the aforementioned lists, their IV were calculated using the software JUICE (Tichý 2002). The calculation was based on the IV of the taxa which present high fidelity value with those taxa of which IV were to be calculated. The ϕ-coefficient (Legendre & Legendre 1998) was used as fidelity coefficient and the value 0.3 was chosen as fidelity cut level. This fidelity value is high and enables the calculation to be based on a small but sociologically and thus environmentally and phytogeographically related number of taxa. For 26 taxa (7.6 % of the total number) the calculation of IV was not possible as no taxa with known IV and fidelity value higher than

0.3 occurred with them. According to Ewald (2003), the exclusion of less than 20 % of the taxa from the relevés, affects the environmental indication values only weakly. Moreover, most of the taxa excluded from environmental indication calculation were rare. The indicator values for each relevé were calculated as weighted (by relative cover) average of the occurring taxa. The relative cover was calculated on the basis of the power transformed values of the cover percentages. As power the value 0.3 was used. The IV of relevés together with the altitude were ranged according to the method proposed by Sneath & Sokal (1973) and comprised the ecological variables of the explanatory data set.

Longitude and latitude of relevés were used to calculate their X and Y coordinates. The latter comprised the geographical variables of the explanatory data set.

Data analysis

Classification was assisted by the divisive method TWINSPAN (Hill 1979, 1994). Three pseudospecies cut-levels were used, corresponding to the cover values 0, 2 and 20 %. In each level of division, the classification was interpreted with the help of ordination diagrams, which were conducted applying Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980). DCA diagrams helped greatly to evaluate whether the groups created by TWINSPAN were ecologically or phytogeographically meaningful. From the several data sets which have been analysed by DCA, three are presented in the results section, one with all relevés (data set A), and two others which include the relevés from NE Greece (data set B) and C Greece (data set C). TWINSPAN was performed in JUICE 6.2 (Tichý 2002).

DCA was performed using CANOCO 4.5 (ter Braak & Šmilauer 2002). Detrending by segments and square-root transformation of the cover abundances of taxa were applied. The explanatory variables were used in DCA in order to support the interpretation of the diagrams. Correlations between DCA relevé scores and explanatory variables were calculated using the non-parametric Kendall coefficient.

In order to partition the variation that is accounted for by the first two DCA axes of the three data sets among the two groups of explanatory variables (ecological and geographical), multiple linear regressions were computed in which the response variable was the DCA relevé scores on each of the two first DCA axes and the explanatory variables were the ecological or geographical or both groups of variables. The corresponding values of the $R_\alpha{}^2$ (adjusted coefficient of determination) of these regressions represent the variation that is accounted for by the explanatory variables (Legendre & Legendre 1998). The fractions of variation accounted for by each group of explanatory variables, as well as by both groups of variables jointly, were computed for each DCA axis. By this way of variation partitioning, the amount of variation of the DCA relevé scores, which can by explained by the two groups of explanatory variables was calculated. Correlation coefficients and multiple linear regressions were computed using SPSS 12 (Anon. 2003).

The synoptic table (App. 1) is divided into two parts. The first part presents the fidelity values of the taxa based on the ϕ-coefficient (Legendre & Legendre 1998; Chytrý et al. 2002). The second part presents the constancy classes of the taxa. The vegetation units and taxa were re-arranged manually in order to obtain a better presentation of the differentiation.

Fig. 1. Distribution of the vegetation units of App. 1. Each bar represents the number of relevés (second number above bars) of a vegetation unit (first number above bars) in a mountain.

Table 1. Eigenvalues, length of gradient and total inertia for the DCA of the three data sets.

Data set	Eigenvalues		Gradient length		Total
	Axis 1	Axis 2	Axis 1	Axis 2	inertia
A	0.370	0.312	3.230	3.004	10.139
B	0.379	0.238	3.525	2.665	9.516
C	0.430	0.334	3.188	3.225	7.890

Results

Classification of relevés

The 1404 relevés were classified by means of TWINSPAN into 14 relevé groups, of which 8 occur in NE Greece and 6 in EC and NC Greece. The synoptic table of these units is found in App. 1. The relevé groups correspond to ecologically and phytogeographically interpretable vegetation units. The distribution of the vegetation units is presented in Fig. 1.

Unit 1 corresponds to the *Geranium macrorrhizum-Fagus sylvatica* community (Schreiber 1998; Bergmeier & Dimopoulos 2001) representing the beech forests of Mt. Falakro, near the timberline, on calcareous stony soil.

Unit 2 consists of mesophytic beech forests (*Soldanello rhodopaeae-Fagetum sylvaticae* and *Pulmonaria rubra-Fagus sylvatica* community in Bergmeier & Dimopoulos 2001; Tsiripidis et al. 2007) of NE Greece. They occur mainly on acidic soil with very good water and nutrient supply.

Unit 3 represents acidophytic forests of NE Greece, chiefly on gneiss. Most of these forests have been classified as *Calamagrostis arundinacea-Fagus sylvatica* community by Tsiripidis et al. (2007).

Unit 4 represents the beech forests of NE Greece occurring on calcareous substrate (mainly marble). Relevés of this unit from the Rodopi range were classified as *Brachypodium pinnatum-Fagus sylvatica* community (Tsiripidis et al. 2007).

Units 5 and 6 concern thermophytic beech forests of NE Greece, growing on acidic soils (mainly on gneiss). The relevés of unit 5 from the Rodopi range comprise *Hieracium olympicum-Fagus sylvatica*, *Luzula forsteri-Fagus sylvatica*, *Melittis melissophyllum* ssp. *albida-Fagus sylvatica* and *Quercus frainetto-Fagus sylvatica* communities (Tsiripidis et al. 2007). Unit 6 corresponds to the *Fagus sylvatica* ssp. *orientalis* community of lower altitudes (Bergmeier & Dimopoulos 2001).

Unit 7 corresponds to the *Lamiastro montani-Fagetum sylvaticae* (Bergmeier & Dimopoulos 2001). It includes the mesophytic beech forests of Mt. Voras, growing on humid nutrient-rich soils.

Unit 8 includes forests of Mt. Voras occurring in warmer and drier sites than those of the previous unit, treated as '*Galio-odorati-Fagetum festucetosum drymeii*' by Smiris (1980), and classified within the *Galium odoratum-Fagus sylvatica* community by Bergmeier & Dimopoulos (2001).

Unit 9 corresponds to the *Orthilio secundae-Fagetum sylvaticae* (Bergmeier & Dimopoulos 2001). It represents the acidic forests of C Greece.

Units 10 and 11 occur on Mt. Olimbos. The first represents forests on calcareous substrate at high elevations, classified as *Cardamine graeca-Fagus sylvatica* community by Bergmeier & Dimopoulos (2001). Forests of the second unit occur at much lower altitudes and represent the subcommunity with *Fraxinus ornus* of the *Lathyro alpestris-Fagetum sylvaticae* (Bergmeier & Dimopoulos 2001).

Unit 12 consists of the thermophytic beech forests of C Greece which grow on various substrates. It corresponds to the *Lathyro alpestris-Fagetum sylvaticae* (Bergmeier & Dimopoulos 2001).

Units 13 and 14 represent a group of local thermophytic beech forests in the mountains of Cholomon and Chortiatis (in the southwestern part of NE Greece) (Tsiripidis et al. 2005a). They were classified as *Rubus canescens-Fagus sylvatica* community by Bergmeier & Dimopoulos (2001).

Table 2. Correlations (Kendall's coefficient) between DCA relevé scores and the explanatory variables. * = Significance at the 0.01 level. For abbreviations see Fig. 2.

Data set	Axis	Axis1	Axis2	T	M	R	N	Alt	Lon	Lat
A	1	1	-0.036	0.240*	-0.339*	-0.033	-0.280*	-0.545*	0.185*	-0.132*
A	2	-0.036	1	0.222*	-0.017	0.093*	0.001	0.053*	-0.484*	-0.571*
B	1	1	0.051	0.306*	-0.330*	0.064*	-0.277*	-0.657*	0.332*	-0.310*
B	2	0.051	1	0.050	0.022	-0.372*	-0.227*	-0.105*	0.285*	-0.050
C	1	1	0.058	0.259*	-0.300*	-0.143*	-0.338*	-0.339*	0.452*	-0.317*
C	2	0.058	1	0.109*	0.001	0.073*	0.186*	-0.444*	0.092*	0.323*

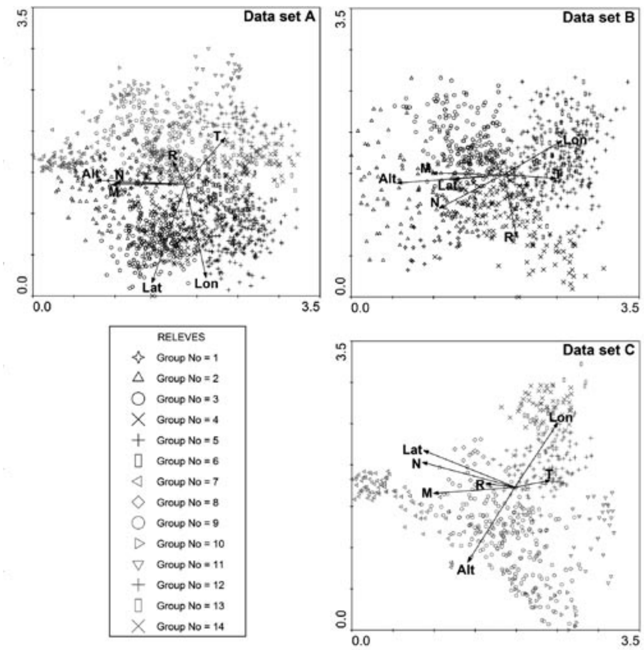

Fig. 2. DCA biplot of the first two axes. Scaling factor was set to three. The three diagrams correspond to the three data sets A (all relevés), B (NE Greece) and C (Central Greece). Alt: altitude, T: temperature, M: moisture, R: reaction, N: nitrogen, Lon: longitude, Lat: latitude. Group numbers correspond to the vegetation units in App. 1.

Indirect gradient analysis

The most important results of the DCA for the three data sets are summarized in Table 1. The DCA diagram of all relevés (data set A) (Fig. 2) revealed a differentiation along two major gradients, one ecological and one geographical. The first axis was significantly correlated with altitude, moisture, nitrogen and temperature as well as with all geographical variables (Table 2). However, the correlations of the geographical variables with axis 2 were much stronger than those with axis 1. Significant, yet weak correlations of ecological variables with axis 2 exist with temperature, reaction and altitude. Consequently, axis 1 represents chiefly an ecological gradient expressing altitude, moisture and nitrogen, while axis 2 represents a geographical gradient. This conclusion is supported by the clear discrimination of the relevés of NE Greece (black colour) from those of C Greece (grey colour) along axis 2 (Fig. 2). However, the relevés from the southwestern part of NE Greece (Mt. Cholomon and Mt. Chortiatis; vegetation units 13 and 14) appeared together with the ones of C Greece. This is why relevés of the first six units in App. 1 will be assigned to NE Greece (data set B) and relevés of the units 7-14 will be assigned to C Greece and comprise data set C.

In the DCA diagram of the relevés of NE Greece (data set B) the units were more distinct than with all relevés included (Fig. 2). The first two axes were correlated with environmental as well as with geographical variables (Table 2). The first axis is stronger correlated with altitude, the second with reaction. Axis 1 represents an altitudinal gradient with which temperature, moisture and nitrogen present relatively highly significant correlations. The correlations of the geographical variables with axis 1 may be attributed to the geographical structure of the ecological variables (viz., higher elevations in the western part of the Rodopi mountain range than in the eastern part). Axis 2 seems to represent mainly soil reaction, which is also geographically structured since calcareous substrates are restricted to the western part of NE Greece.

In the DCA of the relevés of C Greece (data set C; Fig. 2) the vegetation units were also more distinct than with all relevés. Axis 1 was correlated with both ecological and geographical variables (Table 2), and it is quite unclear which gradient it represents. However, it contributes to the discrimination of the relevés of vegetation unit 7 from all the others of the data set C. Axis 2 presents the strongest correlation with altitude and supports the discrimination of the more thermophytic vegetation units 12-14 from the more cool and humid units 9 and 10.

Table 3. Partitioning of the variation accounted for by DCA axes 1 and 2; a = variation explained by ecological variables; b = variation explained by ecological and geographical variables jointly; c = variation explained by geographical variables; d = residual variation.

Data set	Axis	a	b	c	d
A	1	43.4	30.0	2.4	24.2
A	2	4.2	15.6	53.6	26.6
B	1	54.8	28.7	0.5	16.0
B	2	40.4	7.3	5.0	47.3
C	1	23.2	45.8	9.5	21.5
C	2	27.4	27.2	11.5	33.9

Variation partitioning

The variation partitioning was conducted separately for each axis and data set. The results are presented in Table 3. In data set A the variation of the relevé scores along the first DCA axis was attributed mainly to ecological variables, while the proportion of variation explained jointly by both groups of variables was also relatively high. The second axis represents variation attributed mainly to the geographical variables. This differentiation of the first two DCA axes regarding the groups of variables was clear only in data set A. In data set B the relevé scores of both DCA axes were explained to a much higher extent by the ecological variables. In data set C the variation of DCA relevé scores explained by ecological or geographical variables, was more or less the same and rather low, while the joint effect of the above two types of variables was relatively high.

Discussion and Conclusions

Classification

The TWINSPAN classification reflects both the ecological and the phytogeographical gradient. The first four groups (second level of division) correspond to the main ecological groups of Greek beech forests (mesophytic, acidophytic, calcareous at high altitudes, thermophytic) (Bergmeier & Dimopoulos 2001; Tsiripidis et al. 2005b). Similarly, the TWINSPAN classification of the beech forests of the southern part of Central Europe (Willner 2002), also based on TWINSPAN, revealed a main ecological gradient.

The differential taxa of the synoptic table (App. 1) may be grouped roughly into four categories:

(1) taxa differentiating vegetation units of NE Greece from those of C Greece;

(2) taxa differentiating ecological units throughout Greece;

(3) exclusive taxa for one vegetation unit;

(4) taxa exclusive for certain areas (single or connected mountain ranges).

The first category indicates a geographically structured floristic differentiation among beech forests, while categories 3 and 4 may be due to specific ecological conditions in certain areas (ecological differentiation) or to their specific species pools (geographical differentiation or both geographical and ecological differentiation). The second category reflects the well-known ecological differentiation of European beech forests.

The first two categories of differential taxa produce two major gradients of differentiation. In the synoptic table we preferred the arrangement of the units according to the geographical gradient since the geographically differential taxa (31) outnumber by far the ecological ones (15).

Gradients in the Greek beech forests

The variation explained by the first two DCA axes in all three data sets is low, ranging from 6.5 to 9.7 % of the total floristic variation. However, low proportions of explained variance may nonetheless be informative considering the noise that large data sets of plant community data commonly have (Økland 1999; ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003). The diagrams of all the three data sets are interpretable and reveal the main gradients of floristic differentiation. Specifically, the first two axes of the DCA diagram of data set A represent the two types of gradients in the beech forests of C and NE Greece.

In this study, variation partitioning is conducted only for the variation accounted for by the first two DCA axes and not for the whole variation of the data set. The approach of variation partitioning proposed by Borcard et al. (1992) was not used in the present study in order to avoid the use of explanatory variables derived from the species composition in a canonical correspondence analysis. The method used here avoids this problem as it correlates the explanatory variables with the DCA scores calculated only on the basis of the floristic composition of the relevés (ter Braak & Šmilauer 2002).

The proportions (V) of the total floristic variation which can be attributed to the geographical or ecological variables, on the basis of the first two DCA axes, can be calculated using the formula: $V = (V_{\text{axis1}} * V_{x1}) + (V_{\text{axis2}} * V_{x2})$, where V_{axis1} and V_{axis2} are the proportions of variation that DCA axes 1 and 2 explain, and V_{x1} and V_{x2} are the proportions of variation in the DCA relevé scores (along axes 1 and 2, respectively) that the ecological or geographical variables explain. In data set A, these proportions are approximately 1.7 % for both types of variables. Of course the proportions of explained variation are too small to decide which category of variables is most responsible for the floristic variability. Nevertheless, the results of variation partitioning clearly suggest that in beech forests of C and NE Greece a gradient of regional scale occurs which strongly supports a plant geographical differentiation of beech forest vegetation.

The results of this study combined with those of Dzwonko & Loster (2000) and Bergmeier & Dimopoulos (2001) show a strong plant geographical differentiation between the beech forest vegetation units in the southern Balkan Peninsula directed both west to east and north to south. The former gradient is described also by Strid (1997) on the basis of the Greek flora differentiation. Strid (1997) suggests the Axios River as phytogeographical border between NE and NC Greece and the lowland area east of the Pindos range as a phytogeographical border between the latter and the mountains of C Greece.

The results of this study will not put an end to the discussion on the nature of the gradients underlying the differentiation of the southern Balkan beech forest vegetation. It will depend on the scale of the study area, its position along a possible regional gradient, as well as the size and quality of the data set used which gradients could be revealed in an analysis (Knollová & Chytrý 2004; Fortin & Dale 2005). The fact that a north-south geographical gradient was not revealed in the present study may be attributed to the fact that C Greece comprises only a part of the gradient that Dzwonko & Loster (2000) found in the southwestern Balkan Peninsula. Furthermore, the west to east geographical gradient found in the present study emerged thanks to almost 600 new relevés from the Rodopi range (Tsiripidis 2001), an area insufficiently represented in the analysis of Bergmeier & Dimopoulos (2001). The results of the present study summarize the available data and help to formulate more detailed hypotheses, for instance on the identification of geographical borders between the two geographically differentiated vegetation groups as well as why the geographical differential taxa are distributed in the way that is reflected by our data. A wider study area and a more tightly knotted network of data may help to improve our knowledge on the gradients of differentiation of beech forest vegetation in the southern Balkans and beyond.

Acknowledgements. This paper is dedicated to Dimitrios Babalonas, Professor of Systematic Botany and Phytogeography at the Aristotle University of Thessaloniki and one of the main contributors to the knowledge of Greek vegetation who suddenly passed away in October 2004. We thank Helge Bruelheide and three anonymous reviewers for their valuable comments and suggestions.

References

Adamis, M. 1989. *Vegetationskundliche Untersuchungen in Buchenwäldern und verwandten Gesellschaften in Nordost-Griechenland*. Dipl. Thesis, Georg-August-Universität, Göttingen, DE.

Anon. 2003. *SPSS for Windows, Rel. 12.0.0.* SPSS Inc., Chicago, IL, US.

Bergmeier, E. 1990. Wälder und Gebüsche des Niederen Olymp (Káto Olimbos, NO-Thessalien). Ein Beitrag zur systematischen und orographischen Vegetationsgliederung Griechenlands. *Phytocoenologia* 18: 161-342.

Bergmeier, E. & Dimopoulos, P. 2001. *Fagus sylvatica* forest vegetation in Greece: Syntaxonomy and gradient analysis. *J. Veg. Sci.* 12: 109-126.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

Braun-Blanquet, J. 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. 3rd. ed. Springer, Berlin, DE.

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, J. 2002. Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13: 79-90.

Dierschke, H. 1990. Species-rich beech wood*s* in mesic habitats in central and western Europe: a regional classification into suballiances. *Vegetatio* 87: 1-10.

Dierschke, H. 1998. Syntaxonomical survey of European beech forests: some general conclusions. *Ann. Bot.* (*Roma*) 55: 17-26.

Dzwonko, Z. & Loster, S. 2000. Syntaxonomy and phytogeographical differentiation of the *Fagus* woods in the Southwest Balkan Peninsula. *J. Veg. Sci.* 11: 667-678.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot.* 18: 1-248.

Ewald, J. 2003. The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés. *Basic Appl. Ecol.* 4: 507-513.

Fortin, M.-J. & Dale, M.R.T. 2005. *Spatial analysis; a guide for ecologists*. Cambridge University Press, Cambridge, UK.

Gamisans, J. & Hebrard, J.-P. 1980. A propos de la vegetation des forêts en Grèce du nord-est (Macédoine orientale et Thrace occidentale). *Doc. Phytosociol.* 5: 243-289 + App.

Gerasimidis, A. 1985. *Standortkundliche Verhältnisse und postglaziale Vegetationentwicklung der Wälder Lailias, Bez. Serres und Katafygi im Pieria-Gebirge (Nordgriechenland).* Ph.D. Thesis. *Sci. Ann. Dept. Forest. Nat. Env. Aristotle Univ. Thessaloniki* 26 (7): 1-133. (In Greek.)

Greuter, W., Burdet, H.M. & Long, G. (eds.) 1984-1989. *Med-Checklist 1, 3, 4*. Conservatoire et Jardin botaniques, Genève, CH.

Habeck, F. & Reif, A. 1994. Die Waldgesellschaften der montanen und subalpinen Stufe des Ostabfalls des Olymp, Griechenland. *Phytocoenologia* 22: 501-536.

Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, a comprehensive database management system for vegetation data. *J. Veg. Sci.* 12: 589-591.

Hill, M.O. 1979. *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two way table by classification of the individuals and the attributes*. Ecology & Systematics, Cornell University, Ithaca, NY, US.

Hill, M.O. 1994. *DECORANA and TWINSPAN, for ordination and classification of multivariate species data: a new edition, together with supporting programs, in FORTRAN 77*. Institute of Terrestrial Ecology, Huntingdon, UK.

Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

Horvat, I., Glavač, V. & Ellenberg, H. 1974. *Vegetation Südosteuropas*. G. Fischer, Stuttgart, DE.

Karagiannakidou, V. 1993. Site research in beech forests of the Chortiatis Mountain Range, NE Greece. *Bot. Helv.* 103: 23-37.

Knollová, I. & Chytrý, M. 2004. Oak-hornbeam of the Czech Republic: geographical and ecological approaches to vegetation classification. *Preslia* 76: 291-311.

Kuželová, I. & Chytrý, M. 2004. Interspecific associations in phytosociological data sets: how do they change between local and regional scale? *Plant Ecol*. 173: 247-257.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*, 2nd. English ed. Elsevier Science, Amsterdam, NL.

Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK.

Moravec, J. 1985. Chorological and ecological phenomena in the differentiation and distribution of the *Fagion* associations in Bohemia and Moravia (Czechoslovakia). *Vegetatio* 59: 39-45.

Moulopoulos, C. 1965. The beech woods of Greece. Part 1. The beech species and their distribution in Greece. *Epist. Epet. Geopon. Dasol. Shol. Arist. Panepist. Thessalonikis* 1965: 1-85. (In Greek.)

Økland, R.H. 1999. On the variation explained by ordination and constrained ordination axes. *J. Veg. Sci*. 10: 131-136.

Pignatti, S., Menegoni, P. & Pietrosanti, S. 2005. Bioindicazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italia. *Braun-Blanquetia* 39: 1-97.

Raus, T. 1980. Die Vegetation Ostthessaliens (Griechenland). III. Querco-Fagetea und azonale Gehölzgesellschaften. *Bot. Jahrb. Syst*. 101: 313-361.

Reif, A. & Löblich-Ille, K. 1999. Sind die Rotbuchenwälder im Pieria-Gebirge (Nordgriechenland) höhenzonal oder extrazonal? Eine Studie zum Übergang zwischen temperaten und submediterranen Wäldern in Nordgriechenland. *Phytocoenologia* 29: 87-146.

Schreiber, H.J. 1998. Waldgrenznahe Buchenwälder und Grasländer des Falakro und Pangäon in Nordostgriechenland. Syntaxonomie, Struktur und Dynamik. *Arb. Inst. Landschaftsökol. Westf. Wilhelms-Univ. Münster* 4: 1-171.

Smiris, P. 1980. *Standortskundliche und waldbauliche Untersuchungen von naturnahen Buchenwäldern im Voras-Gebirge (Nordgriechenland)*. Ph.D. Thesis, Georg-August-Universität, Göttingen, DE.

Smiris, P. 1985. Die Struktur im Urwald von Paranestion. *Sci. Ann. Dept. Forest. Nat. Env. Aristotle Univ. Thessaloniki* 28: 597-670. (In Greek.)

Sneath, P. & Sokal, R. 1973. *Numerical taxonomy – The principles and practice of numerical classification*. W.H. Freeman, San Francisco, CA, US.

Strid, A. (ed.) 1986. *Mountain flora of Greece,* Vol.1. Cambridge University Press, Cambridge, UK.

Strid, A. 1997. Introduction. In: Strid, A. & Tan, Kit (eds.) *Flora Hellenica* Vol. 1. Koeltz, Königstein, DE.

Strid, A. & Tan, Kit (eds.) 1991. *Mountain flora of Greece*, Vol. 2. Edinburgh University Press, Edinburgh, UK.

Strid, A. & Tan, Kit (eds.) 1997, 2002. *Flora Hellenica* 1-2. Koeltz, Königstein, DE.

ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination* (version 4.5). Microcomputer Power, Ithaca, NY, US.

Theodoropoulos, K. 1991. *Bestimmung und Klassifizierung der pflanzensoziologischen Vegetationseinheiten im Universitätswald Taxiarchis Chalkidiki*. Ph.D. Thesis. *Sci. Ann. Dept. Forest. Nat. Env. Aristotle Univ. Thessaloniki* 32 (18): 1-200. (In Greek.)

Tichý, L. 2002. JUICE, software for vegetation classification. *J. Veg. Sci*. 13: 451-453.

Török, K., Podani, J. & Borhidi, A. 1989. Numerical revision of the Fagion illyricum alliance. *Vegetatio* 81: 169- 180.

Tsiripidis, I. 2001. *Plant communities of beech forests in Rodopi mountain range and their environmental assessment for reforestation*. Ph.D. Thesis, Aristotle University of Thessaloniki, Thessaloniki. (In Greek.)

Tsiripidis, I. & Athanasiadis, N. 2003. Contribution to the knowledge of the vascular flora of NE Greece: Floristic composition of the beech (*Fagus sylvatica* L.) forests in the Greek Rodopi. *Willdenowia* 33: 273-297.

Tsiripidis, I., Fotiadis, G., Karagiannakidou, V. & Babalonas, D. 2005a. Classification problems of forest vegetation in Greece: Transition from beech to deciduous oak zone. *Bot. Chron*. 18(1): 253-268.

Tsiripidis, I., Karagiannakidou, V. & Athanasiadis, N. 2005b. Ecological and phytogeographical differentiation of beech forests in Greek Rodopi (Northeast Greece). *Biologia* 60: 57-67.

Tsiripidis, I., Karagiannakidou, V., Alifragis, D. & Athanasiadis, N. 2007. Classification and gradient analysis of the beech forest vegetation of the southern Rodopi (Northeast Greece). *Folia Geobot*. 42: 249-270.

Tutin, T.G. et al. (eds.) 1968-1993. *Flora Europaea*, Vols. 2-5 and Vol. 1, 2nd. ed. Cambridge University Press, Cambridge, UK.

Tzonev, R., Dimitrov, M., Chytrý, M., Roussakova, V., Dimova, D., Gussev, C., Pavlov, D., Vulchev, V., Vitkova, A., Gogoushev, G., Nikolov., I., Borisova, D. & Ganeva, A. 2006. Beech forest communities in Bulgaria. *Phytocoenologia* 36: 247-279.

Volpers, T. 1989. Changes in microclimate and vegetation after thinning in a montane virgin forest. *Phytocoenologia* 17: 71-104.

Willner, W. 2002. Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. *Phytocoenologia* 32: 337-453.

Zoller, H., Geissler, P. & Athanasiadis, N. 1977. Beiträge zur Kenntnis der Wälder, Moos- und Flechtenassoziationen in den Gebirgen Nordgriechenlands. *Bauhinia* 6: 215-255.

Received 24 July 2006;
Accepted 20 February 2007;
Co-ordinating Editor: H. Bruelheide.

For App. 1, see also JVS/*AVS Ele*ctronic Archives;
www.opuluspress.se/