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The effects of stand characteristics on the understory vegetation in Quercus petraea and Q. cerris dominated forests

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Abstract. Different types of forest use significantly changed the structure and species composition of European temperate forests. Herbaceous species and seedlings are important parts of the forest ecosystem, thus it is necessary to understand the effects of stand characteristics on the species composition of the understory. In our study we assessed the main factors that affect the species composition of herb and tree seedling assemblages in *Quercus petraea* and *Q. cerris* dominated stands (age 50-150 years) in the Bükk Mountains, Hungary. The relationship between the studied assemblages and explanatory variables (tree species composition, stand structure, canopy closure and topography) were explored by Redundancy Analysis (RDA). The occurrence of herbaceous species was affected by canopy closure, stand structure (mean DBH and DBHcv of trees), topography and the density and diversity of shrub layers. Oak forest species were related to more open stands with sparsely distributed large trees, while mesic forest species were positively related to heterogeneous stand structure, low shrub density, and western exposure. Seedlings of trees and shrubs showed a dispersal limited phenomenon. The composition of seedlings was significantly influenced by the mean DBH of trees, the structural heterogeneity of the overstory, the tree species diversity and the density of shrub layers. However the seedlings of both dominant oak species required the same stand structure, sessile oak was able to regenerate almost exclusively in those stands where it was dominant in the overstory, which is significant for the management of the species. Generally, forest management affects species composition and structure of the overstory, accordingly it had direct and indirect effects on the understory community as well.

Abbreviations: DBH – Diameter at breast height

Nomenclature: Tutin et al (1964-1993)

Introduction

From the Roman age, human impact has been growing in the European forests (Bengtsson et al 2000, Rackham 2000, Szabó 2005). The different types of forest use such as harvesting, coppicing, fuel and litter collecting, grazing and hunting significantly changed the species composition, structure, production and dynamics of forests (Bengtsson et al 2000, Rubio et al 1999). The establishment and growth of seedlings, their composition, spatial and temporal pattern creates the basis of forest dynamics and regeneration. Herbaceous layer contributes to species diversity, primary production, carbon storage and nutrient supply; it can also serve as habitat and food for other organism groups (Whigham 2004). In addition, herbaceous species can respond to the changed environmental conditions quickly, hereby they are potential ecological indicators (von Oheimb and Härdtle 2009, Standovár et al 2006). It is essential to understand the factors that affect the species composition of the understory assemblages (including herbs and seedlings).

One of the most important factors directly affecting understory vegetation is the amount and pattern of light (Van Calster et al 2008, von Oheimb and Brunet 2007, Tinya et al 2009). In shaded stands generalist and shade tolerant species dominate the herb layer (von Oheimb and Brunet 2007, Rogers et al 2008, Tybirk and Strandberg 1999). Higher canopy openness increases not only the proportion of light-demanding and ruderal species (Brunet et al 1996, Pérez-Ramos et al 2008, Tybirk and Strandberg 1999), but species richness and diversity as well (von Oheimb and Härdtle 2009). The amount of light reaching the understory is also essential for the regeneration of some arboreals – including oak species (von Oheimb and Brunet 2007, Rogers et al 2008, Schumann et al 2003). The second group of influential stand variables are soil properties, such as pH, nutrient content and soil moisture (Tybirk and Strandberg 1999). These variables determine which species can establish and survive in a stand (Brunet et al 1996, Dzwonko and Gawroński 2002), in addition, they determine the microbe and mycorrhiza community of the soil, thus influencing the species composition of the herb layer in an indirect way as well (Pérez-Ramos et al 2008). Finally, herb and seedling species composition is mainly affected by propagule source. In forest conditions, dispersal distance is a potential limitation even for anemochore species (Hermy et al 1999), in addition, shelterwood silvicultural system creates broad cutting sites, which further increase the importance of the propagule source (Decocq et al 2005). Species composition and the structure of the shrub and overstory layers have great impact on these stand characteristics (Van Calster et al 2008, Kirby 1988, Rogers et al 2008). Tree species of the overstory serve as the propagule source for the seedlings; the density and structure of the canopy and shrub layers determine moisture and light availability for the understory (Barbier et al 2008, Horn 1971, Rogers et al 2008, Tinya et al 2009), and the quality and quantity of litter affect soil moisture, temperature, pH and C:N ratio (Sharpe et al 1996, Graae and Heskjaer 1997).

The relationship between the overstory and the understory is better revealed in mesic forests (Burrascano et al 2011, Graae and Heskajer 1997, Härdtle et al 2003, Kelemen et al 2012, Standovár et al 2006). In case of dry, oak dominated forests, our knowledge is more incomplete, in spite of their economic and conservational significance. The extension of *Quercus cerris* and *Q. petraea* dominated forests is 120 000 ha in Hungary (Bölöni et al 2008). These forests were used for grazing, masting, firewood collecting in the past (Kotroczó et al 2007), and most of them are managed in the present as well. Additionally, these turkey oak – sessile oak forests provide habitat to several forest species in Hungary (Borhidi et al 2012, Bölöni et al 2011, Chytrý and Tichý 2003, Csapody et al 1962, Roleček 2005).

This study tries to ascertain the most important factors influencing the composition of the understory. In our paper we explore the relationships between forest stands (tree species composition, stand structure, topography) and the species composition of herbaceous and seedling assemblages.

Methods

Study area

The study was carried out in the southern part of the Bükk Mountains, in Hungary, at elevations between 300 m and 600 m. In the oak dominated area of the Bükk Mountains average annual precipitation is 600-700 mm, average annual mean temperature is 8.5˚C (Mersich et al 2002). Monthly mean temperature in January ranges from -4.1 ˚C to -3.4˚C, while in July from 17.7˚C to 19.2˚C (Mersich et al 2002). In the studied area the bedrock is mainly limestone, but dolomite, loess and sandstone also occur. Main soil types are brown forest soil and rendzina.

Pannonian-Balkanic turkey oak – sessile oak forests (91M0, Directive 92/43/EEC. 1992) dominated by *Q. cerris* and *Q. petraea* create the dominant forest type in Hungary between 200-600 m a.s.l. This forest type covers 120 000 ha in Hungary, circa 6% of the total forest cover (Bölöni et al 2008). Beside the two dominant oak species, *Acer campestre*, *Sorbus torminalis* and *Fraxinus excelsior* can occur with a higher ratio, while *Q. pubescens* and *Carpinus betulus* are less frequent associate tree species. In the well developed shrub layer *Cornus mas*, *Crataegus monogyna*, *Ligustrum vulgare*, *Prunus spinosa*, *Rosa canina s.l.* and *A. campestre* are common species. The presence of light-demanding and drought tolerant forest species is typical in the species-rich understory. Sedges (*Carex michelii*, *C. montana*, *C. muricata*) and grasses (*Brachypodium sylvaticum*, *Dactylis glomerata*, *Festuca heterophylla*, *Melica uniflora*, *Poa nemoralis*) dominate the herb layer. Frequent herbs of the understory are *Tanacetum corymbosum, Campanula* spp. *Clinopodium vulgare*, *Galium schultesii*, *Geum urbanum, Hieracium* spp., *Lathyrus* spp., *Symphytum tuberosum*, *Trifolium* spp., *Vicia* spp. and *Vincetoxicum officinale*. *Q. cerris* and *Q. petraea* dominated forests can be found on various bedrocks, on neutral or slightly acidic soil. In the past, these forests have been used intensively for grazing, masting and firewood production in the framework of a coppicing silvicultural system (Kotroczó et al 2007). They have been converted to high forests, managed by a uniform shelterwood silvicultural system with an 80-90 year long rotation period.

Data collection

Thirty-one forest stands (compartments of forest management) were selected from the Database of Hungarian Forest Stands (ÁESZ 2008) using stratified random sampling. The selected stands represented the same region, forest type, elevation range (300 – 600 m), excluding northern exposure. The selection was based on the age of the dominant tree layer. Stands were grouped into three age categories: young (below 80 yr), mature (80-120 yr) and overmature (dominant layer older than 120 yr, not managed for 40 yr). From the young and mature categories 29 stands were selected randomly, while from the overmature category all (two) potential stands were studied. The number of overmature stands is very limited in the region; these are abandoned forests for conservation purposes, which belong to forest reserves (Kecskés-Galya Forest Reserve, Vár-hegy Forest Reserve, Horváth and Borhidi 2002, www.erdorezervatum.hu). One hundred and twenty-two sampling plots were selected, usually two to five in each stand (more in unmanaged forests, because of the scarcity of forest reserves). Their minimum distance from roads and forest edges was 50 m to avoid edge effect, and also 50 m was the minimum distance between plots in the same stand. Stand age was more or less evenly distributed in the whole sample (between 48 and 150 yr).

Vegetation was sampled in four layers: (1) overstory - trees larger than 5 cm in DBH (diameter at breast height); (2) high shrub layer - woody plants higher than 130 cm, DBH smaller than 5 cm; (3) low shrub layer - woody plants between 50 cm and 130 cm height; (4) understory layer – woody plants (seedlings) lower than 50 cm height and herbaceous species. The understory layer was surveyed from June to August 2009, the two shrub layers and the overstory in the spring and autumn of 2009. The sampling design of the different layers is shown on **Fig. 1**. The study of the overstory was carried out in the entire circular sampling plots, each 500 m^2 in size. For each tree the following variables were recorded: species, circumference and vitality (using healthy, stem damaged, crown damaged, stem and crown damaged and dead tree categories). For each tree we recorded whether its crown reaches the average canopy height (dominant tree) or it is lower (suppressed tree). The volume of logs was estimated by line-intercept method using three 12.6 m long lines, starting from the centre of the sampling plots to three directions (0, 120 and 240 degree, Ståhl et al 2001, Warren and Olsen 1964, Van Wagner 1968). Canopy closure was measured by a spherical densiometer, with a standard method: at four spots (5.6 m from the centre in the cardinal directions), facing to north, east, south and west (Lemmon 1956). For every plot, the average of the sixteen measured values was used as the representative estimation. We measured the height of 1-3 trees per sampling plot using Haglöf Vertex III height and distance meter, and we noted the exposure and slope at each sampling plot. In the case of shrub layers, we counted the individuals (abundance) of species (when we could not determine individuals accurately, we counted main shoots). The low shrub layer was studied in four circular subplots, each 7 m^2 in size, to 5.6 m from the centre, in the cardinal directions. For the high shrub layer, one 100 m^2 circular subplot was studied in each sampling plot. The understory layer was surveyed in 28 0.5 m^2 circular subplots in each plot, systematically arranged along 3 circles (with 4 m, 7 m and 11 m radius). Presence/absence of herb and seedling species was recorded in all subplots. Herbaceous species were classified as oak forest species or mesic forest species, based on their habitat preference. (Horváth et al 1995, Simon 2000) *(App. 1)*. During the analysis names of the species were abbreviated using the first three letters of the genus and species names *(App. 1, 2)*.

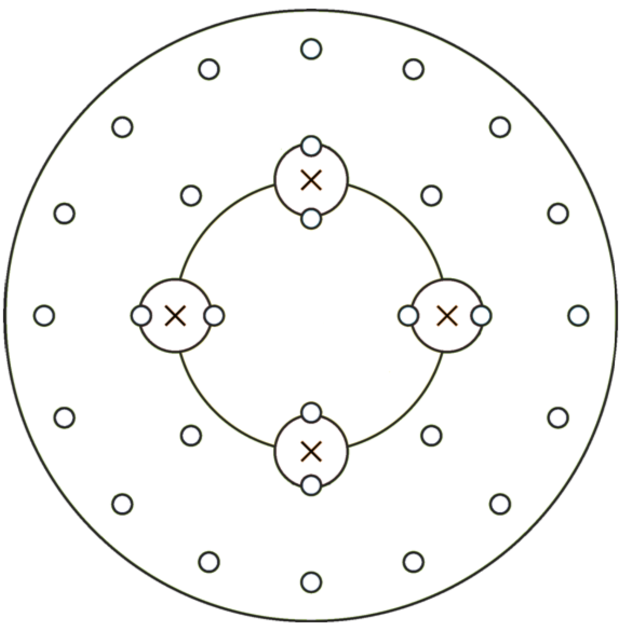

Figure 1. Sampling arrangement. The circles symbolize the sampling units: major circle (r = 12.6 m) – overstory: medium circle (r = 5.6 m) – high shrub layer; 4 circles (r = 1.5 m) – low shrub layer; 28 small circles (r = 0.4 m) – understory; four crosses – sampling points of canopy closure.

Data analysis

The relationships between explanatory variables and studied assemblages were explored by Redundancy Analysis; Principal Component Analysis and Detrended Correspondence Analysis were used as preliminary indirect ordinations (Podani 2000, Ter Braak and Smilauer 2002). Herb and seedling assemblages were analysed separately, the importance of species were expressed by their local frequency values. Rare (low frequency) species were eliminated from the multivariate analyses, the frequency limit was 21 for herbs and 13 for seedlings, therefore the analysis comprised 51 herbaceous and 22 seedling species. Before the analyses, the collinearity of explanatory variables was tested, and highly correlated variables (correlation value exceeds +/- 0.55) were excluded from the analysis (**Table 1**). Explanatory variables were standardized and log transformed, if necessary for better fit to normal distribution. The effect of geographical coordinates was tested in a separate RDA, they were influential on the composition of herbs and seedlings, therefore geographical coordinates got into the final RDA as covariables. During the Redundancy Analysis, manual forward selection was used on the potential explanatory variables. The significance of their conditional effects was tested by F statistics via Monte Carlo simulations with 1000 permutations, the limiting p values were 0.05. After the selection procedure, the significance of all canonical axes was tested similarly (Ter Braak and Smilauer 2002). Multivariate analyses were carried out with Canoco 4.5 program (Ter Braak and Smilauer 2002).

Results

On the course of the survey, one hundred and eighty-three herbaceous and thirty-one seedling species were recorded in the understory. The average number of herbaceous species was 29 per plot, the minimum 7, the maximum 56 species. In the case of seedlings, average species number was 10, the minimum 2 and the maximum 17 species. The most frequent herbaceous species were *Dactylis glomerata*, *Melica uniflora*, *Clinopodium vulgare*, *Galium schultesii*, *Fragaria vesca*, *Geum urbanum*, *Veronica chamaedrys*, *Poa nemoralis*, and *Viola odorata (App. 1)*. The most frequent seedling species were *A. campestre*, *Q. cerris*, *R. canina*, *C. mas*, *F. excelsior* and *L. vulgare (App. 2)*.

In both shrub layers the most frequent species were *L. vulgare*, *C. mas*, *R. canina*, *A. campestre* and *C. monogyna*, with an average 12 000 stems per hectare low shrub density and 2000 stems per hectare high shrub density (**Table 1**).

The dominant species of the overstory were *Q. cerris* and *Q. petraea*, while the most frequent associate tree species were *A. campestre*, *Sorbus torminalis*, *Q. pubescens*, *F. excelsior* and *C. betulus*. Average tree density was approximately 600 stems per hectare, varying between 125 and 2480 stems per hectare, while the stand height varied between 13 and 27 m, with an average of 20 m (**Table 1**).

Table 1. The abbreviations and descriptions of explanatory variables.

Abbreviation	Description of the Variable	Unit	Average/Median	SD/Quantile
Slope	Slope	Degree	27	12
DNorth	Deviation from North	Degree	133	37
DEast	Deviation from East	Degree	77	47
Height	Average stand height	m	20	3
Openness	Canopy openness	percent	9.2	4.1
DBH	Mean DBH of trees	cm	23.0	7.6
DBHcv	Coefficient of variation of DBH of trees		0.50	0.28
DomDBH	DBH of dominant trees	cm	33.6	9.4
DomDBHcv	Coefficient of variation of DBH of dominant trees		0.18	0.08
TreeDiv	Tree species Shannon diversity based on relative basal area of the species		1.02	0.49
QuCeRat	Q. cerris ratio between the two dominant oak species	percent	42	33
HShrub	Density of high shrubs	stem/ha	2043	1843
LShrub	Density of low shrubs	stem/ha	11938	10794
ShrubDiv	Shrub species Shannon diversity		1.18	0.54

Table 2. Significant explanatory variables of the Redundancy Analysis that determine the composition of seedlings. Explained variance of all canonical axes was 43.2 %.
Significance levels: *** <0.001; ** <0.01; * <0.05

Abbreviation	Variable	Explained variance	F-value
LShrub	Density of low shrubs	8 %	1512.10***
TreeDiv	Tree species Shannon diversity	7 %	11.55***
QuCeRat	Q. cerris ratio between the two dominant oak species	6 %	10.42***
DBH	Mean DBH of trees	4 %	7.67***
HShrub	Density of high shrubs	4 %	6.28***
DNorth	Deviation from North	2%	2.69*
DomDBHcv	Coefficient of variation of DBH of dominant trees	1 %	3.19**
ShrubDiv	Shrub species Shannon diversity	1 %	2.71**

Seedling species

Variance explained by the four axes of the Principal Component Analysis was 74.1 %; the samples were not clustered. The gradient length of the Detrended Correspondence Analysis was between 2 and 3 standard deviation units. The variance covered by all the canonical axes of the Redundancy Analysis was 32.9 % (explained variance of the first four axes: 11.7 %, 10.4 %, 6.2 % and 2.8 %, respectively). Based on the Redundancy Analysis, the most important factors affecting the occurrence of seedling species were high and low shrub density, mean DBH of trees, DBHcv of dominant trees and tree species diversity (**Table 2**). Most of the seedling species (*C. monogyna*, *C. mas*) can be found in *Q. cerris* dominated stands with heterogeneous stand structure, high low and high shrub density and southern exposure (**Fig. 2**). The occurrence of *L. vulgare* seedlings was mostly correlated with high and low shrub density, while the seedlings of *P. spinosa* and some other species (*Acer tataricum, Cornus sanguinea, Lonicera xylosteum)* preferred stands with dense shrub layers and low tree diversity. The seedlings of the two most frequent associate tree species – *A. campestre* and *F. excelsior* – preferred stands with high tree diversity, heterogeneous stand structure and southern exposure. The seedlings of both

dominant oak species preferred sessile oak dominated stands with relatively large tree size, homogeneous stand structure and low tree diversity.

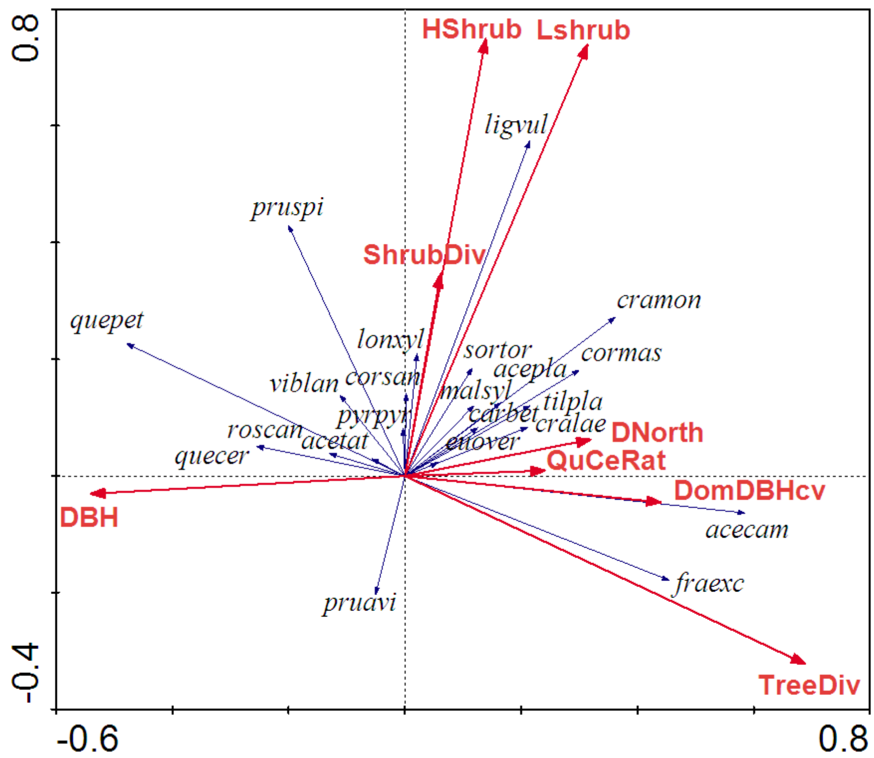

Figure 2. Explanatory variables and species biplot of the first (horizontal) and the second (vertical) axes of the Redundancy Analysis of seedlings. Significant explanatory variables are represented by thick lines, their abbreviations are explained in Table 1, species are abbreviated by the first three letters of the genus and species names (App. 2). Variance covered by the first axis is 11.7%, by the second axis is 10.4%.

Herbaceous species

In the case of herbaceous species, the four axes of the Principal Component Analysis covered 59.6 % of the variance; the sampling units were not clustered either. The gradient length of the Detrended Correspondence Analysis was between 2 and 3 standard deviation units. The explained variance of all the canonical RDA axes was 25.7 % (variance covered by the first four axes were 13.6 %, 4.9 %, 2.8 % and 1.6 %, respectively). The most important factors that affecting the occurrence of herbaceous species were average DBH and DBHcv of all the trees, deviation from east, canopy openness, and species diversity and density of the shrub layers. (**Table 3**, **Fig. 3**).

Oak forest species were located on the positive side of the first axis. They preferred stands with relatively open canopy, large mean DBH and sparse shrub layer. In the case of mesic forest species, the second axis was determinant with a positive correlation. These species preferred stands with structurally heterogeneous overstory, diverse shrub layers, well developed low shrub layer and western exposure.

Fig. 3. Explanatory variables and species biplot of the first (horizontal) and the second (vertical) axes of the Redundancy Analysis of herbs. Significant explanatory variables are represented by red lines, their abbreviations are explained in Table 1., species (black) are abbreviated by the first three letters of the genus and species names (App. 1). Variance covered by the first axis and second axis are 13.6 % and 4.9 %, respectively.

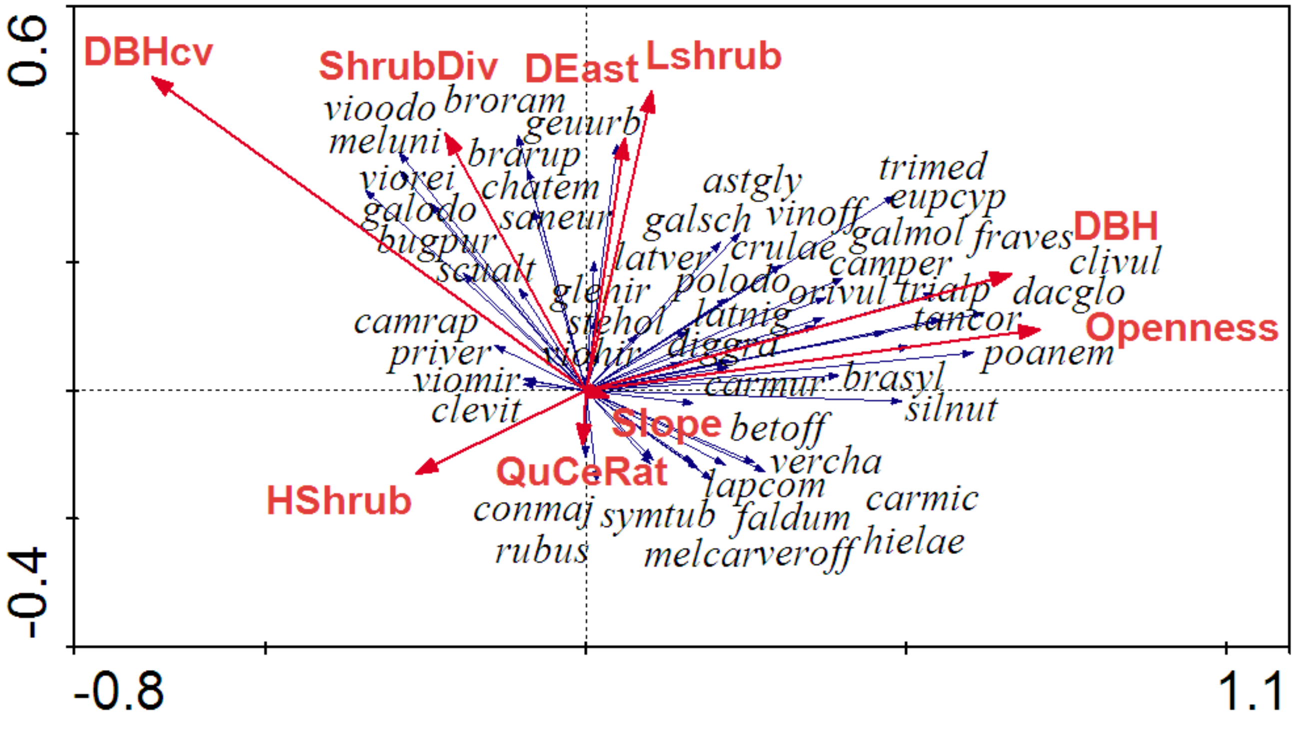

Table 3. Significant explanatory variables of the Redundancy Analysis that determine the composition of herbaceous species. Explained variance of all canonical axes was 35.9 %.
Significance levels: *** <0.001; ** <0.01; * <0.05

Abbreviation	Variable	Explained variance	F-value
DBH	Mean DBH of trees	8 %	12.73 ***
DBHcv	Coefficient of variation of DBH of trees	5 %	7.46 **
Openness	Canopy openness	3 %	4.44 ***
DEast	Deviation from East	2 %	4.57***
ShrubDiv	Shrub species Shannon diversity	2 %	3.45***
QuCeRat	Q. cerris ratio between the two dominant oak species	2 %	2.85**
HShrub	Density of high shrubs	2 %	2.44**
LShrub	Density of low shrubs	1 %	2.56**
Slope	Slope	1 %	2.25*

Discussion

Seedling species

The occurrence of seedling species was influenced by the characteristics of the shrub layer and the species composition and structure of the overstory. Kirby (1988) also found that changes in the understory are mainly affected by changes of tree species composition and age structure.

The structure of the overstory was a very important stand characteristic for the seedlings of the two dominant oak species. Both *Q. cerris* and *Q. petraea* seedlings could be found at homogeneous stands, where mean DBH of trees was bigger, tree species diversity and *Q. cerris* ratio were low, thus *Q. petraea* dominated the overstory. In these forest stands the trees stand sparsely, no associate tree species can be found, and even if there is a second canopy layer, it has low cover, accordingly more light can reach the understory. In more closed stands, the regeneration of light-demanding oak species was less successful, generating a realignment of tree species composition (von Oheimb and Brunet 2007, Tinya et al 2009). In closed stands, reduced *Q. robur* regeneration was described by von Oheimb and Brunet (2007), while Schumann et al (2003) showed stronger *Q. rubra* regeneration in gaps. According to Rogers et al (2008), the ratio of *Q.* species (*Q. rubra, Q. velutina, Q. alba*) showed a long-trem decrease in the overstory because of the closed canopy. Although the two dominant oak species require the same conditions for recruitment, there is an important difference between them. In case of a proper stand structure, lower overstory *Q. cerris* ratio was sufficient for regeneration. Contrarily, *Q. petraea* was able to regenerate only where it dominated the overstory. This strong dispersal limitation phenomenon can be useful for forest management, because the natural regeneration of sessile oak is often problematic.

The seedlings of the two most frequent associate tree species –field maple (*A. campestre*), and European ash (*F. excelsior*) – can be found in those sampling plots where tree species diversity is relatively high. This phenomenon also indicates spatial limitation of propagules, because high tree species diversity is related to the high proportion of these species in the overstory. It is controversial to the general expectations that for these anemochore trees regeneration is not related to the proximity of parent plants. However, Hermy et al (1999) concluded that dispersal is often a limiting factor for the establishment of anemochore forest species. These species also preferred structurally heterogeneous stands, where the coefficient of variation of dominant trees is high. A possible explanation may be that in these stands the overstory had been disrupted in the past (by either forest management or natural disturbance), thus associate tree species could strengthen and become a propagule source. Additionally, their seedlings have a better chance to find a proper habitat in heterogeneous stands.

The seedlings of frequent shrub species were present in stands with a high density of at least one of the shrub layers. Most of these species are not anemochore, thus it is comprehensible that propagule source was one of the most important variables in the case of their regeneration. Dense shrub layers were the most important stand characteristics in the case of *L. vulgare* seedlings. This clonal shrub can tolerate the shaded conditions under a closed shrub layer better than light demanding herbs and seedlings (Borhidi et al 2012, Bölöni et al 2011, Horváth et al 1995, Roleček 2005). The species composition of the overstory had an important effect on the species composition of the seedlings of the shrub layer as well. *C. monogyna*, *C. mas* and *L. vulgare* seedlings preferred stands where *Q. cerris* dominated the overstory. Probably soil characteristics and bedrock type are responsible for the observed oak ratio, which are also influential on the composition of shrub seedlings. The seedlings of *C. monogyna* and *C. mas* also preferred southern exposure and heterogeneous stand structure. They are typical shrub species of dry oak forests (Borhidi et al 2012, Bölöni et al 2011, Horváth et al 1995, Roleček 2005); they probably prefer a warmer microclimate for their regeneration. The preference of the structurally diverse overstory can be explained similarly to the case of the two most frequent associate tree species. These shrub species could have strengthened in a disrupted forest stand (as a consequence of forest management or natural gap formation), resulting a notable propagule source for the present. *P. spinosa* seedlings – unlike the other three frequent shrub species – did not prefer the *Q. cerris* dominated areas with dense shrub layer. They occurred in stands where stand structure was homogenous, stem density was low and *Q. petraea* dominated the overstory. Since *P. spinosa* is basically a light-demanding forest edge species (Gencsi and Vancsura 1992, Horváth et al 1995, Simon 2000) it is fairly understandable that it preferred more open stands.

Contrarily to most arboreal species, the seedlings of *Prunus avium* avoided stands with dense shrub layers. We have no obvious explanation to this phenomenon, probably weaker competition in the understory enhances their survival.

Herbaceous species

The concept of a close relation between the overstory and understory is generally accepted (Barbier et al 2008, Tobisch and Standovár 2005). Stand structure has many indirect effects on the species composition of the understory: it determines the amount and pattern of light, influences the soil and litter properties and moisture.

One of the most important factors determining the species composition of herb assemblages is light. In our study oak forest species occurred in stands where the shrub layers were scantily developed, the canopy closure was low and the mean DBH was relatively large, while mesic forest species preferred stands with a dense shrub layer. Each of these stand characteristics define the amount of light that reaches the understory. It seems that light availability is the most relevant factor influencing the occurrence and cover of oak forest species, whereas mesic forest species tolerate shaded conditions better. The relation between the amount of light reaching the herbs and the species composition of the understory is partly revealed. Based on several studies, it seems obvious that the amount, pattern and quality of light are among the most important factors that affect the understory vegetation (Van Calster et al 2008, von Oheimb and Brunet 2007, Tinya et al 2009). Canopy closure and species composition of the overstory and shrub layer mostly determine the light reaching the understory (Barbier et al 2008, Brunet et al 1996, Maranón et al 1999, von Oheimb and Härdtle 2009). In stands where trees stand sparsely and shrub layer is scarce, more light reaches the forest floor, which increases the diversity of the understory (von Oheimb and Härdtle 2009) and the proportion of light-demanding and ruderal species (Brunet et al 1996, Pérez-Ramos et al 2008, Tybirk and Strandberg 1999). With the closing of the canopy, diversity and species richness of the understory decrease, cover and frequency of light demanding species diminish, while the ratio of shade tolerant and generalist species increases (von Oheimb and Brunet 2007, Rogers et al 2008, Tybirk and Strandberg 1999). Von Oheimb and Härdtle (2009) suggest that canopy openness is one of the best indicators of species composition and species richness of the understory in temperate forests.

The second important stand characteristic that affects herbaceous species composition is moisture. Canopy openness and the density of shrub layers define not only the amount and pattern of light that reaches the understory, but also the air humidity of the herb layer. The density of the overstory and shrub canopy determines the temperature and air humidity of the lower layers (Sharpe et al 1996). Rogers et al (2008) have shown that in stands with a dense shrub layer, humidity is higher, therefore mesic species appear in the understory. In our study we came to similar results. Mesic forest species preferred more humid habitats - stands with dense low shrub layer and heterogeneous structure, which enhance the occurrence of more humid patches in a forest stand. On the contrary, oak forest species were positively correlated to dryer, more open stands with scantily developed shrub layers. In our study, exposure was an other influential characteristic for herb composition; mesic forest species preferred west facing slopes. There is not an obvious explanation for this phenomenon, but it is assumable that the microclimatic conditions of the western slopes are more humid than those of the eastern.

The species composition of the herb layer is affected by the soil nutrient content as well. Mesic forest species were positively related to the DBHcv of trees and the density of low shrub layer. The coefficient of variation of DBH of trees is related to stand age. In older forest stands, the accumulated litter increases nutrient supply and the dense shrub layer can further increase the amount of litter, accordingly, mesic forest species can find an appropriate habitat. The density of trees and shrubs defines the amount of litter, and the species composition of the overstory affects the decay rate, C:N ratio and pH of the litter (Graae and Heskjaer 1997). Brunet et al (1996) found that the organic matter content of the soil has a great impact on the understory vegetation in oak forests. In addition, the amount and availability of nutrients have an effect on the microbe and mycorrhiza community of the soil, thus affecting the species composition of the understory in an indirect way (Pérez-Ramos et al 2008).

Stand age can also influence the composition of herb assemblages. In our study, mesic forest species seemed to prefer older stands (high stands with large diameter of dominant trees). Different studies arrive at controversial conclusions concerning the effect of stand age on understory diversity. Forest age influences the chemical and structural properties of the soil and consequently understory vegetation (Honnay et al 1999), although it is not the only way in which stand age affects the species composition of herbs. Decocq et al (2005) found it also influential on understory composition; many species need a long time for recolonization after harvesting, species diversity decreases by the ageing of a forest, but the ratio of real forest species – geophytes, shade-tolerant and moisture-demanding species (Hermy et al 1999) – increases. The strong effects of forest management intensity and the time elapsed since the last cutting on understory species composition were shown by Fredericksen et al (1999). Contrarily, according to Graae and Heskjaer (1997), the effect of stand age on understory vegetation is not significant in forests between 50 and 150 years. Ford et al (2000) did not find the effect of stand age significant on species richness, diversity and evenness of the understory either. Ito et al (2004) have found that former land use overwrites the effects of current stand structure and microtopography.

Conclusion

As a summary of our results we conclude that different factors affect the occurrence of herbaceous and seedling species. The herb species composition of the understory is mainly influenced by canopy openness, stand structure and shrub layer density, therefore the most important factors seem to be related to light and humidity conditions. The occurrence of seedling species was defined by the species composition of the overstory and the shrub layer, thus in the case of arboreal species, the proximity of the propagule source has great importance. This phenomenon is particularly relevant in the case of *Q. petraea*, because it is an important species for forest management, but difficult to regenerate. Based on our study, the presence of *Q. petraea* is not sufficient for successful regeneration, it has to be dominant in the overstory. More detailed investigations of soil conditions could considerably contribute to the overview of the studied relationships.

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Appendix

App. 1. Abbreviations, frequency data and classification of the herbaceous species.

Abbreviations	Binomial name	Frequency (%)	Classification
astgly	Astragalus glycyphyllos	59.0	Oak forest species
betoff	Betonica officinalis	18.0	Oak forest species
brarup	Brachypodium rupestre	31.1	Oak forest species
brasyl	Brachypodium sylvaticum	25.4	Mesic forest species
broram	Bromus ramosus	63.1	Mesic forest species
bugpur	Buglossoides purpureo-coerulea	37.7	Oak forest species
camper	Campanula persicifolia	23.8	Oak forest species
camrap	Campanula rapunculoides	51.6	Mesic forest species
carmic	Carex michelii	54.1	Oak forest species
carmur	Carex muricata	58.2	Oak forest species
chatem	Chaerophyllum temulum	41.0	Mesic forest species
clevit	Clematis vitalba	45.9	Mesic forest species
clivul	Clinopodium vulgare	83.6	Oak forest species
conmaj	Convallaria majalis	29.5	Mesic forest species
crulae	Cruciata laevipes	22.1	Oak forest species
dacglo	Dactylis glomerata	86.9	Oak forest species
diggra	Digitalis grandiflora	19.7	Oak forest species
eupcyp	Euphorbia cyparissias	31.1	Oak forest species
faldum	Fallopia dumetorum	54.1	Mesic forest species

fraves	Fragaria vesca	73.8	Oak forest species
galmol	Galium mollugo	29.5	Oak forest species
galodo	Galium odoratum	33.6	Mesic forest species
galsch	Galium schultesii	77.9	Oak forest species
geuurb	Geum urbanum	73.0	Oak forest species
glehir	Glechoma hirsuta	29.5	Mesic forest species
hielae	Hieracium laevigatum	27.9	Oak forest species
lapcom	Lapsana communis	25.4	Mesic forest species
latnig	Lathyrus niger	36.1	Oak forest species
latver	Lathyrus vernus	59.8	Mesic forest species
melcar	Melittis carpatica	49.2	Oak forest species
meluni	Melica uniflora	85.2	Oak forest species
orivul	Origanum vulgare	19.7	Oak forest species
poanem	Poa nemoralis	69.7	Oak forest species
polodo	Polygonatum odoratum	18.9	Oak forest species
priver	Primula veris	20.5	Oak forest species
rubus	Rubus sp.	20.5	Mesic forest species
saneur	Sanicula europea	27.0	Mesic forest species
scualt	Scutellaria altissima	33.6	Mesic forest species
silnut	Silene nutans	28.7	Oak forest species
stehol	Stellaria holostea	32.8	Mesic forest species
symtub	Symphytum tuberosum	46.7	Oak forest species
tancor	Tanacetum corymbosum	64.8	Oak forest species
trialp	Trifolium alpestre	18.9	Oak forest species
trimed	Trifolium medium	49.2	Oak forest species
vercha	Veronica chamaedrys	71.3	Oak forest species
veroff	Veronica officinalis	17.2	Oak forest species
vinoff	Vincetoxicum officinale	60.7	Oak forest species
viohir	Viola hirta	26.2	Oak forest species
viomir	Viola mirabilis	20.5	Mesic forest species
vioodo	Viola odorata	68.0	Mesic forest species
viorei	Viola reichenbachiana	64.8	Mesic forest species

App. 2. Abbreviations and frequency data of the seedling species.

Abbreviation	Binomial name	Frequency (%)
acecam	Acer campestre	91.8
acepla	Acer platanoides	27.0
acetat	Acer tataricum	10.7
carbet	Carpinus betulus	49.2
cormas	Cornus mas	77.9
corsan	Cornus sanguinea	14.8
cralae	Crataegus laevigata	29.5
cramon	Crataegus monogyna	63.1
euover	Euonymus verrucosus	29.5
fraexc	Fraxinus excelsior	77.9
ligvul	Ligustrum vulgare	75.4
lonxyl	Lonicera xylosteum	13.9
malsyl	Malus sylvestris	16.4
pruavi	Prunus avium	36.1
pruspi	Prunus spinosa	68.0
pyrpyr	Pyrus pyraster	16.4
quecer	Quercus cerris	87.7
quepet	Quercus petraea	69.7
roscan	Rosa canina	85.2
sortor	Sorbus torminalis	33.6
tilpla	Tilia platyphyllos	13.1
viblan	Viburnum lantana	13.9