



Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability

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Abstract

The effect of soil type and light availability on a natural regeneration community comprising of several shade tolerant species was studied in 120-year-old managed, beech-dominated, forest in the Czech Republic. Full inventory of natural regeneration was conducted and a light climate (canopy openness, DSF, ISF, TSF) determined from hemispherical photographs on 81 sampling plots (3.14 m² each) belonging to two distinctly different soil types (Calcaric regosol and Calcaric cambisol). The effect of light and soil on basal diameter and height of nine naturally regenerated tree species was examined. The mean density of natural regeneration was about 160 000 ind./ha, which is several times higher than recommended afforestation rates. Density of natural regeneration was independent of soil type and negatively regressed to canopy openness, probably as a result of increased competition with herbal vegetation in open spots. Mean height of natural regeneration was significantly related to soil type and available light. Although species composition of the regeneration community was similar on both soil types, the partitioning of species differed greatly. Influence of soil and light availability on seedling diameter and height differed among species. Soil had significant effect on height of elm and sycamore maple and on basal diameter of elm. Light climate had significant effect on height of beech and diameter of beech and Norway maple. Browsing by deer was found to be an important factor determining natural regeneration community development. Ash, maple and elm were the most preferred with up to 100% of individuals being browsed while less than 15% of beech seedlings were damaged.

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1. Introduction

Natural regeneration of production forests is a viable option for sustainable forest management in Europe and has drawn major attention to natural

regeneration processes (Emborg, 1998; Tarp et al., 2000; Swagrzyk et al., 2001). Financial profitability (Peti, 1976; Tarp et al., 2000), better plant establishment (Mauer and Palátová, 2000), native regeneration material and high seedling densities (Madsen and Larsen, 1997; Holgén and Hånell, 2000) are main advantages of naturally regenerated forests. However, the initial growth of naturally regenerated seedlings is slower than that of planted individuals (Holgén and Hånell, 2000); slower growth makes them more

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sensitive to competition with herbal vegetation, which in many cases can retard seedling development (Dolling, 1996). As a result of above-mentioned advantages, the proportion of naturally regenerated forest stands in the Czech Republic has increased 4-fold in the last 10 years (Ministry of Agriculture ČR, 2001).

Factors affecting success of natural regeneration of forests dominated by shade tolerant tree species have received major attention. Site factors (Madsen and Larsen, 1997; Minotta and Pinzauti, 1996), canopy characteristics (e.g. Emborg, 1998; Wellander and Ottosson, 1998), understorey vegetation (e.g. Dolling, 1996) and individual species performance (e.g. Wellander and Ottosson, 1998) were recognized to play crucial roles in natural regeneration of forest. In general, tree seedlings under forest canopy react positively to increased light level (e.g. Madsen, 1994, 1995; Minotta and Pinzauti, 1996) but in a natural setting, the living environment of seedlings is shared with other understorey vegetation, which can retard seedling development (e.g. Dolling, 1996).

Although differential performance between species is probably the force standing behind species composition dynamics and forest development, natural regeneration studies in Europe are almost exclusively restricted to beech (e.g. Minotta and Pinzauti, 1996; Swagrzak et al., 2001 and others) and oak (e.g. Wellander and Ottosson, 1998). Other species (e.g. maple, ash, elm, lime, etc.) have been neglected in natural regeneration studies although they may form an important part of the natural regeneration community, with far reaching consequences for further forest development. The differential performance between tree species defines the management possibilities and the limits of natural regeneration systems and knowledge of these differences may add to promoting sustainable forest management in European mixed forests.

In this study we targeted the differences in performance of European shade tolerant tree species on two soil types and under various light availability. We hypothesized that various tree species will perform differently under different soil and light conditions and that these differences in performance will determine patterns and development of natural regeneration. To explore the influence of soil and light on complex natural regeneration development we have selected a homogenous beech-dominated forest stand with abundant multi-species natural regeneration.

2. Methods

2.1. Study area and layout of plots

Production beech stand (306 B 12), approximately 120-year-old, in the vicinity of Brno, Czech Republic (49°17'03"N, 16°41'47"E) was selected for this study. Shelterwood regeneration had been started 10 years ago by the first selection cut. European beech (*Fagus sylvatica*) dominated the canopy, accounting for 95% of stems. Sessile oak (*Quercus petraea*), Norway spruce (*Picea abies*), maples (*Acer platanoides* and *A. pseudoplatanus*) and European hornbeam (*Carpinus betulus*) co-occur in the canopy. Two distinctly different (Table 1) soil types—Calcaric cambisol (CMs) and Calcaric regosol (RGc) occur within the stand.

In the stand, 81 sampling plots were established in the regular matrix with 30 m × 30 m spacing over an area of approx. 7.3 ha. Plots were circular with 2 m diameter (area 3.14 m²), making up the total sampling area approx. 254 m². 36 of the plots were situated on RGc, 45 on CMc.

2.2. Field and laboratory methods

All fieldwork was carried out during August 2001. Light available under forest canopy was estimated from hemispherical photographs, which were taken at the center of each plot at 1.5 m height with a Canon T70 camera with a Canon 7.5 mm fish-eye lens on Fujicolor Superia 100 ASA color negative film. Films were scanned, converted to BW images and analyzed for canopy openness, direct site factor (DSF), indirect site factor (ISF) and total site factor (TSF) with Winphot 5.0 (Ter Steege, 1996).

To explore basic patterns, an inventory of natural regeneration (tree individuals lower than 2 m) was conducted for all plots. There were no trees between 2 and 15 m high. We recorded species, height class (10 cm intervals) and damage by herbivores for each individual. The proportional cover of woody regeneration and herb vegetation in plots was estimated during inventory.

To compare seedling growth of major species, sample individuals representing both soil types, a broad range of canopy openness and the majority of height classes were collected in the vicinity of plots

Table 1

Basic physical and chemical properties (mean \pm S.E.) of the two soil types (Modrý and Hubený, 2003)^a

	Calcaric regosol (RGc)			Calcaric cambisol (CMc)		
	Ah1	Ah2	C	Ahck	Bck1	Bck2
Horizon	Ah1	Ah2	C	Ahck	Bck1	Bck2
Boundaries (cm)	1–22	1–22	22+	2–9	9–40	9–40
Specific density (g cm ⁻³)	2.1 \pm 0.07 a	2.5 \pm 0.07 b	2.6 \pm 0.07 b	2.1 \pm 0.07 a	2.6 \pm 0.07 b	2.7 \pm 0.07 b
Porosity (%)	63.9 \pm 1.85 c	60.2 \pm 1.85 bc	54.7 \pm 1.85 ab	61.7 \pm 1.85 bc	48.1 \pm 1.85 a	46.4 \pm 1.85 a
Moisture content (%)	35.9 \pm 1.94 b	30.3 \pm 1.94 ab	23.3 \pm 1.94 a	35.6 \pm 1.94 b	24 \pm 1.94 a	21.2 \pm 1.94 a
Actual aeration (%)	33.2 \pm 2.76 a	30.9 \pm 2.76 ab	25.1 \pm 2.76 ab	23.6 \pm 2.76 ab	19.6 \pm 2.76 b	18.5 \pm 2.76 b
Potential reaction (pH/CaCl ₂)	5 \pm 0.57 ab	5.6 \pm 0.57 ab	6.3 \pm 0.57 b	3.5 \pm 0.57 a	3.3 \pm 0.57 a	3.3 \pm 0.57 a
CEC (mmol 100 g ⁻¹)	74 \pm 5.21 b	57.3 \pm 5.21 ab	45.4 \pm 5.21 a	72.1 \pm 5.21 b	61.7 \pm 5.21 ab	58 \pm 5.21 ab
Exchangeable cation content (mmol 100 g ⁻¹)	32.9 \pm 5.64 b	34.8 \pm 5.64 b	37.1 \pm 5.64 b	6.3 \pm 5.64 a	4.5 \pm 5.64 a	7.3 \pm 5.64 a
Base saturation (%)	47.3 \pm 11.27 ab	68.9 \pm 11.27 b	81.3 \pm 11.27 b	8.6 \pm 11.27 a	7.4 \pm 11.27 a	12.8 \pm 11.27 a
Particle size classes						
Clay (<0.002 mm)	19.6 \pm 3.6 a	24.3 \pm 3.6 ab	19.1 \pm 3.6 a	25.3 \pm 3.6 ab	31.2 \pm 3.6 b	30.9 \pm 3.6 b
Silt (0.002–0.02 mm)	16.5 \pm 2.9 ab	17.8 \pm 2.9 ab	14.9 \pm 2.9 a	21.5 \pm 2.9 c	17.9 \pm 2.9 ab	15.8 \pm 2.9 ab
Fine sand (0.02–0.2 mm)	11.4 \pm 2.7 ab	9.5 \pm 2.7 a	10.1 \pm 2.7 ab	15.9 \pm 2.7 c	11.3 \pm 2.7 ab	11.2 \pm 2.7 ab
Coarse sand (0.2–2 mm)	52.6 \pm 8.0 bc	48.4 \pm 8.0 b	55.9 \pm 8.0 c	37.3 \pm 8.0 a	39.6 \pm 8.0 ab	42.1 \pm 8.0 ab

^a The same letters show means without significant difference (Tukey's Post Hoc test, $P \leq 0.05$).

(1.1–1.5 m from plot center). For each individual, we measured total height from root-neck to terminal bud by tape, basal diameter by shifting measure and age by counting growth rings on the basal transversal cut. The attempt was made to collect individuals without visible damage by herbivores, but for some species (European ash, sycamore maple) it was impossible to find an adequate amount of undamaged individuals. In such cases the browsed individuals were also taken into account and noted in results.

2.3. Data analyses

The characteristics and growth of regeneration communities have been related to soil type and light characteristics. All analyses have been carried out separately for canopy openness, DSF, ISF and TSF to show the most suitable light characteristics. One-way ANOVA (significance test criterion $P \leq 0.05$) was used to test differences among means of various characteristics, with Tukey's Post Hoc test applied to show the homogenous sets of means. Linear regression was used to test the influence of light on regeneration community characteristics. Characteristics that did not differ significantly among soil types (ANOVA, $P > 0.05$) were examined for the whole dataset; characteristics differing significantly among soil types (mean size of seedlings, growth of elm

seedlings) were treated for each soil type separately as well as all analyses with DSF and TSF. A general linear model with soil type as a factor and age and light characteristics as covariates was used to analyze the influence of soil type, age and light on growth of seedlings of the most abundant tree species. Shannon–Weaver index ($H' = -\sum pi \times \ln(pi)$, where pi is the relative abundance of species i) was used to express the heterogeneity of the regeneration community. All data analyses were undertaken with Systat 10.0.

3. Results

3.1. Light patterns

The light availability in the understorey is highly variable. The canopy openness ranges from 5.6 to 24.1%, mean value is 15.4%. The DSF ranges from 0.01 to 0.50 with mean value of all plots 0.19, ISF ranged from 0.01 to 0.39 with mean 0.23. The plots of the two soil types did not differ significantly among each other in canopy openness and ISF but significant differences (ANOVA, $P \leq 0.05$) were found in DSF and TSF (Table 2). Values of all examined light characteristics are closely related; there is a significant linear regression between canopy openness and DSF, ISF and TSF ($P \leq 0.001$ in all cases). The weakest

Table 2
Light characteristics (mean \pm S.E.) of plots of the two soil types^a

Soil type	Openness	DSF	ISF	TSF
RGc	14.8 \pm 0.71 a	0.16 \pm 0.01 a	0.23 \pm 0.01 a	0.17 \pm 0.01 a
CMc	15.8 \pm 0.69 a	0.21 \pm 0.01 b	0.24 \pm 0.01 a	0.21 \pm 0.01 b

^a DSF, ISF and TSF were calculated as the proportion of direct, indirect and total light available below canopy of those above canopy (Ter Steege, 1996).

relation is between canopy openness and DSF ($R^2 = 0.57$). Unless mentioned, results of analyses carried out with DSF, ISF and TSF are analogical to those obtained with canopy openness.

3.2. Nature regeneration patterns

Seedlings of nine tree species (Table 3) and two shrub species (European elder, *Sambucus nigra* and hawthorn, *Crataegus oxyacantha*) were recorded in

the forest stand. Only slight differences were found in species composition of the two soil types (fir was restricted to CMc and hawthorn to RGc, two individuals of each species only).

The mean density of natural regeneration did not differ significantly between soil types (16.2 and 14.0 ind./m² for RGc and CMc, respectively). The mean size of individuals in plots was significantly higher (ANOVA, $P = 0.05$) on CMc (25.7 cm) than on RGc (20.9 cm). There is a negative significant

Table 3
General characteristics of natural regeneration community—density (mean \pm S.E.), height (mean \pm S.E.) and percentage of individuals damaged by herbivores of recorded tree species for soil types^a

Species	Soil type					
	RGc			CMc		
	Density (ind./m ²)	Height (cm)	Browsing (%)	Density (ind./m ²)	Height (cm)	Browsing (%)
Silver fir <i>Abies alba</i>	–	–	–	0 \pm 0.01	5 \pm 0	0
Hedge maple <i>Acer campestre</i>	0.4 \pm 0.11 b	22.3 \pm 2.18 A	60	0.2 \pm 0.05 a	23.1 \pm 3.28 A	86
Norway maple <i>A. platanoides</i>	6.0 \pm 1.10 b	13.7 \pm 0.32 B	88	2.9 \pm 0.80 a	11.5 \pm 0.36 A	94
Sycamore maple <i>Acer pseudoplatanus</i>	1.1 \pm 0.17 b	15.4 \pm 0.79 A	98	0.5 \pm 0.08 a	20.7 \pm 1.4 B	94
European hornbeam <i>C. betulus</i>	0 \pm 0.01 a	10 \pm 5 A	95	0.5 \pm 0.21 b	35 \pm 2.56 A	90
European beech <i>F. sylvatica</i>	4.9 \pm 0.73 a	23.1 \pm 0.7 A	15	7.5 \pm 0.79 b	30.1 \pm 0.67 B	12
European ash <i>Fraxinus excelsior</i>	3.2 \pm 0.49 a	22 \pm 0.62 A	100	2.2 \pm 0.40 a	26 \pm 0.91 B	100
Small-leaved linden <i>Tilia cordata</i>	0.2 \pm 0.05 b	15.6 \pm 1.89 A	12	0.1 \pm 0.02 a	21.3 \pm 4.6 A	24
Smooth-leaved elm <i>Ulmus carpiniifolia</i>	0.3 \pm 0.10 a	40 \pm 3.55 A	100	0.2 \pm 0.06 a	37.9 \pm 5.03 A	98

^a Different letters show significant differences among mean number of individuals (Tukey's Post Hoc test, significance criterion $p \leq 0.05$). Capital letters show differences between mean heights of individuals of the two soil types.

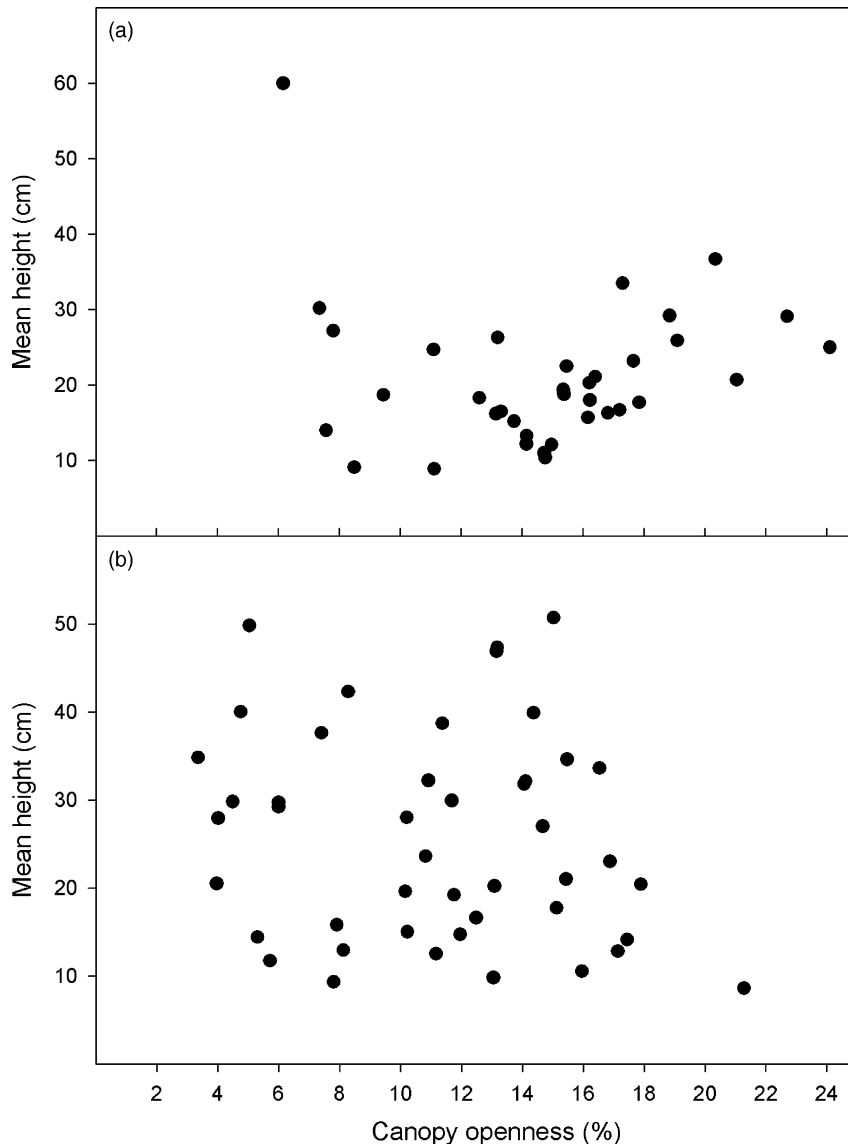


Fig. 1. Relation between canopy openness and mean height of natural regeneration in plots for (a) RGc and (b) CMc.

regression between canopy openness and mean density of seedlings ($P = 0.02$, $R^2 = 0.07$, Fig. 5) but there is not a significant relationship with other light characteristics. Since the mean size of individuals differed among soil types, the relation between canopy openness and mean size was examined separately for CMc and RGc. While there was no trend observed between canopy openness and mean size of individuals for CMc (Fig. 1b), RGc showed a positive significant

relationship between canopy openness and mean size of woody regeneration ($P = 0.04$, $R^2 = 0.12$, Fig. 1a).

The mean cover of natural regeneration and understorey herbal vegetation (14.1 and 19.6% for herbal vegetation and regeneration on RGc, 14.0 and 18.4% on CMc, respectively) did not differ significantly between soil types. Significant positive influence of canopy openness on cover of herbal vegetation was found (linear regression, $P = 0.009$, $R^2 = 0.16$); a

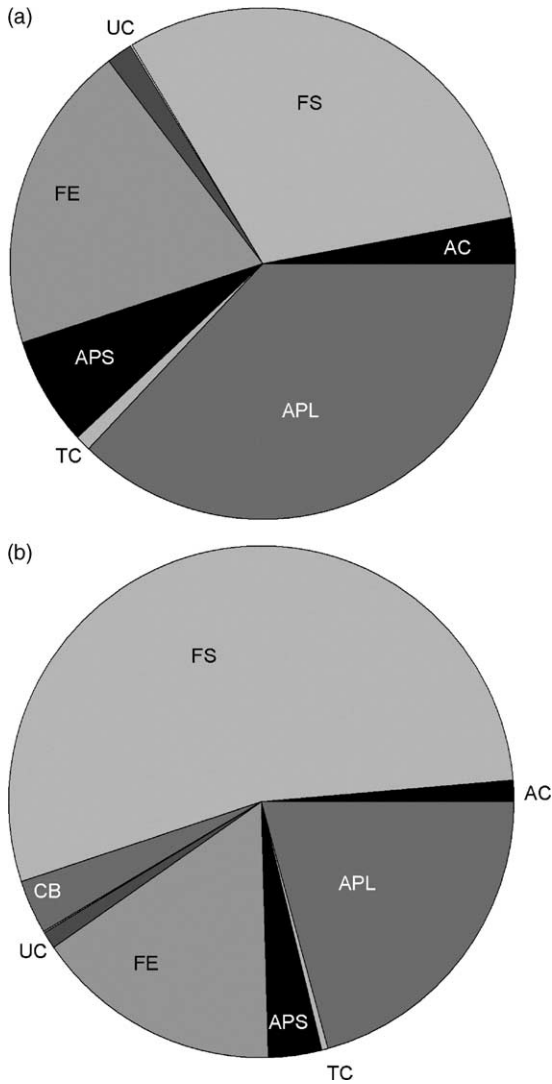


Fig. 2. Species composition and partitioning on (a) RGc and (b) CMc. FS: beech, FE: ash, UC: elm, APS: Sycamore maple, APL: Norway maple, AC: Hedge maple, TC: lime, CB: hornbeam.

stronger relationship appeared between cover of herbal vegetation and DSF ($P < 0.002$, $R^2 > 0.20$ for both soil types). No interaction was found among cover of herbal vegetation and cover of woody regeneration or mean size of woody individuals.

Although the species composition of the regeneration of the two soil types is very similar, major differences were observed among density and share of separate species in total regeneration (Fig. 2). Beech seedlings accounted for over half of total regeneration

on CMc while Norway maple dominated RGc. The minor species (Sycamore maple, linden, ash, elm) were more abundant on RGc and increased the regeneration community heterogeneity represented by Shannon–Weaver index (1.46 and 1.32 for RGc and CMc, respectively). The mean size of individuals differed significantly between soil types for ash only (Table 3).

The mean density of hornbeam was positively related to canopy openness whereas the mean density of ash was negatively related to canopy openness. The density of elm was positively related to canopy openness on RGc although the relation was not significant for the whole dataset. The mean seedling size was positively related to canopy openness for hedge maple, sycamore maple and elm. There was a positive significant relation between canopy openness and mean seedling density for ash on RGc, but the trend was not significant on CMc. Both size and density of beech, Norway maple and linden were independent of all light characteristics.

3.3. Seedling growth

The growth of seedlings was examined separately for the most abundant species to determine factors influencing seedling growth. Age played an important role in both the total height and basal diameter growth for all examined species except ash, where total height seemed to be independent of age, probably as a result of nearly 100% damage by herbivores. The influence of canopy openness on seedling height and diameter was significant for both the height and diameter of beech and for the diameter of Norway maple, it was not found to be important for other species. Soil type had a significant effect on elm growth only (Table 4, Figs. 3–5).

3.4. Influence of herbivores

The proportion of individuals influenced by herbivores differs among species. The beech is the least preferred with 14% damaged individuals; also linden seedlings almost escaped browsing (15% damaged individuals). On the other hand, the terminal buds of all three maple species and elm as well as all individuals of ash were almost completely snapped off. No difference in damage caused by herbivores was found between soil types (Table 3).

Table 4

Results of ANCOVA model describing the effect of soil type, age and canopy openness on seedling growth represented by height and basal diameter^a

Species	Variable	Height		Basal diameter	
		<i>P</i>	<i>R</i> ²	<i>P</i>	<i>R</i> ²
<i>F. sylvatica</i> (<i>N</i> = 312)	Soil type	0.129	0.73	0.062	0.84
	Age	<0.001		<0.001	
	Openness	<0.001		0.001	
<i>Ulmus carpiniifolia</i> (<i>N</i> = 33)	Soil type	0.023	0.34	<0.001	0.47
	Age	0.003		0.001	
	Openness	0.8		0.4	
<i>A. platanoides</i> (<i>N</i> = 119)	Soil type	0.6	0.44	0.9	0.69
	Age	<0.001		<0.001	
	Openness	0.7		<0.001	
<i>Acer pseudoplatanus</i> (<i>N</i> = 90)	Soil type	0.08	0.61	0.7	0.71
	Age	<0.001		<0.001	
	Openness	0.8		0.22	
<i>Fraxinus excelsior</i> (<i>N</i> = 30)	Soil type	0.4	0.35	0.25	0.79
	Age	0.13		0.01	
	Openness	0.6		0.9	
<i>C. betulus</i> (<i>N</i> = 26)	Soil type	0.3	0.41	0.4	0.59
	Age	0.001		0.048	
	Openness	0.6		0.9	

^a Significance of each independent and *R*² of the model are shown for each species.

4. Discussion

Natural regeneration of forests usually results in high seedling densities (e.g. Madsen and Larsen, 1997; Holg n and H nell, 2000); this case is not an exception. Mean density of regeneration (14 and 16 ind./m²) is several times higher than the afforestation rates recommended for any of the species (maximum 10 000 ind./ha). Even the density of beech as a major commercial species in this forest is 5–7-fold higher than the recommended afforestation rate. In beech forests, these high seedling densities do not incur increased early management costs as beech forests perform self-thinning in early development.

Selection of a forest stand with homogenous canopy and rich natural regeneration situated on two distinctly different soil types enabled us to describe the influence of soil on early growth of various shade tolerant European tree species. The forest stand was in the first phase of shelterwood regeneration. The canopy structure of the forest was quite homogenous (canopy openness 5–24%) without major gaps resulting in a

relatively narrow range of light conditions. This narrow range influences the outcomes of community analyses and results in a weak relationship between available light and mean regeneration height. Detailed species-specific growth analyses revealed differences in growth among species and showed the importance of minor differences in light climate on early seedling growth.

Consistent with results of other studies (e.g. Madsen, 1995; Minotta and Pinzauti, 1996), soil was found to have a significant effect on regeneration community growth. Differences in performance related to soil properties among species resulted in completely different partitioning of species in the natural regeneration community of the two soil types. The effect of soil in determining natural regeneration patterns is underlined by similar canopy composition and light climate in the understorey.

The individual growth analysis showed that the diameter growth of beech and elm is slower on RGc than on CMc, while the soil type has no influence on growth of maples and ash. Development of elm on

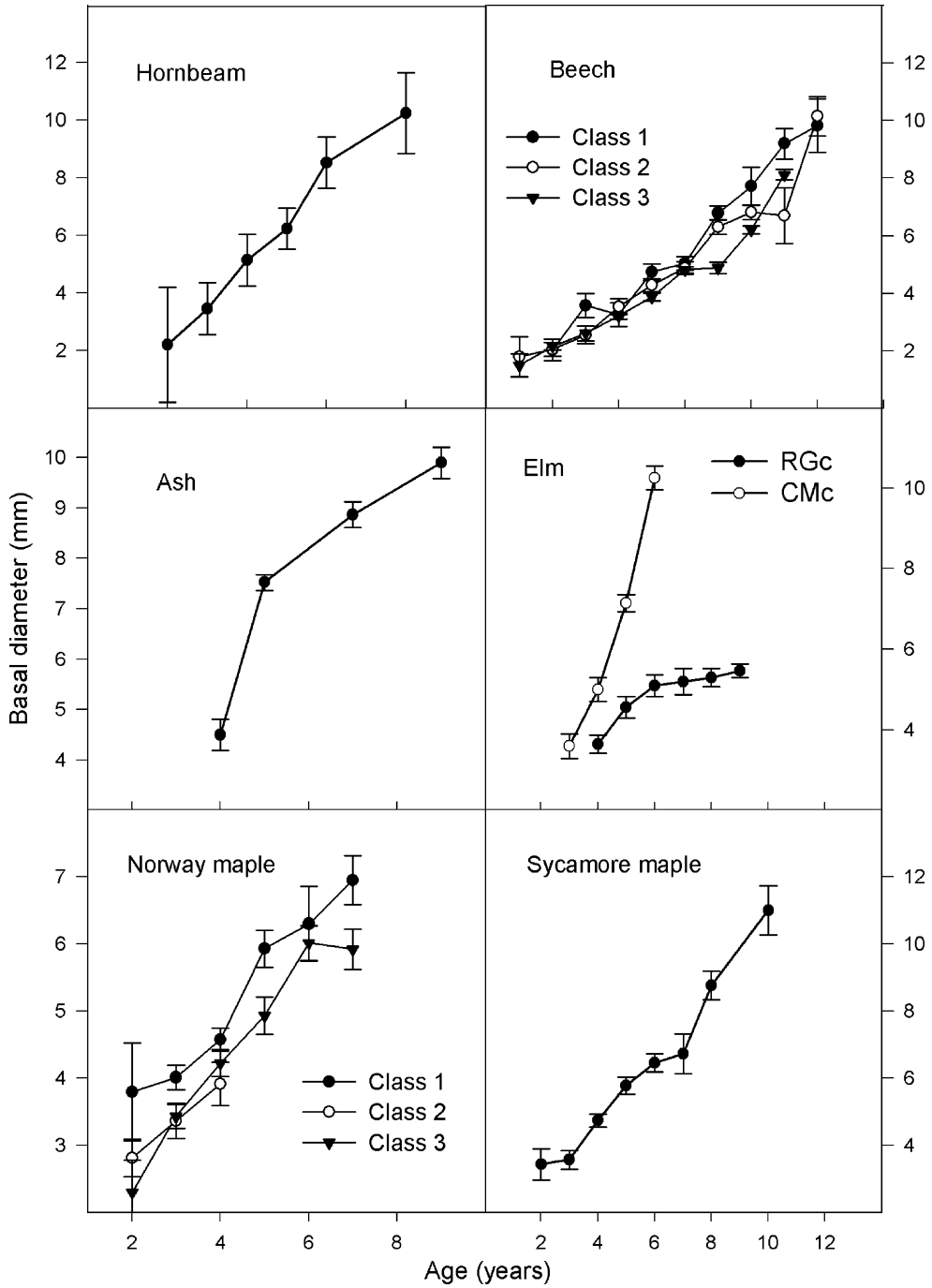


Fig. 3. Basal diameter as a function of age for selected species. Three lines for beech and Norway maple show significant effect of light, two lines for elm show significant effect of soil type.

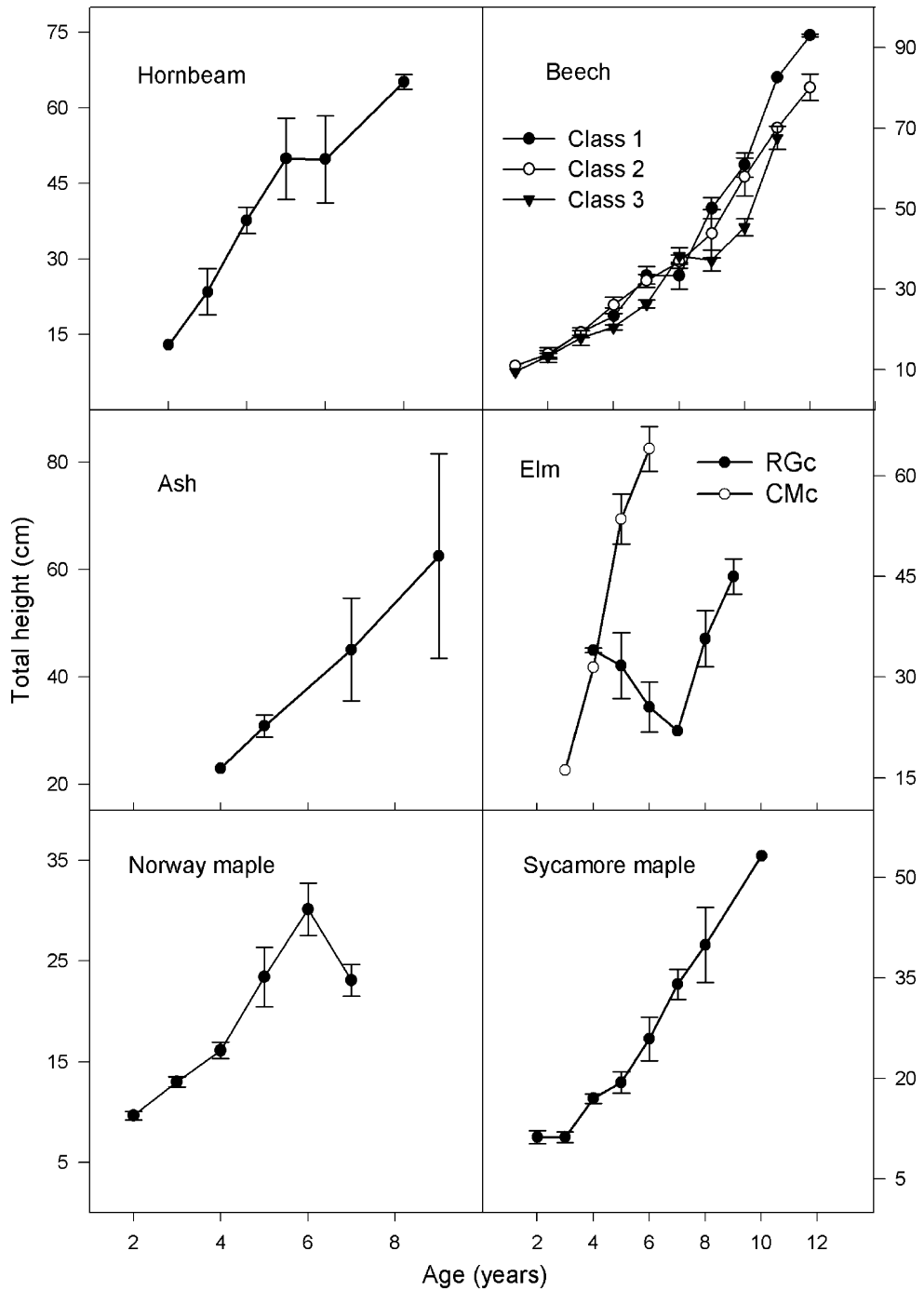


Fig. 4. Total height as a function of age for selected species. Three lines for beech show significant effect of light, two lines for elm show significant effect of soil type.

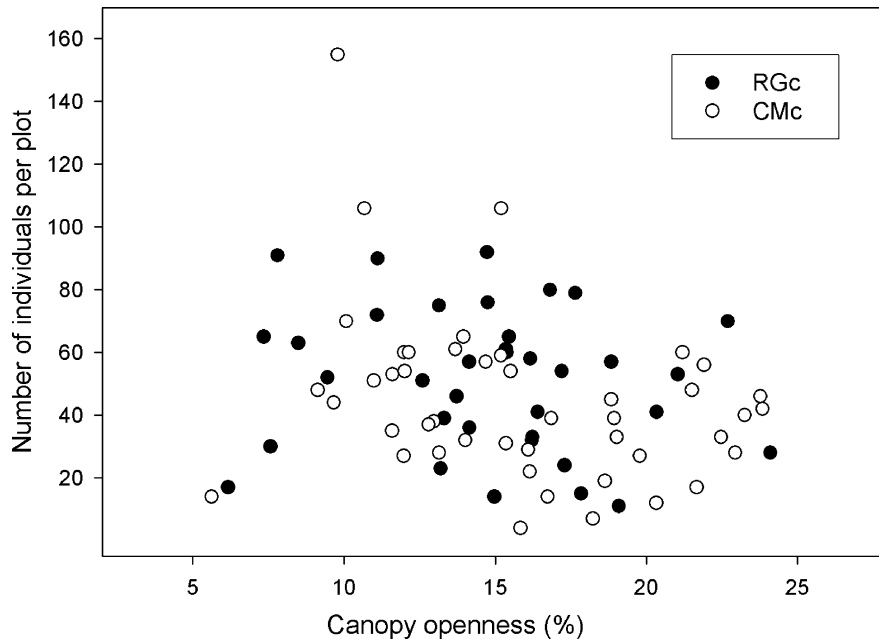


Fig. 5. Relation between canopy openness and total number of seedlings per plot.

RGc is retarded to a degree, in which it is not a suitable commercial species. These trends can be attributed to lower base saturation and exchangeable cation capacity of RGc. Direct influences of separate soil characteristics on species performance can be revealed by controlled experiments only.

The relationship between regeneration community and light climate was analogical for all light characteristics examined (canopy openness, DSF, ISF, TSF). None of the species investigated have shown different relationships to direct light availability than to canopy openness. This suggests that seedlings of shade tolerant European tree species utilize light dispersed under the forest canopy and do not profit strongly from direct light input. The relationship between cover of herbal vegetation was much stronger with DSF than with canopy openness showing that herbal vegetation reacts more sensitively to direct light than present tree regeneration. Increased direct irradiation thus may lead to a decrease in performance and density of woody regeneration as a result of increased competition for resources. This trend was many times verified in practical temperate forest management.

Mean height of regeneration was positively related to light availability on RGc only, corresponding to

increased importance of light on nutrient poor sites. The general effect of light availability on mean seedling height can be weakened by browsing rates, variability in age of seedlings in each plot and the narrow range of light availability in the forest stand.

Although increased light level is generally reported to positively affect seedling growth (e.g. Madsen, 1994; Madsen and Larsen, 1997; Collet et al., 2001), only height of beech was significantly influenced by canopy openness. Since high browsing rates of other species are likely to be responsible for biased results, diameter growth analysis provides more information. Even in diameter growth, only beech and Norway maple showed significant effects of light availability.

The browsing preferences of deer may play an important role in nature regeneration dynamics. For some species, the browsing rates are very high, reaching up to 100% of individuals (ash seedlings). Fenced plots in the vicinity of experimental plots showed that maples and ash would dominate the stand in the age of 15–25 years if not heavily browsed by deer. In this forest stand, deer browsing helps to maintain the desired commercial species composition with strong dominance of beech even on less suitable Calcaric Regosols where maples would probably take over.

5. Conclusion

This study has revealed the influence of soil and light on natural regeneration community patterns and development. The interspecific differences in performance of tree seedlings with respect to soil and light will determine the development of the regeneration community unless target species composition is maintained by forest manager. Although deer browsing is generally considered to be an important obstacle in natural regeneration success, in cases such as this it helps to maintain the desired species composition.

Knowledge of processes and factors influencing nature regeneration is essential for its successful application. Factors affecting natural regeneration of beech have received major attention lately. This study showed that performance of other European shade tolerant tree species differs from that of beech but these species (e.g. ash, maples and elm) have been mostly omitted in recent studies. As shown, these species may play a dominant role in natural regeneration processes and thus the knowledge of their performance is of key importance for management of European mixed forests.

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