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ORIGINAL PAPER

Regeneration patterns of the late-successional *Abies alba* Mill.: inhibition in monospecific stands and colonization in mixed stands

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Abstract
· *Key message* In *Abies alba* Mill. stands and mixed stands of *A. alba* and *Picea abies* L. (H. Karst), microsites neighbouring the trunks of adult trees were more conducive to *A. alba* regeneration. Although at the stand level, the effect of *Fagus sylvatica* L. was positive; the local effect of the adult *F. sylvatica* neighbourhood was insignificant. Hence, forming mixed stands with a fine-grained mosaic of admixed species might better facilitate natural regeneration of *A. alba* than monospecific stands.
· *Context* The establishment of natural regeneration in *Abies alba* Mill. stands is a slow, spatially heterogeneous and stochastic process. Recent studies based on inventory data indicate that *A. alba* more readily regenerates in mixed stands than in monospecific stands.
· *Aims* The objective was to examine how this positive association evidenced at the stand level operates on the scale of microsites with contrasting local species composition and stand density.
· *Methods* In 8 monospecific and 22 mixed stands with *Fagus sylvatica* L. or *Picea abies* L. (H. Karst), microsites with a contrasting density of *A. alba* seedlings were selected and compared in terms of local species composition, stand density, canopy characteristics and topsoil properties.
· *Results* In *A. alba* stands, seedling density was positively associated with the proximity of adult trees. In mixed stands of *A. alba* and *P. abies*, adult trees of both species exerted a positive effect on *A. alba* regeneration, but the *P. abies* neighbourhood influenced regeneration occurrence more strongly than the *A. abies* neighbourhood. In mixtures with *F. sylvatica*, however, the effect of local stand density and local species composition was not evidenced at all.
· *Conclusion* Although at the stand level, *P. abies* and *F. sylvatica* exert a positive effect on *A. alba* regeneration, on the microsite scale, their influences differ. In stands with a dominance of *A. alba*, the hampered seedling establishment in gaps may be considered an inhibitive effect that facilitates the emergence of other species.

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1 Introduction

In temperate zones, although late-successional tree species frequently show similar life strategies and compete for similar resources in relatively homogeneous environments, they form

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mixed stands in a wide range of sites (Roženbergar et al. 2007; Szwagrzyk et al. 2012). Species coexistence under such conditions contravenes the logic that species with the highest long-term relative population growth rate in admixture with other species should oust all others (Wilson 2011). It is therefore reasonable to assume that the temporal persistence of mixed stands involves mechanisms that stabilize complex species composition and counteract exclusion of certain of its components through density-dependent processes.

Although shifts in species abundance may appear at different development stages (Mori and Komiyama 2008; Rousset and Lepart 2000), one crucial prerequisite for mixture persistence is successful reproduction. In particular, mixed species composition may be stabilized at this stage by negative feedback versus conspecific regeneration and/or positive effects versus the regeneration of heterospecific species (Busing 1996; Catovsky and Bazzaz 2002). These associations potentially may involve a range of factors, including seed dispersal (Snyder and Chesson 2004), light regime (Roženbergar et al. 2007), density-dependent and host-specific pests (granivory, herbivory, pathogens) (Baraza et al. 2006; Nopp-Mayr et al. 2012), topsoil properties (Bigelow and Canham 2015) or allelopathic effects (Becker and Drapier 1985). The spatial scale at which these factors operate may differ strongly and range from an area encompassing the entire stand to close proximity of single trees. In fact, research shows that in mixed forests, microsites occupied by different species may differ from the neighbouring background in many properties important for establishing regeneration, including light conditions (Stadt and Lieffers 2000), topsoil moisture and pH (Paluch and Gruba 2012), ectohumus layer thickness (Bens et al. 2006; Buck and St Clair 2014), forest floor vegetation (Saetre 1999), abundance of soil fungi (Frankland 1998) and fungal pathogens (Kotanen 2007) and mycorrhiza colonization rates (Cline et al. 2007) or seedling mycorrhiza diversity (Grebenc et al. 2009).

Several examples have been documented of certain tree species regenerating more easily in mixtures with another species than in monospecific stands (Arbour and Bergeron 2011; Yamazaki et al. 2009). In most cases, however, this situation is exemplified by tree species of different successional status with few well-documented examples of interactions between species coexisting at the same stage of a succession sequence. One example is forests with late-successional *Abies alba* Mill. In pure stands, natural regeneration of *A. alba* accumulates slowly because gaps (including small inter-crown openings) and close-to-trunk locations can be unfavourable for seedlings: the former are associated with increased fungal pathogen attacks and the latter with water deficiency that hinder seedling growth (Paluch and Stępniewska 2012). In effect, in monospecific stands, the spatial pattern of regeneration is very irregular, and *A. alba* seedlings are mostly absent in canopy openings, the microsites with the lowest competitive

pressure from surrounding adult trees and hence the highest chances of successful recruitment. On the other hand, several studies have indicated that *A. alba* regenerates more readily in mixed stands with late-successional *Fagus sylvatica* L. and/or *Picea abies* L. (H. Karst) than in monospecific stands (e.g. Šimak 1951; Jaworski 1973; Hofmeister et al. 2008; Paluch and Jastrzębski 2013), although little is still known about mechanisms, spatial scale and intensity of this positive effect.

The aim of this present study, therefore, is to test whether the regeneration facilitation effect evidenced in mixed stands at the stand level also operates on the level of intra-stand variation in microsites with different local species composition and stand density. The specific hypotheses are as follows: (i) microsites with different regeneration density will differ in local species composition and local stand density attributes, (ii) microsites with a higher regeneration density will show a higher proportion of *F. sylvatica* and *P. abies* trees in the upper canopy, (iii) the positive effect of admixtures will diminish with a decreasing proportion of *A. alba* trees and reduced availability of their seeds and (iv) the spatial effect of *P. abies* and *F. sylvatica* will differ because of differences in these species' properties, including tree architecture, litter properties and spatial pattern of litter dispersal.

2 Material and methods

2.1 Study site

The study was conducted in the Western Carpathians (southeastern Poland) in stands located in the lower montane belt of the altitudinal zone 500–950 m a.s.l., between 18.794° E and 22.722° E longitude and 49.133° N and 49.784° N latitude. In this region, *A. alba* commonly grows on eutric, loamy cambisols developed on flysch sediments. Depending on altitude, location and aspect, the growth period (with a mean daily temperature above 5 °C) is ca 180–200 days, the average annual temperature is 5–7 °C and the annual precipitation is 750–1450 mm, 60 % occurring between May and October. The mean annual temperature increases by about 0.5 °C per each 100 m increase in altitude (Paszyński and Niedzwiedź 1999).

For this study, 8 pure *A. alba* stands (hereafter, Abies stands) were selected together with 11 mixed stands of *A. alba* and *F. sylvatica* (hereafter, Fagus-Abies stands) and 11 mixed stands of *A. alba* and *P. abies* (hereafter, Picea-Abies stands). Each species composition variant was represented by two to four stands in the eastern, middle or western part of the Western Carpathian massif. In addition to species composition, the criteria for stand selection were homogeneity of site conditions, the occurrence of a naturally established *A. alba* seedling bank of largely young individuals (i.e. not older than 25 years with a mean height between 0.1 and 0.3 m), low

competition from forest floor plants (less competitive, low herbal plants and arborescent species forming a loose and discontinuous cover) and a low intensity of silvicultural operations during recent decades (only thinning operations without cuttings aimed directly at promoting regeneration). The stands were between 80 and 130 years in age and originated from natural regeneration in the shelterwood system. According to field measurements, the stand basal area ranged between 29 and 54 $m^2 ha^{-1}$ (mean = 42.2 $m^2 ha^{-1}$) in the Abies and Picea-Abies stands and between 31 and 44 $m^2 ha^{-1}$ (mean = 36.9 $m^2 ha^{-1}$) in the Fagus-Abies stands. In the Abies stands, the contribution of *A. alba* trees to the stand basal area was above 90 % (mean = 94 %); in the Fagus-Abies stands, it ranged between 16 and 61 % (mean = 34 %); and in the Picea-Abies stands, it fell between 34 and 85 % (mean = 73 %).

2.2 Data collection

In the 30 stands selected, based on stand shape and size, between two and five transects 5 m wide and 1500 m in total length were traced out. These transects were divided into 50-m-long sectors, and in each segment, a patch about 10 m^2 in area with a locally maximal density of *A. alba* regeneration was identified (hereafter, favourable microsite). The minimal distance between the neighbouring favourable microsites was limited to 25 m. Between each pair of favourable microsites selected, a patch with a locally minimal density of *A. alba* regeneration was identified (hereafter, unfavourable microsite). This sampling procedure resulted in the identification of 30 favourable microsites and 30 unfavourable microsites in each of the stands.

In the centre of every selected patch, a circular sample plot 1 m^2 in area was placed and all *A. alba* seedlings were counted. The term "seedlings" as used here refers to all individuals under 50 cm in height (but usually between 0.1 and 0.3 m) except for the current year's germinants. Trees growing within a 10 m radius (horizontal distance) of the plot centres were mapped using a compass and an ultrasonic distance meter. The 10-m radius was assessed as sufficient to capture local variation in stand density and species composition. Measurements were then taken of all live trees with a diameter at breast height (dbh) ≥ 7 cm and all the stumps of trees removed approximately during the last two decades with a diameter at 0.3 m ≥ 20 cm. The measurement records included species, the dbh of live trees and the diameters of the removed trees.

To characterize canopy openness (i.e. the fraction of open sky unobstructed by vegetation in a specified canopy region) and light conditions in the favourable and unfavourable microsites, in June–August 2014, 60 hemispherical images were taken of each stand in the selected sample plots. All these photos were obtained in overcast conditions from 0.6 m above the ground using a Nikon E4500 camera with a Nikon FC–E8

fisheye converter affixed to a tripod and a universal O-mount with a northfinder (Régent Instruments Inc., Canada).

In each stand, in both favourable and unfavourable microsites, topsoil samples were taken using a soil sampler tool (50 mm in diameter) up to a depth of 20 cm (inclusive of the organic layer). The samples from plots with the same regeneration status (i.e. 30 samples from favourable microsites or 30 samples from unfavourable microsites) were pooled, packed in plastic bags, tied up, marked and transported to a refrigerator in which they were kept at −3 °C until laboratory analysis began. In total, the Abies ($N = 8$), Picea-Abies ($N = 11$) and Fagus-Abies stands ($N = 11$) were represented by16, 22 and 22 soil samples, respectively, collected from both favourable and unfavourable microsites.

2.3 Soil analysis

Before the soil could be sieved, the living roots and rock particles were removed and the soil samples air-dried for about 1 week at room temperature. The samples were then sieved using a 2-mm sieve. The fractions of clay (<0.002 mm), silt (0.05 to 0.002 mm) and sand particles (0.05 to 2 mm) were determined using laser diffraction (Analysette 22, Fritsch GmbH, Germany). Soil pH was measured electrochemically with a combination electrode in a suspension with distilled water and 1 mol dm^{-3} KCl solution (1:5 mass-to-volume ratio) after 24 h of equilibration (Buurman et al. 1996). Exchangeable calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+) were extracted with 1 mol L^{-1} CH_3COONH_4 at pH = 7. The soil samples were then mixed with an extractant (10 g in 30 mL) and equilibrated. After 24 h, the suspensions were filtered (0.45 μm millipore membrane), the soil was washed with additional extractant and the total volume was made up to 100 mL (Jackson 1958). Lastly, the concentration of cations was determined by means of ICP (ICP-OES Thermo iCAP 6500 DUO, Thermo Fisher Scientific Inc., USA). The total carbon (C) and total nitrogen (N) contents of the soil were determined in fine subsamples ground in a ball mill using an LECO CNS TrueMac Analyzer (Leco Co., USA).

2.4 Data analysis

The canopy pictures were analysed using the WinSCANOPY Pro 2006a programme (Régent Instruments Inc., Canada) with manufacturer-suggested camera and lens specifications. In most cases, the automatic pixel classification method based on grey levels yielded acceptable results because of the good picture quality. Sporadically, the threshold values were adjusted manually (usually between 235 and 250 on a 0–255 scale). For every sample plot, the analysis determined gap fractions in the canopy regions given by the zenith angles 0–10°, 0–20°

and 0–30°; the total light factor and direct light factor (the ratios of the average daily direct and diffuse radiation and the average daily direct radiation, respectively, received under and over the canopy during the growing season) and the indirect light factor (the ratio of indirect radiation received under and over the canopy assuming a standard overcast sky model).

The set of variables adopted as potential indicators of favourable versus unfavourable microsites were as follows: the gap fractions in the canopy regions as defined above; the direct, indirect and total light factors; the basal areas of live or removed trees and the proportion of admixed species (i.e. *F. sylvatica* in Fagus-Abies stands or *P. abies* in Picea-Abies stands) in local basal areas within a 2, 3, …, 10 m radius from the sample plots; and soil characteristics (fraction of sand, silt and clay particles, pH, total N, total C, C:N ratio, the sum of base cations: Ca^{2+}, K^+, Mg^{2+}, Na^+).

Preliminary computations included routine analyses of the variable distributions, spatial autocorrelations (Moran's I tests) and associations between predictors and response variables (scatterplot analyses and Pearson correlations). These were followed by a comparison of the mean values of the variables in the favourable versus the unfavourable microsites. Skewed distribution problems were eliminated by the application of bootstrap procedures testing the equality of means (10,000 bootstrap samples, Efron and Tibshirani 1993, pp. 220–224). For multiple comparisons in the distance gradients, Bonferroni corrections were used. Differences between the topsoil characteristics were tested via one-sample bootstrap procedure (10,000 bootstrap samples, Efron and Tibshirani 1993, pp. 224–227) that serves as a simulation-based alternative for Wilcoxon signed-rank tests and sign tests. Data analysis was carried out using Statistica (Stat Soft Inc., USA), version 9.1.

3 Results

3.1 Variation in regeneration density

In the Abies stands, the average seedling density per m^2 was 22.4 in the favourable microsites and 1.8 in the unfavourable microsites. In the Picea-Abies stands, seedling density in both types of microsites was lower than in the Abies stands (18.5 and 0.9 per m^2, respectively). The lowest regeneration densities were registered in the Fagus-Abies stands in which the average number of seedlings per m^2 was 11.0 in the favourable microsites and 0.7 in the unfavourable microsites. The regeneration densities in favourable and unfavourable microsites in the stands studied are illustrated in Fig. 1. Overall, the analysis reveals no significant relations between stand-level seedling density and either stand basal area ($r = -0.16$, n. s.) or light conditions as determined by the total light factor ($r = 0.18$, n. s.).

3.2 Effect of local stand density

In the Abies stands, the favourable microsites were characterized by a significantly higher local basal area than the unfavourable microsites (Fig. 2a). These differences were highest at the smallest spatial scale analysed (i.e. within a 2 m radius), decreased with the increasing radius of the surroundings and maintained statistical significance up to a radius of 4 m. The differences in local basal area (within a 2 m radius) between the favourable and unfavourable microsites amounted to 69 cm^2 m^{-2} on average (about 70 % of the standard deviation unit in terms of stand-level variation) and ranged between 29 and 194 cm^2 m^{-2} in individual stands. Similar differences between the favourable and unfavourable microsites were observable in the Picea-Abies stands (on average 40 cm^2 m^{-2}) (Fig. 2c). In the individual stands, the differences ranged between 15 and 82 cm^2 m^{-2} and attained negative values in two stands with the highest stand basal area. In contrast to the conifer stands, no differences related to local basal area manifested between the favourable and unfavourable microsites in the Fagus-Abies stands (Fig. 2b), in which the differences ranged between 18 and 35 cm^2 m^{-2} and amounted to 10 cm^2 m^{-2} on average. Nor were any such differences observable for removed trees in the surroundings of favourable versus unfavourable microsites.

In the Abies and Picea-Abies stands, the favourable microsites differed from the unfavourable microsites in a lower gap fraction in canopy regions defined by the zenith angles 10° ($p < 0.001$) and 20° ($p < 0.001$) (Fig. 3a, c). These differences diminished and ceased to be statistically significant, however, as the zenith angle and canopy region increased. Although this tendency was also discernible in the Fagus-Abies stands (Fig. 3b), the differences were smaller and statistically significant only for the zenith angle of 10° ($p < 0.001$). The total radiation received by favourable and unfavourable microsites differed only insignificantly by 0.4–1.1 %.

3.3 Effect of local species composition

The analysis of the Fagus-Abies series revealed no differences between the two types of microsites in the basal area of *F. sylvatica* trees (Fig. 4a). In the Picea-Abies stands, however, the favourable microsites were characterized by a significantly higher proportion of *P. abies* in the local basal area than found for the unfavourable microsites (Fig. 4b). The highest differences occurred on the smallest spatial scale analysed, within a 2 m radius. In the single stands, these differences ranged between 11 and 33 % and amounted to 15 %, on average. The significantly higher proportion of *P. abies* in the favourable microsites was statistically assured up to a distance of 3 m and discernible in the entire spatial range analysed.

Fig. 1 Regeneration density in favourable and unfavourable microsites (median values, 10th and 90th percentiles): **a** Abies stands, **b** Fagus-Abies stands, **c** Picea-Abies stands. The stands are arranged by ascending basal area
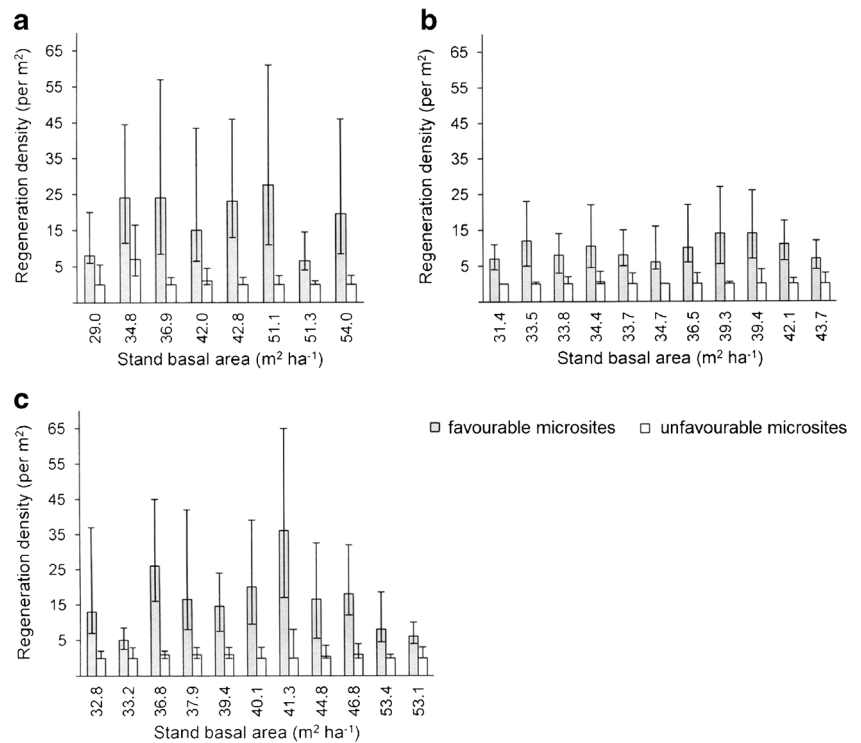
3.4 Topsoil characteristics

Except for a higher proportion of clay fraction (9.9 versus 6.6 %, $p = 0.02$) and a lower C:N ratio (14.7 versus 16.6, $p = 0.02$) in the Abies stands relative to the Fagus-Abies stands, the majority of the topsoil characteristics analysed showed no significant differences between the stand composition series. In the Abies and Picea-Abies stands, however, the favourable microsites showed a higher C content and C:N ratio than the unfavourable microsites, together with a lower topsoil pH, Ca^{2+} concentration and sum of base cations (Table 1). These tendencies were not discernible in the Fagus-Abies stands. Nonetheless, some Fagus-Abies stands did have considerable C content (between 5.3 and 8.9 %) together with

Fig. 2 Mean values and bootstrapped 95 % confidence intervals for local basal area of live trees in radii between 2 and 10 m from the favourable and unfavourable microsites: **a** Abies stands, **b** Fagus-Abies stands, **c** Picea-Abies stands. The significantly different pairs of values (two-sided bootstrap tests with the Bonferroni correction for multiple comparisons, $\alpha = 0.05/9$) are designated by enlarged marks
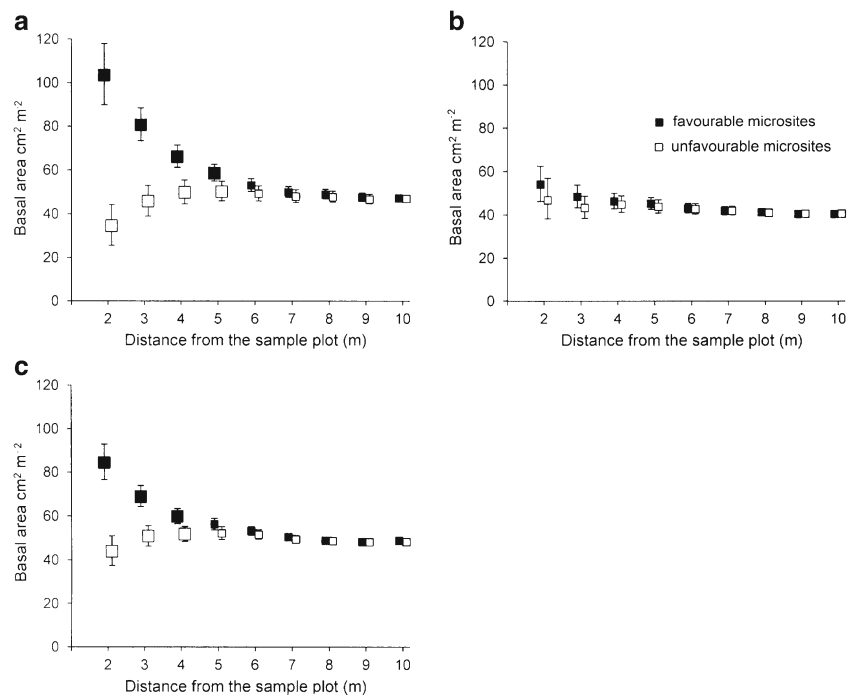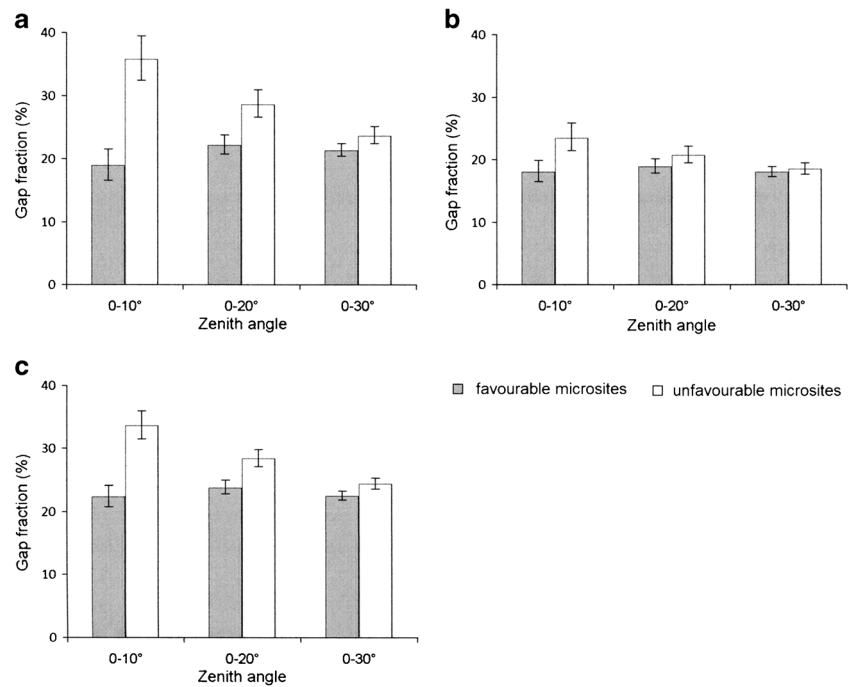
Fig. 3 Mean values and bootstrapped 95 % confidence intervals for canopy gap fractions in favourable and unfavourable microsites for different zenith angles: **a** Abies stands, **b** Fagus-Abies stands, **c** Picea-Abies stands

□ favourable microsites   □ unfavourable microsites

low topsoil pH values (below 4.0). In these stands, however, in contrast to the conifer stands, the higher C levels and lower pH occurred in the unfavourable microsites. In general, in the Fagus-Abies stands, the microsites contrasting in regeneration density differed significantly only in Ca^{2+} concentration and the sum of base cations (Table 1).

4 Discussion

4.1 Availability of seeds versus availability of favourable microsites

The associations analysed here should be considered from the perspectives of two different factor categories: the availability of seeds and the availability of favourable microsites in which seeds can survive and germinate, and germinants can establish

seedling banks (Nuttle and Haefner 2005; Snyder and Chesson 2004). Dependent on stand density, the median dispersal distance in forest interiors of the winged and relatively heavy seeds produced by *A. alba* (on average, 50-55 g per 1000 dried seeds, Schütt 1991; Suszka 1983) has been estimated at between 6.0 and 21.5 m, and the maximum density of fallen seeds per area unit has been observed at a distance between 3.0 and 6.0 m from the mother tree (De Andrés et al. 2014; Marczyk 2012; Sagnard et al. 2007). Paluch (2011) also identified a significant spatial and temporal correlation of ground seed density in *A. alba* stands that could be linked to the arrangement of seed-bearing trees, variation in these trees' seed output and local stand density. Hence, a higher ground seed density could be expected in patches with a higher basal area of adult *A. alba* exemplars.

The mixed stands studied here, however, yielded no evidence of close association between seed rain intensity and
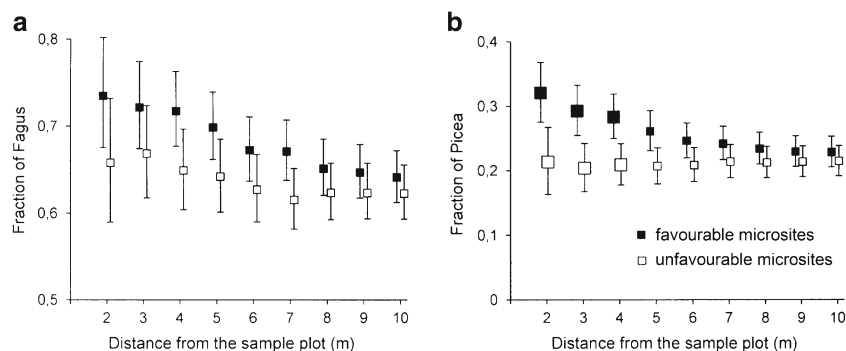

Fig. 4 Proportion of admixed species in local basal area in different radii from favourable and unfavourable microsites (mean values and bootstrapped 95 % confidence intervals): **a** Fagus-Abies stands, **b**

Picea-Abies stands. The significantly different pairs of values (two-sided bootstrap tests with Bonferroni correction for multiple comparisons, $\alpha/9 = 0.05$) are designated by enlarged squares

Table 1 Topsoil characteristics (means and standard errors) in the microsites favourable (+) and unfavourable (−) for *A. alba* regeneration

Characteristics		Abies (N = 8 stands)			Fagus-Abies (N = 11 stands)			Picea-Abies (N = 11 stands)		
		(+)	(−)		(+)	(−)		(+)	(−)	
Sand	(%)	24.9 (2.9)	20.6 (2.9)		33.1 (4.3)	31.3 (4.6)		29.5 (3.6)	25.2 (4.7)	
Silt	(%)	66.9 (2.7)	67.0 (3.3)		60.1 (3.8)	62.2 (4.0)		63.3 (3.3)	66.8 (4.4)	
Clay	(%)	8.1 (0.7)	11.7 (2.6)		6.8 (0.6)	5.2 (0.7)		7.2 (0.5)	7.9 (0.5)	
pH (H$_2$O)	N/A	4.1 (0.09)	4.4 (0.13)	**	4.3 (0.11)	4.3 (0.15)		4.1 (0.07)	4.4 (0.09)	***
Total N	(%)	0.22 (0.012)	0.21 (0.011)		0.23 (0.03)	0.26 (0.04)		0.22 (0.02)	0.21 (0.02)	
Total C	(%)	3.6 (0.3)	2.9 (0.3)	**	3.8 (0.5)	4.5 (0.8)		3.9 (0.3)	3.1 (0.2)	***
C:N ratio	N/A	15.4 (0.7)	14.0 (0.6)	**	16.4 (0.8)	16.8 (0.9)		16.3 (0.6)	15.2 (0.5)	***
Sum of base cations	cmol kg^{-1}	1.4 (0.3)	2.6 (0.8)	*	1.4 (0.2)	2.3 (0.4)	*	1.6 (0.3)	2.9 (0.9)	*

The significantly different pairs of values (one-sample bootstrap test) are designated by *($\alpha < 0.01$), **($\alpha < 0.05$) or ***($\alpha < 0.01$), respectively

microsite preferences of *A. alba* regeneration. In the Fagus-Abies stands with a relatively low density of adult *A. alba* trees (mean basal area of *A. alba* = 12.3 m^2 ha^{-1}), no positive effect of seed-bearing trees was observable, and in the Picea-Abies stands, the positive effect of *P. abies* in local species composition held approximately constant irrespective of the proportion of *A. alba* in the stand species composition, which ranged between 34 and 85 %. This finding suggests that the more favourable conditions for regeneration establishment created by *F. sylvatica* and *P. abies* were capable of counter-balancing the lower availability of seeds. The relevance of such microsite filtering for *A. alba* regeneration was also emphasized by de Andrés et al. (2014), who found spatially uncoupled patterns of seed and seedling density in both a Pyrenean monospecific and a mixed Fagus-Abies stand.

4.2 Effect of local stand density

In line with several research conclusions that microsites under too open canopies are not conducive to *A. alba* regeneration (Diaci 2002; Grassi and Bagnaresi 2001; Paluch 2005a; Roženbergar et al. 2007), the results obtained in the Abies and Picea-Abies stands point to a positive association between regeneration occurrence and local stand density as expressed by local basal area. The temporal permanence of such a pattern of regeneration establishment was also validated for uneven-aged stands of *A. alba* in the Western Carpathians, in which advance regeneration was positively correlated with adult trees and trees of the lower stand layer (Paluch 2005b).

This positive association, however, may not be directly linked to seedbed characteristics because topsoil features that matter for regeneration establishment, like ectohumus layer depth or seedbed moisture, tend to deteriorate with decreasing distance from the tree trunks of conifer species (e.g. Liski 1995; Paluch and Gruba 2011; Penne et al. 2010). In fact, this effect was also observable in the present research, which found a higher organic C content and C:N ratio together with

a lower pH and base cation concentration in the microsites characterized by higher local stand density. Other explanations such as seed burying, seed predation or vegetation competition (Hunziker and Brang 2005) stemming from the lower attractiveness of *A. alba* seeds for rodents (Schreiner et al. 2000) also seem less probable, as does the moderate vegetation cover in the stands under study (i.e. <50 % maximal coverage by a loose and discontinuous layer of less competitive, low herbal plants). It is also worth mentioning that no notable differences were observable in the germination and juvenile survival of a control group of seedlings sown on mingled topsoil samples taken from the favourable and unfavourable habitats in Abies, Picea-Abies and Fagus-Abies stands and then artificially sheltered in a nursery and subjected to contrasting watering regimes (unpublished data).

One explanation proposed for the positive association between abundant regeneration occurrence and local stand density is a mechanism involving spatial diversification of fungal infections in below-crown zones and inter-crown openings (Paluch and Stępniewska 2012). This explanation assumes that germinants growing in gap environments are more frequently moistened, exposed to contact with soil particles spread onto their cotyledons by rain drops splashing on the ground and thus more subject to infections by aeroaquatic and aquatic fungi (e.g. *Gyoerffyella rotula*, *Pseudaegerita* sp., *Varicosporium elodeae*, Jankowiak et al., submitted to *Fungal Ecology*). The ectohumus layer, which is thicker in the neighbourhood of stems and frequently absent under canopy openings on eutric sites in the Western Carpathians (Paluch and Gruba 2011), may additionally separate plants and diminish their contact with mineral soil, thereby reducing the seedling mortality caused by fungal pathogen attacks.

Canopy openings with moderately developed ground vegetation are usually regarded as hot-spots characterized by reduced competition from the over-story stand and a higher availability of resources, which offer better chances of successful recruitment to the canopy layer than do the below-

crown zones (e.g. Woods 1984; Nagel et al. 2010). Hence, in stands with a dominance of *A. alba*, the hampered seedling establishment in gaps may be treated as an inhibitive effect that facilitates the emergence of other species, which are given more chances of successful advancement.

4.3 Species effect

The species examined here differed in their influence on *A. alba* regeneration dependent on spatial scale. The effect of *A. alba* and *P. abies* was maximal in the shortest distance analysed (i.e. 2 m), decreased as the distance from stems increased and corresponded approximately to the horizontal crown projections. The similarity of the spatial pattern of regeneration establishment in the proximity of adult *A. alba* and *P. abies* trees suggests the same mechanism of spatial diversification of fungal infections in below-crown zones and intercrown openings (Paluch and Stępniewska 2012). It remains unexplained, however, why below-crown zones in the proximity of *P. abies* were more preventive of pathogen attacks than those in the proximity of *A. alba*. Both species have a similar rate of precipitation interception (between 20 and 80 %, depending on stand characteristics and rain intensity) (Otto 1994), meaning that the zones sheltered by their crowns should potentially have experienced no difference in wetting frequency. One possible working hypothesis is that the ectohumus layer, which tends to be roughly double the thickness in the neighbourhood of *P. abies* trunks as compared to *A. alba* trunks (Paluch and Gruba 2012), may have modified pathogen behaviour and/or infection mechanisms and hindered the spreading of fungal spores onto the above-ground parts of juvenile seedlings.

In comparison to *A. alba* and *P. abies*, the effect of *F. sylvatica* was more spatially diffused. *F. sylvatica* is a broad-leaved species characterized by a more efficient stem flow, a higher pH and a lower C:N ratio of litter-fall and atmospheric deposition interception than *A. alba* and *P. abies* (Augusto et al. 2002). As a result, on eutric cambisols, the neighbourhoods of this species have a weaker effect on the decrease of topsoil moisture and pH than *A. alba* and *P. abies* (Paluch and Gruba 2012). Yet in spite of these contrasting characteristics, at the stand level, *F. sylvatica* exerts a similarly positive effect on *A. alba* regeneration as *P. abies* (Paluch and Jastrzębski 2013). Although the findings of this present study suggest that this positive stand-level effect does not operate at the local scale, the mechanism underlying *F. sylvatica*'s positive influence may be similar to that in other species; that is, the influence may be linked to the ectohumus layer's preventive effect against fungal infections. Given the wider litter-fall shadows of broad-leaved species and the more homogenous distribution of their litter on the ground (Jonard et al. 2006; Staelens et al. 2003), in mixed stands with *F. sylvatica*, the stand-level effect may be more pronounced than the local

effects attributable to the proximity of tree stems. At the same time, changes in stand species composition may also be accompanied by shifts in the frequency of occurrence and the virulence of pathogens.

5 Conclusions

The above analysis has clearly demonstrated that microsites with differing regeneration density also differ significantly in local species composition and that favourable microsites are characterized by a higher proportion of *P. abies*. Although at the stand level, the effect of *F. sylvatica* ranked between that of *P. abies* and *A. alba*, the local effect of the *F. sylvatica* neighbourhood was insignificant. Hence, although forming mixed stands of *A. alba* with *P. abies* and *F. sylvatica* may ameliorate conditions decisive for establishing *A. alba* regeneration, the limited spatial scale of tree influence identified in this study implies that significant improvement might be achieved using homogenous distribution and considerable partitioning of the admixed species. One viable candidate could be a fine-grained mixture of *P. abies* and *A. alba*, although in the case of the highly competitive *F. sylvatica*, mixtures with small clumpings or two-layered stands with a subordinate beech layer would be preferable.

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