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ORIGINAL PAPER

Responses of crown architecture in *Betula pendula* to competition are dependent on the species of neighbouring trees

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Abstract We measured the growth responses of individual shoots and branches of *Betula pendula* when growing next to trees of the same species or *Pinus sylvestris*, *Larix sibirica* or *Alnus glutinosa*. We used the three-dimensionally digitized response variables and the size and distance of trees growing within a 5-m radius of the study trees to establish a relationship between tree performance and the effect of competing neighbouring tree species on crown architecture. *B. pendula* was able to modify its crown architecture and thus alter its strategy to compete with different neighbours. Trees of *B. pendula* growing beside species counterparts had the highest growth of new long shoots in relation to the already existing branch length [growth vigour (GV)], while GV was the lowest next to *L. sibirica*. With *B. pendula* or *P. sylvestris* as its main neighbour, *B. pendula* invested in short shoots by growing them rather densely in short branches with limited numbers, whereas with *L. sibirica* the number, length and angle of the branches were high. The competitive response was also strongly dependent on tree ontogeny and the shoot and branch characteristics were significantly affected by their location inside the crown. *B. pendula* was able to respond to the challenges posed by its neighbours, which was also reflected in the GV. The ability to maintain steady growth with alternative crown designs in different neighbourhoods reflects plasticity in the crown responses.

Keywords Acclimation · *Betula pendula* · Competition · Crown architecture · Shoot growth · Neighbour effect

Introduction

The architecture of a tree crown follows some species-specific growth rules and ways of reacting to the environment (Hallé et al. 1978; Bell 1991). Within these genetic limits, acclimation occurs as the structure of a tree develops during its lifespan to reflect the dynamic changes in its environment (Bonser and Aarssen 1994). A tree crown maintains the efficiency of vital functions by allocating limited growth resources, which are under constant change and often unevenly distributed inside a crown, among different structures and functions (Chelle 2005). This allocation is proposed to happen through a complex optimization process where within-plant signalling and environmental factors are integrated (Vandenbussche and Van Der Straeten 2004). The growth of the surrounding vegetation continuously modifies the environment: i.e. light conditions and available growing space. Growth responses occurring as a consequence of neighbouring plants and their competitive effects are called the competitive responses of the target plant (Weiner 1990).

Silvicultural competition studies have traditionally used stand averages of neighbouring effects and responses, as is also the case with *Betula pendula* Roth. (e.g. Lappi-Seppälä 1930; Mielikäinen 1980; Valkonen and Ruuska 2003). The use of individual target trees and distance-dependent competition indices (CIs), which incorporate the number, size and location of the neighbouring trees

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(e.g. Tomé and Burkhart 1989), has not substantially improved the detection of competitive responses compared to stand averages (e.g. Biging and Dobbertin 1992, 1995). Today, distance-dependent CIs are most often used for measuring aboveground competition interpreted as competition for light affecting the area occupied by tree crowns. Stand-level measurements, on the other hand, are used to illustrate belowground competition for water and nutrients which affects larger, rather unpredictable areas (Stiell 1970; Ledermann and Stage 2001).

Studies separating the effects of different neighbouring species on competitive response have typically used simple response variables, such as increase in height, and have not aimed at revealing the more detailed responses of the target tree crown architecture. Yet, it is clear that the complex and dynamic crown architecture also reacts to competition at lower levels of organization inside the crown (e.g. Osada et al. 2002, 2004; Kaitaniemi and Lintunen 2008). Responses to mild stress entails much more than direct effect of resource deprivation on growth rate (Aphalo and Ballaré 1995). Therefore, detailed measurements of crown architecture may be crucial to understanding the growth responses of trees in various ecological conditions where the crown interacts with its environment through the action of individual branches (Sprugel et al. 1991; Sachs 2004) and shoots, each growing and surviving semi-independently in response to its local environment (Takenaka 2000; Nikinmaa et al. 2003; Kaitaniemi and Ruohomäki 2006). Crown architecture may vary as a plastic response depending on the neighbouring species due to differences between species in growth rates, use of resources (see Goldberg 1987), crown profiles, light interception structures and ability to cause mechanical disturbance.

Recent theoretical advances have also suggested that several functionally equivalent strategies for maintaining efficient performance may exist in trees growing in similar environmental conditions (Marks and Lechowicz 2006). Although functional equivalence is mainly considered to be a mechanism which generates variability between species (Hubbell 2005), it is a mechanism that could operate analogously also within species (Kaitaniemi 2007), thereby providing alternative ways for achieving equal performance with variable combinations of traits.

To examine this theoretical question as well as to address the general importance of tree architecture in competition, which has only been superficially covered in the literature, the objectives here were: (1) to determine which of the measured competition and ontogenetic factors, and factors related to the spatial location inside the crown, contribute to shoot- and branch-scale components of crown architecture in up to 30-year-old *B. pendula* growing in mixed forests additionally composed of *Pinus sylvestris* L., *Larix sibirica* Ledeb., *Alnus glutinosa* (L.) Gaertner, or other individuals of *B. pendula*; (2) to determine whether the crown architecture varies according to neighbouring species and, most importantly; 3) to study the consequences of the various crown architectures formed on tree performance in *B. pendula* when interacting with different neighbours using growth vigour (GV) as a measure of performance.

Growth responses were characterized according to the number of long and short shoots, length of long shoots, number of first-order branches, length and angle of branches. These variables were directly associated with the GV of the study trees and thus likely indicate the lifetime performance of those trees that were still young and actively competing for their status inside the stands (Landis and Peart 2005). The location of shoots and branches inside the crown was also considered since the fates of shoots in *B. pendula* change depending on shoot position (Maillette 1982). Tree age or height was used as an indicator of the ontogenetic stage. The environmental factors included the main species of close neighbours and the amount of aboveground competition, which was characterized by several optional distance-dependent CIs.

Materials and methods

Study species

The study species *B. pendula* is a deciduous pioneer tree species. It extends axially with a sympodial growth pattern by producing long shoots, which are important modular units of tree growth, crown development and structure (Maillette 1982; Jones and Harper 1987b). The axillary buds of the long shoots develop into new long or short shoots. It was suggested that short shoots, which bear the majority of the leaves, are more specialized for leaf display (Jones and Harper 1987b) since they grow monopodially only a few millimetres per year. It is also possible for a short shoot bud to produce a long shoot. Short shoots have from two to three leaves, whereas new long shoots produce numerous leaves throughout the summer by indeterminate growth (Maillette 1982).

All the tree species included in the study are light-demanding species actively competing for light. The study trees were selected so as to have a clear dominant tree species surrounding each of them to distinguish the influence of different neighbouring species. *B. pendula* and *P. sylvestris* together with Norway spruce *Picea abies* (L.) H. Karst. are the three most common tree species forming forests in Finland. *A. glutinosa* also grows naturally in Finland. Combinations of these three studied species are native to most of Europe and Southwest Asia, whereas the fourth study species, *L. sibirica*, can be found with

B. pendula from Western Russia to Central Siberia (Hämet-Ahti et al. 1992).

Sampling design

Twelve unconnected study sites were located in the southern half of Finland along a southwest–northeast transect between latitudes 60°N and 63°N, and longitudes 21°E and 29°E, in the boreal forest zone. A substantial geographical range was covered to eliminate the potential effects of local adaptation from the results. A factor common to all study sites was that they were mixed partially planted areas representing the *Myrtillus* forest site type (Cajander 1909). Furthermore, they comprised plots of up to 50 m × 50 m, where *B. pendula* was abundant together with at least one of the other tree species studied (Table 1). *Betula pubescens* Ehrh. was also frequently found and some infrequent individuals of *P. abies* were typically present in the undergrowth. The sites were defined as largely homogeneous stands in the local forest management plan. None of the sites had undergone recent management procedures that could have affected the responses.

In all, 6 of the 12 study sites were experimentally established replacement series of mixed-species plantations. Four of them were planted with *P. sylvestris* and in part with *B. pendula* in 1982 and 1983 at a density of 2,060 seedlings per hectare. In the case of *B. pendula*, seedlings were also planted 8 years later or occurred naturally. Two of the experimentally established sites were planted in 1999 and 2000 with *P. sylvestris*, *B. pendula*, *L. sibirica* and *A. glutinosa* with 4,400 seedlings per hectare. The other six study sites were planted as mixed stands for silvicultural demonstrations in 1979, 1981, 1986 or 1988, and were often complemented by naturally occurring individuals of the species studied. The initial seedling density of at least four of these sites was 2,000 seedlings per hectare. Information regarding the establishment year of one of the oldest sites as well as initial density for two sites was lacking.

The sampling scheme conformed to a fractional factorial design in order to balance between the need to obtain a representative sample of trees for testing the most important explanatory variables and the huge amount of work required for measuring the tree architecture using point-by-point digitizing (Sinoquet et al. 1997). Accordingly, not all the factor combinations were available, e.g. not all species combinations were present at all sites, but those available partially overlapped to facilitate analysis of the most ecologically interesting effects (e.g. Zaluski and Golaszewski 2006). In all, 73 *B. pendula* trees distributed among the 12 study sites were selected for the study. The trees studied represented 4–33-year-old individuals and thus encompassed the developmental phase in which *B. pendula* grows most rapidly and establishes its competitive status. Within each site, two or three trees were typically measured per species combination available (Table 1). To enable the

Table 1 Characteristics of the study sites in mixed forests

Study site	Neighbouring species	Study tree information				Site characteristics		
		No. of study trees	Mean age (years)	Mean height (m)	Max height (m)	Site index (H^a_{50})	Mean height (m)	Basal area (m^2/ha)
1	*B. pend.*[a], *P. sylv.*[b]	6	21	9	13	24	8	10
2	*B. pend., P. sylv., L. sib.*[c]	7	13	7	9	22	6	13
3	*B. pend., P. sylv., L. sib.*	4	11	5	6	22	5	8
4	*B. pend., P. sylv.*	6	17	13	17	30	9	15
5	*B. pend., P. sylv., A. glut.*[d]	7	29	17	21	26	15	25
6	*B. pend., P. sylv.*	6	21	10	13	22	10	12
7	*B. pend., L. sib.*	4	23	15	17	24	13	33
8	*B. pend., P. sylv., L. sib.*	3	32	14	16	22	15	18
9	*B. pend., P. sylv.*	6	22	10	12	22	8	12
10	*B. pend., P. sylv., L. sib., A. glut.*	14	4	2	3	26	2	2
11	*B. pend., L. sib., A. glut.*	8	4	2	2	24	2	<1
12	*P. sylv.*	2	21	11	13	22	9	20

All the sites were classified in the same fertility class based on forest floor vegetation. The site index was calculated to further estimate the capability of the study trees to produce wood at different sites

[a] Site index is an estimated dominant height (mean height of 100 trees per ha with highest diameter-at-breast-height) in the 50-year-old trees for *Betula pendula* in Southern Finland. It was defined for each site from a height bonitet table with maximum study tree height and age of that tree

B. pend., Betula pendula; P. sylv., Pinus sylvestris; L. sib., Larix sibirica; A. glut., Alnus glutinosa efficient detection of neighbour-specific responses at each site, the sizes and ages of trees selected within each site were as uniform as possible (Table 1). The stands representing different age or height classes were also replicated to avoid ontogenetically systematic variation by always ensuring that at least two sites had a maximum difference of 2 m in the average tree height (Table 1).

The neighbouring trees were defined as those that touched or could have touched the study tree crowns by extending their branches straight through an open space within a circle with a maximum radius of 5 m. This criterion excluded those trees inside the 5 m radius that were situated behind another tree, as crown collision with the target tree or intense light reflectance reaching the target tree was hardly possible in these cases. Since only aboveground competition was estimated, we assumed that significant competitive stress in individual trees was induced only by the ring of competitors immediately surrounding the subject tree crown (Cole and Lorimer 1994). Previous studies used a radius 3.5 times the mean crown radius of the canopy trees (Lorimer 1983; Mailly et al. 2003); in our data the mean crown radius of all the study trees was 1.2 m. In addition, the CIs used in this study decreased as a function of the distance between the target tree and the neighbour following an inverse J-shaped curve form (Ledermann and Stage 2001); thus neighbours beyond the 5-m radius would have had a minor effect on the total CI.

The neighbours shared approximately the same height as the study trees, and the coefficient of variation for the different traits characterizing the neighbours was generally half of the value detected among the sites. The total basal area of the main neighbouring species exceeded the total basal area of all the other neighbouring trees, except for three study trees growing at a single 4-year-old stand. In these three cases, the competitive status of the trees was likely yet unsettled, so we considered it safer to define the neighbouring species based on the large number of small competitors belonging to a single species instead of a single tree with a high basal area belonging to another species. The average total basal area for the main neighbouring species varied from 75 to 89%, with the coefficient of variation ranging from 11 to 24%.

Measurements

To examine the growth responses of the study trees with different neighbours, the architecture of the study trees was measured by digitizing the structure of the sample branches. In summer 2003, the study trees were felled gently using a pulley as an aid, and their stems cut into 1.5-m lengths before digitizing. Digitizing was performed to record the detailed architecture of the treetop and, in addition, 2–5-sample branches were systematically chosen to represent all vertical sections of the crown from the base to the top. For *B. pendula*, such a sample is sufficient to detect most of the pattern of shoot production and elongation (Maillette 1982). The growth direction of the sample branches was selected randomly. Additionally, the positions of the base and tip of each first-order branch extending from the stem were recorded. From the treetop and sample branches, the three-dimensional (3D) position of the base and tip of each shoot and branch of every gravelius order (GO) (MacDonald 1983) was recorded together with information concerning the age of shoots younger than 3 years. Since the measurements were performed during the growing season, long shoot information from the previous year (2002) was utilized. Conversely, information regarding short shoots and branches originated from the measurement year 2003. The mean number of measured long shoots per tree was 70, short shoots 715 and first-order branches 52. Digitizing was performed using a Polhemus Fastrak equipped with a digitizing stylus and a Longranger transmitter (Polhemus Inc., Colchester, VT, USA). To maintain accuracy in capturing the coordinates in the field, the digitizing site was covered with a wind shelter.

The coordinates recorded were used to rebuild the 3D architecture of the trees with a computer and further to calculate various crown variables in order to analyse GV, shoot growth, and the numbers and locations of shoots, as well as branch number, length and angle. Growth vigour is a relative growth rate describing current, overall tree performance. It was derived from the total length of the long shoots (*totlong*) located in both the digitized treetop and the sample branches in the year prior to sampling (t), and from the total length of the same tree parts (*totlength*) 2 years prior to sampling ($t - 1$); it was represented as $\mathrm{GV} = totlong_t/totlength_{t-1}$.

Number of shoots was calculated as the number of living long and short shoots per sample branch, and for branches as the number of living branches per 10% of the crown length. Length of branches was measured as the distance between the branch base and the furthest situated living shoot inside the branch. Angle of branches was defined as the angle between the trunk and the direction of the branch at about 5–10 cm from the branch base.

The location of individual shoots and branches inside the crown was considered by calculating the effects of relative height-within-the-crown (RHC) and GO (MacDonald 1983) in the case of long shoots. The RHC is the relative height of the shoot or branch base position expressed as a percentage of the crown length, with 0% referring to the crown bottom and 100% to the crown top. The crown length was defined as the distance between the base of the lowest living branch and the highest living shoot in a crown. However, in the case of branch scale analysis current-year shoots were excluded from the crown length because older branches do not yet exist in that part of the crown where new long shoots are growing. The GO assigns the same order number to segments belonging to the same axis and one order number higher to lateral segments. The stem is the main axis, which is assigned the order 1; lateral branches attached to the stem are assigned the order 2 etc.

Trees that were defined as neighbours were measured to obtain distance to a sample tree (L_{ij}), diameter-at-breast-height (d_j) and tree height (h_j). A group of 14 distance-dependent CIs (Rouvinen and Kuuluvainen 1997) was compared separately for each analysis to find the best index for measuring the amount of neighbouring tree competition since a single index which would be superior with all species in all situations has yet to be pinpointed (Biging and Dobbertin 1992). Six CIs were selected for the final models:

$$\mathrm{CI}_1 = \sum_{j=1}^{n} \arctan\left(d_j/L_{ij}\right) \quad (1)$$

$$\mathrm{CI}_2 = \sum_{j=1}^{n} \arctan\left(d_j/L_{ij}\right),\ d_j > d_i \quad (2)$$

$$\mathrm{CI}_6 = \sum_{j=1}^{n} \arctan\left(h_j - 0.8h_i/L_{ij}\right),\ h_j > 0.8h_i \quad (3)$$

$$\mathrm{CI}_8 = \sum_{j=1}^{n} \arctan\left[\left(h_j - h_i\right)/L_{ij}\right],\ h_j > h_i \quad (4)$$

$$\mathrm{CI}_9 = \sum_{j=1}^{n} \frac{d_j}{L_{ij}} \quad (5)$$

$$\mathrm{CI}_{12} = \sum_{j=1}^{n} \frac{\left(d_j/d_i\right)^2}{L_{ij}} \quad (6)$$

where i denotes the study tree, j the neighbouring tree and n the number of competitors in a 5-m radius from the study tree. Rather than stand level measurements, distance-dependent indices were used because species-specific competition is detectable in field studies mainly through aboveground competition, which results in variation in growth between neighbouring trees. Belowground competition, on the other hand, decreases the growth evenly between trees over a wider area and hence the competitive effect is difficult to separate between trees (Weiner 1990). In addition, the study trees grew in stands with sufficient nutrients and water, and the majority of them had already undergone the youngest sapling phase when root competition is most important (Morris et al. 1993). Therefore, light was likely the most important competition resource (Holmes and Reed 1991).

Ecological context of the variables

Seven dependent variables and 13 explanatory variables (Table 2) derived from the data were examined in statistical tests. The dependent variable GV together with the number of short and long shoots and length of long shoots represented the effect of factors describing the current growth responses. Conversely, the number, length and angle of first-order branches indicated the past influences on the current tree architecture.

The explanatory variables RHC and GO represented the location of shoots or branches inside the crown. We assumed that RHC indicated both the relative light level and relative branch age within the crown. In previous studies on *Betula*, the age of branches clearly affected the number of different shoot types (Maillette 1982; Jones and Harper 1987a, b) and vertical position of branches affected long shoot length (Goulet et al. 2000). Gravelius order described the hierarchical position of a shoot reflecting apical dominance, and it also correlated with an index suggested by Nikinmaa et al. (2003) to explain shoot growth. The variables tree height and age were used to describe the developmental stage of a tree. These two variables were correlated, thus only one of them was included in the analysis at a time.

The neighbouring species and the CIs were explanatory variables representing mainly the aboveground effect of neighbouring trees on the architecture of a target tree. Another explanatory variable was branch length, which was an exception among the variables in the sense that it served as both a dependent and explanatory variable in different analyses: it was used to explain the number of shoots and angle of branches. Explaining the number of long and short shoots by branch length was quite straightforward since branch length described the number of potential shoots on a branch. The relationship between angle and length of branches, in turn, is not that clear; anatomically, branch angle is determined partly during branch formation and partly during its growth history (Wilson 1998). We assumed that during growth, long branches may bend downwards because branch weight can promote formation of tension wood and growth in the upper side of the branches (Alméras and Fournier 2009; Wang et al. 2009).

The use of a fractional factorial design allowed us to include some interaction variables in the models (Table 2). An interaction variable, neighbouring species with CI, described possible species-specific effects on the target tree related to differences between species in the competition effect of a given CI unit. Large individuals of a neighbouring species with a high light-interception rate would have a stronger competitive effect than large trees with a low interception rate. The amount of foliage per basal area

Table 2 *P* values from type-3 GEE analysis for the model explaining dependent crown variables with selected combinations of explanatory variables

Explanatory variables	Growth vigour $R^2 = 0.64$	Long shoot number in a branch $R^2 = 0.36$	Long shoot length (cm) $R^2 = 0.34$	Short shoot number in a branch $R^2 = 0.60$	Branch number[a] $R^2 = 0.49$	Branch length (cm) $R^2 = 0.43$	Branch angle (°) $R^2 = 0.05$
Branch length (cm)	–	**0.0023**	0.6551	**<0.0001**	–	–	**<0.0001**
CI[b]	(CI_{12})	(CI_6)	(CI_9)	(CI_9)	(CI_8)	(CI_1)	(CI_2)
	0.0607	**0.0020**	**0.0427**	0.0960	**0.0177**	0.6739	0.0511
GO[c]	–	–	0.9171	–	–	–	–
Neighbouring species	0.5103	0.3795	0.8897	0.1720	0.1807	0.7015	0.6595
RHC[d] (%)	–	0.1465	**0.0291**	0.5444	**<0.0001**	**<0.0001**	**<0.0001**
Tree height (m)	–	–	–	–	**0.0006**	**<0.0001**	0.3281
Tree age (years)	0.2386	**0.0009**	**0.0274**	**0.0373**	–	–	–
Neighbour × CI	**0.0488**	0.1789	0.6536	**0.0149**	**0.0261**	0.1308	**0.0177**
Neighbour × Tree height/age	0.3428	0.9542	0.4348	0.1060	0.1069	0.0556	0.0750
RHC × GO	–	–	**<0.0001**	–	–	–	-
RHC × Branch length	–	**<0.0001**	0.0546	0.2249	–	–	–
Tree height/age × CI	**0.0167**	**0.0164**	**0.0185**	0.1233	**0.0142**	**0.0006**	0.0794

[a] 10% classes of RHC

[b] Competition index

[c] Gravelius order

[d] Relative height within the living grown

Statistically significant *P* values are written in bold. Coefficients of determination (R^2) are also shown for each analysis. Individual trees were defined as the subjects in the analyses ($n = 73$)

also differs greatly between species (Brown 1978 in Bravo et al. 2001) (in more detail in “Discussion”). Variable interaction of neighbouring species by tree height or age indicated the cumulative long-term effects of different neighbours since the duration of the effects was likely reflected in tree age or size (Mitsuda et al. 2002).

In addition to the interaction variables with neighbouring species, interaction of tree age or height and CIs were added to the models, for it has been shown that competitive effect increases with time (Wagner and Radosevich 1991; De Luis et al. 1998). The interaction of RHC with GO was also added since they both are likely involved in the same hormonal signal: optimal light conditions that depend on RHC enhance auxin formation, and the apical control inside a plant represented here by GO is regulated by auxin hormone (Sachs 2004). Hence, the hormonal signal for shoot growth is actually determined as a combination of the effects of GO and RHC. The RHC and length of branches constituted an additional interaction variable since the number of shoots per branch length may vary in different vertical positions inside the crown. This variation is due to death of the shoots in old branches (low RHC), which typically leads to a smaller number of shoots per branch length. The interaction of RHC and branch length was also used in the analyses of shoot length because branch length alone reveals little about individual shoot growth: length of a branch can be achieved either by high branch age or growth rate.

Statistical analysis

All the explanatory variables describing the phenomenon of interest were included in each model explaining the different crown variables (Table 2). Selection between tree height and age as well as between the alternative CIs was made based on the coefficient of determination (R^2, Table 2).

To examine the multivariate effects on crown architecture, generalized linear models were fitted to the data by generalized estimation equations (GEEs) with the GENMOD procedure (SAS Institute, Cary, NC, USA). The GEE analysis was able to consider the lack of statistical independence due to the correlated repeated measures of the same tree individuals (Orelien 2001). The GEE analysis can be used for any situation in which the emphasis is on understanding the average relationships between the explanatory variables and the dependent variables, and where the data are correlated but the correlations are not the main focus of the analysis (Wu et al. 2001), as was the case in the present study.

To interpret the results with various interaction variables, we used the method presented by Aiken and West

(1991). Let us assume that the model for Y has only three significant explanatory variables X, Z and their interaction XZ (Aiken and West 1991):

$$\hat{Y} = b_1X + b_2Z + b_3XZ + b_0 \tag{7}$$

The interaction variable means that the regression of Y on X is dependent on Z, and vice versa (Aiken and West 1991). To illustrate the effect of the statistically significant interaction variables in the models, the figures were drawn by rearranging the overall regression equation in each model. This was done by including the slopes of the two main effects and the slope of the interaction in a simple regression equation to show the slope of Y on X at a certain level Z (Aiken and West 1991)

$$\hat{Y} = (b_1 + b_3Z)X + (b_2Z + b_0) \tag{8}$$

The main variables of an interaction variable, X and Z, were set to either zero or the value of their estimate, depending on whether the estimate differed significantly from zero in the GEE analysis. Parameter estimates that differed significantly from zero, other than those involved in the interaction variable of interest, constituted the intercept together with b_2Z and b_0 (8) as fixed variables set to the parameter mean value.

Results

Neighbouring species and tree age significantly explained GV in interaction with CI_{12} (Table 2). Growth vigour was highest with *B. pendula* as neighbours and lowest with *L. sibirica* as neighbours (Fig. 1a). In semi-mature trees (approx. 30 years old), GV decreased with all neighbouring species, whereas in younger trees it increased with *B. pendula* as neighbours (latter case in Fig. 1a). Increasing tree age decreased GV, mostly when CI_{12} was high. In younger trees GV increased with increasing CI_{12}, whereas in semi-mature trees CI_{12} decreased GV (Fig. 1b).

The number of long shoots on a branch was not influenced by the neighbouring species (Table 2). It did increase significantly with branch length increment (Table 2), but the interaction between branch length and RHC (Table 2) also contributed significantly to the effect since the positive effect of RHC was strongest in long branches (Fig. 2a). Tree age, CI_6 and their interaction also significantly affected the number of long shoots (Table 2). Though, comparably less in young than in semi-mature trees, the number of long shoots increased with increasing CI_6 (Fig. 2b). The length of long shoots was also independent of neighbouring species (Table 2). Instead, it increased with RHC (Table 2), although the actual parameter estimate for RHC was not significantly different from zero. The change in the length of long shoots with RHC was partly dependent on the GO (Table 2), i.e. shoots in small GOs tended to increase more from the bottom to the top of the crown than shoots in high GOs. Only GO 2 had a parameter estimate significantly different from zero, thus the figure was not presented. CI_9, tree age and their interaction contributed to the model of long shoot length significantly. CI_9 decreased the length of long shoots in the youngest trees, but increased it in semi-mature trees (Fig. 3).

The number of short shoots in a first-order branch was most strongly influenced by branch length (Table 2) since it quite expectedly increased with branch length: the estimate for the increment was 1.1 (95% confidence interval ±0.2) shoots per cm branch length ($P = 0.0001$). In addition, tree age significantly affected the number of short shoots (Table 2), but the parameter estimate itself did not differ significantly from zero. In addition to these main effects, neighbouring species played a significant role in interaction with CI_9 (Table 2; Fig. 4). The number of short shoots in a branch of a certain length (shoot density) increased with CI_9 when the neighbouring species was *B. pendula* or *P. sylvestris*, and decreased with *L. sibirica* and *A. glutinosa* as neighbours. This suggests that when competition was weak or absent, study trees growing with *A. glutinosa* had the highest density of short shoots, but as the amount of competition increased, those trees growing with *B. pendula* exceeded the others in the density of short shoots (Fig. 4).

Neighbouring tree species significantly affected the number of first-order branches in interaction with CI_8 in such a way that the effect of CI_8 was less negative in trees growing with *L. sibirica* than with others. Overall, the number of branches was highest with *L. sibirica* (Fig. 5a). The number of branches increased with tree height and decreased with CI_8, but the interaction of these two variables was also significant since the negative effect of CI_8 was stronger in trees with greater height (Fig. 5b). Furthermore, the number of branches also increased significantly in classes of 10% RHC from the bottom to the upper parts of the crown (Table 2). The increase was fourfold from the bottom to the second uppermost crown class; the number of branches was lowest in the topmost class due to the occurrence of young shoots instead of branches (parameter estimates not presented; nine estimates out of ten were statistically significant).

Branch length was almost significantly dependent on the interaction of neighbouring species with tree height (Table 2). In trees with *A. glutinosa* as neighbours, tree height increased branch length the most, whereas branch length was the highest overall in trees growing with *L. sibirica* as neighbours (Fig. 6a). Branch length decreased towards the crown top by -1.2 (±0.2) cm per 1% increase in RHC ($P < 0.0001$), but increased with total

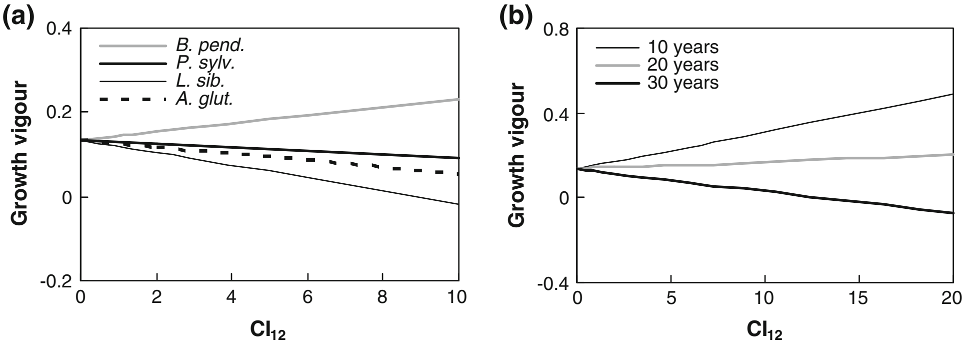

Fig. 1 Regressions of growth vigour on competition index (CI_{12}) in *B. pendula* trees growing (**a**) with different neighbouring species and (**b**) at different ages with *B. pendula* as neighbours are presented. Neighbouring species in the legend denotes *Betula pendula*, *Pinus sylvestris*, *Larix sibirica* and *Alnus glutionsa*. The parameter estimates for the interaction variables were 0.03 for *B. pendula* × CI_{12} (±0.03; $P = 0.0262$), 0.02 for *P. sylvestris* × CI_{12} (±0.01; $P = 0.0116$), 0.007 for *L. sibirica* × CI_{12} (±0.006; $P = 0.0384$), 0.01 for *A. glutinosa* × CI_{12} (±0.006; $P < 0.0001$), and −0.001 (±0.001; $P = 0.0075$) for tree age × CI_{12}. The estimates of the main variables involved in the interaction variables were not significantly different from zero. The model estimation of the intercept was also statistically significant ($P = 0.0411$)

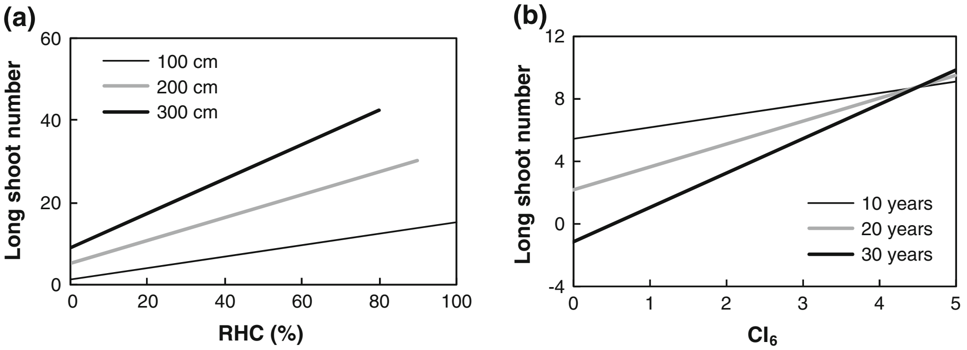

Fig. 2 Regressions of long shoot number per first-order branch (**a**) on relative height within crown (%, RHC) of branches of differing length (cm) and (**b**) on competition index (CI_6) in trees of varying age are presented in *B. pendula* trees growing with intraspecific neighbours. In figure (**a**), the regression lines were cut at those RHCs where the branch length occurred at the highest location from the crown base. The parameter estimates for the interaction variables were 0.001 (±0.0004; $P < 0.0001$) for RHC × branch length and 0.07 (±0.06; $P = 0.0096$) for tree age × CI_6. Of the main variables involved in the interaction, RHC and CI_6 did not have estimates significantly different from zero, whereas branch length and tree age did with values of 0.04 (±0.02; $P = 0.0007$) and −0.3 (±0.2; $P < 0.0001$), respectively. The other parameters that differed significantly from zero were included as fixed parameters in the calculations for each figure: in (**a**) CI_6 and tree age for the means 2 and 15.8 years, and in (**b**) branch length and RHC for the means 76.1 cm and 53.1%, respectively

tree height (Table 2). The increase in branch length with CI_1 was significantly dependent on total tree height for the negative effect of CI_1 only emerged in taller trees (Fig. 6b).

Variation in branch angle was only weakly explained, primarily by RHC and branch length, since it decreased 0.2° (±0.06°) per 1% increase in RHC ($P < 0.0001$) and 0.1° (±0.03°) per 1 cm increase in branch length ($P < 0.0001$) (Table 2). Neighbouring species showed a significant interaction with CI_2 in explaining branch angle (Table 2). CI decreased the branch angle when the neighbour was *P. sylvestris* or *L. sibirica*, but not with *A. glutinosa* or *B. pendula* as neighbours (Fig. 7).

Discussion

Crown architecture of *B. pendula* with different neighbouring species

Several crown variables, which were important constituents of crown size and growth in *B. pendula* under competitive stages of development, showed plastic responses with respect to the influence of neighbouring trees. In combination with indices describing the intensity of competition, the neighbouring tree species influenced the GV, number of short shoots and branches as well as the angle of

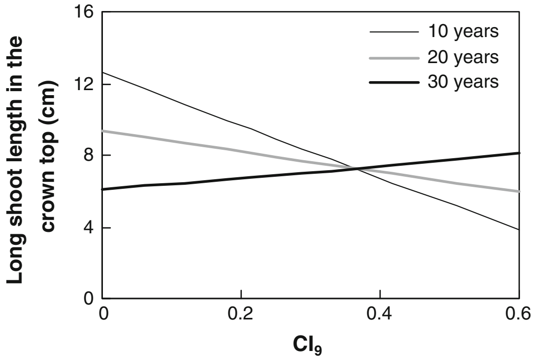

Fig. 3 Regressions of long shoot length (cm) in the crown top of *B. pendula* trees on competition index (CI_9) according to study tree age are presented. The parameter estimate for the interaction variable tree age × CI_9 was 0.9 (±0.8; $P = 0.02$), and the main variables CI_9 and tree age had estimated values of −23.8 (±12.3; $P = 0.0002$) and −0.3 (±0.2; $P = 0.0031$), respectively. The other parameters that differed significantly from zero were included as fixed parameters in the calculations: relative height within the crown was set to 90% and gravelius order to 2 (exceptionally, mean values were not used)

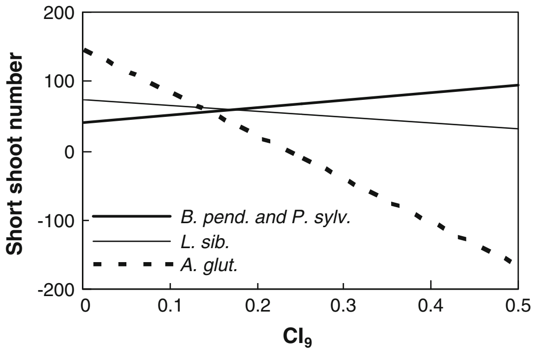

Fig. 4 Regressions of short shoot number per first-order branch on competition index (CI_9) with different neighbouring species are presented for *B. pendula* trees. Neighbouring species in the legend denotes *Betula pendula*, *Pinus sylvestris*, *Larix sibirica* and *Alnus glutionsa*. The relative parameter estimates for the interaction variables were 0 for the reference *B. pendula* × CI_9, −193.1 for *L. sibirica* × CI_9 (±124.2; $P = 0.0023$) and −735.7 for *A. glutinosa* × CI_9 (±233.6; $P < 0.0001$). Neighbouring species *B. pendula* and *P. sylvestris* did not differ from each other significantly. Of the main variables, neighbouring species did not have estimated values significantly different from zero, whereas CI_9 had an estimated value of 110.2 (±81.8; $P = 0.0083$). The intercept estimate ($P < 0.0001$), as well as branch length and tree age (set to the means 76.1 cm and 15.6 years) also had estimated values significantly different from zero and were included as fixed parameters in the calculations

first-order branches significantly, but did not affect long shoot production. Accordingly, the competitive effects were not explained by the CIs alone, suggesting that neighbour-specific modification of crown structure can occur. Two functionally equivalent explanations for the observation remain: either the effects originated from species-specific structural characteristics beyond the CIs affecting growth resources or they were a consequence of species-specific non-resource signals that can be detected by *B. pendula* even before resource competition occurs (Aphalo and Ballaré 1995; Aphalo and Rikala 2006). Without committing ourselves to the reasons behind the phenomenon, the results suggest that neighbour-specific effects were important to *B. pendula.* Effects were found even though it was claimed that shade-intolerant pioneer trees, as all neighbouring species in the present study, are likely to have relatively sparse crowns and thus impose less shade on their neighbours (Canham et al. 1994). On the other hand, as the studied tree species naturally grow together, they likely use the same resources and are thus potentially strong competitors (Goldberg 1987).

The exact mechanism that gives rise to the differences in species-specific competition is unknown (Canham et al. 2004), but several potential mechanisms may contribute to crown responses. The species-specific growth patterns which are visible in the structures of neighbouring trees, very likely affect light conditions in close neighbourhoods. The absorption and transmission spectra of leaves are also dependent on species-specific traits such as leaf size, shape, surface and pigmentation (Gates 1980), and thus neighbouring species not only differ in the amount of light they forward to their neighbours, but also in the quality of that light (de la Rosa et al. 1998). The competitive response of trees to light spectra occurs via different photoreceptors and they respond with morphological acclimations even before shading (Aphalo and Ballaré 1995; de la Rosa et al. 1998; Aphalo and Rikala 2006). Plants may also sense wind velocities modified by neighbours as proximity signals (Aphalo and Ballaré 1995). A more direct effect of wind is crown collision through swaying which has been reported to decrease crown cover, branch length and shoot density of individual branches in the upper half of the crown (Meng et al. 2006). The negative effects of crown collision depend on the ability of the target tree to endure mechanical disturbance, but also on the ability of the neighbour trees to cause it. Root growth and functioning respond to the light environment as well, for the amount of carbohydrates supplied to the roots from the crown is dependent on light via allocation of resources and the activity of enzymes involved in the assimilation of ammonium is regulated by light via certain receptors (de la Rosa et al. 1998 and references therein). Accordingly, the crown responses reflect the state of the root system via water and nutrient supply. Furthermore, the amounts and qualities of the litter produced (e.g. Priha and Smolander 1997, 1999) as well as the structure and size of root systems differ among species (Tremmel and Bazzaz 1993), but direct examination of belowground competition with its wider area of influence was not included in the present study.

Growth vigour was highest when *B. pendula* grew with intraspecific neighbours and lowest with *L. sibirica* as

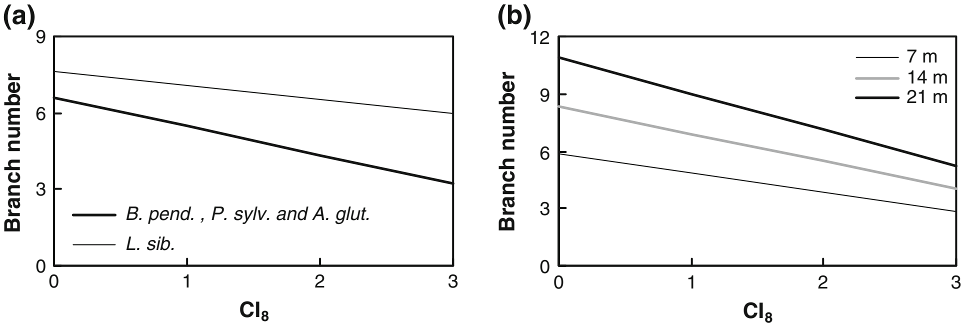

Fig. 5 Regressions of branch number in 10% classes of crown length on competition index (CI_8) (**a**) in *B. pendula* with different neighbouring species and (**b**) in *B. pendula* with varying tree heights and growing with intraspecifics neighbours are presented. Neighbouring species in the legend denotes *Betula pendula*, *Pinus sylvestris*, *Larix sibirica* and *Alnus glutionsa*. The parameter estimates for the interaction variables were 0 for the reference *B. pendula* × CI_8, 0.6 for *L. sibirica* × CI_8 (± 0.4; $P = 0.0092$) and -0.06 (± 0.04; $P = 0.0013$) for tree height × CI_8, whereas the estimated values for *P. sylvestris* × CI_8 and *A. glutinosa* × CI_8 did not differ significantly from zero. Of the main variables, the following had significant estimates had variables CI_8 (-0.5 ± 0.5; $P = 0.0466$), *L. sibirica* (-0.8 ± 0.6; $P = 0.0192$) and tree height (0.4 ± 0.07; $P < 0.0001$). Crown height class and tree height also had estimates significantly different from zero and were included as fixed parameters set to the means 50–60% and 9.2 m in the calculations

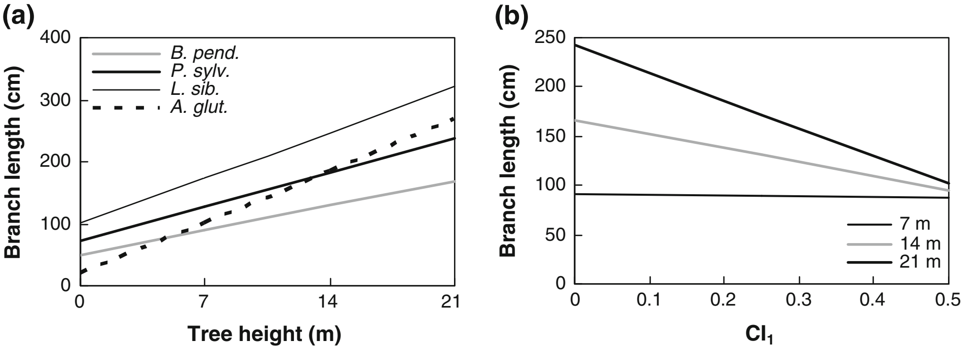

Fig. 6 Regressions of branch length (cm) on (**a**) tree height with different neighbouring species and (**b**) on competition index (CI_1) in trees with varying heights and growing with *B. pendula* as neighbours, are presented for *B. pendula* trees. Neighbouring species in the legend denotes *Betula pendula*, *Pinus sylvestris*, *Larix sibirica* and *Alnus glutionsa*. The parameter estimates for the interaction variables were 0 for the reference *B. pendula* × tree height, 2.2 for *P. sylvestris* × tree height (± 2.0; $P = 0.0270$), 4.8 for *L. sibirica* × tree height (± 4.0; $P = 0.0172$), 6.2 for *A. glutinosa* × tree height (± 2.0; $P < 0.0001$) and -19.4 for tree height × CI_1 (± 7.4; $P < 0.0001$). The main variables tree height and CI_1 had parameter estimates of 10.8 (± 2.5; $P < 0.0001$) and 129.5 (± 97.8; $P = 0.0095$), respectively, whereas neighbouring species did not have estimated values significantly different from zero. The intercept estimate ($P < 0.0001$) and relative height within crown (set to the mean 53.2%) were significantly different from zero and were included as fixed parameters in the calculations

neighbours. The differences in GV between neighbouring species cannot be explained by the number of long shoots or their length because no species-specific differences were found in these parameters. Thus, GV mainly showed differences between neighbours in branch number and length; i.e. when *B. pendula* grew with intraspecific neighbours, total branch length was small, whereas with *L. sibirica* it was high.

The number of short shoots and branch growth in the past played an important role in increasing differences between the effects of neighbouring species on the growth of *B. pendula*. With no aboveground competition, the number of short shoots was higher with *A. glutinosa* than with other neighbouring species, but the situation changed to the positive effect of *B. pendula* and *P. sylvestris* neighbours as the competitive effect increased: the number of short shoots actually increased with higher CI. Dualism in the shoot system of *B. pendula*, i.e. structurally and functionally different short and long shoots whose responses to the light environment are also different, assures that birch crowns can adjust to the changing environment efficiently (Takenaka 2000), as can also be seen from the present results. In general, *B. pendula* growing with intraspecific neighbours or with *P. sylvestris* invested in shoots by growing them rather densely in limited numbers and sizes of branches. This type of growing pattern may minimize energy expenditure on less efficient woody structures by having high densities of short shoots in narrow crowns (Borchert and Tomlinson 1984) and limit the damage caused by crown collision (Meng

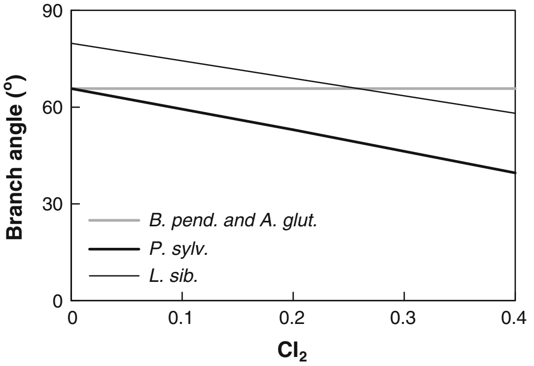

Fig. 7 Regressions of branch angle (°) on CI_2 with different neighbouring species are presented for *B. pendula* trees. Neighbouring species in the legend denotes *Betula pendula*, *Pinus sylvestris*, *Larix sibirica* and *Alnus glutionsa*. The relative estimates for the interaction variables were 0 for the reference *B. pendula* × CI_2, −65.0 for *P. sylvestris* × CI_2 (±46.4; $P = 0.0061$), −55.0 for *L. sibirica* × CI_2 (±27.8; $P = 0.0001$) and not significantly different from zero for *A. glutinosa* × CI_2. The main variables did not have estimated values significantly different from zero. The other parameters in the model whose estimates were significantly different from zero were included as fixed parameters in the calculations: relative height within crown, branch length and tree height were set to the respective means of 53.2%, 102.7 cm and 10 m

et al. 2006). In contrast, when neighboured by *L. sibirica* the high number and length of branches contributed to high growth rates in the past and more investments were made in woody structures that minimized self-shading (Takenaka 1994). Longer branches of *B. pendula* are perhaps possible when growing with *L. sibirica* because the sparse and rather narrow crown of *L. sibirica* (Hämet-Ahti et al. 1992) is well penetrated by light and causes less mechanical damage to neighbouring trees.

Differences in the competitive effect of similar sized neighbouring trees representing different species have also been found in previous studies, of which some have displayed stronger competition within a species and between closely related species (e.g. Canham et al. 2004; Uriarte et al. 2004) while others have provided evidence on behalf of stronger competition between different species (e.g. Sumida et al. 2002; Kaitaniemi and Lintunen 2010). Results on behalf of equal competitive effect per plant biomass among neighbouring species can be found in the literature as well (e.g. Goldberg 1987).

Although *A. glutinosa* positively affects forest soil due to its nitrogen-fixing capacity (Binkley 1983; Prescott 1996), *B. pendula* growing with *A. glutinosa* did not benefit from its neighbour. At fertile sites with high N concentration, *Alnus* does not necessarily increase the average size of other tree species (Binkley 1983), especially not other broad-leaved species (Prescott 2002). On the whole, the differences in crown traits between different neighbouring species are probably not due to other site characteristics because sites with different neighbouring species extensively represented various site indexes and ontogenetic stages (Table 1).

Competition indices

The CIs decreased the GV of nearly 30-year-old *B. pendula* trees while it increased that of younger trees. The trees responded to competition by growing fewer and shorter branches but more long shoots recently. Furthermore, the oldest trees produced lengthier long shoots. In most models, the effect of CI depended on tree age or height. CIs did not affect young trees as much as older trees probably due to the lack of resource competition among young trees. Moreover, in these young trees, the CI may have reflected the growth potential of the small-scale growth habitat around the study tree more than the actual amount of competition.

The effect of neighbouring trees was detected in this study even though the study trees were not under major competition stress. The average crown length of the study trees comprised about 70% of total tree height and the basal areas of the study sites were not high enough compared with the dominant height of the stands to suggest strong competition. In fact, only 3 of the 12 study sites would have required thinning according to Finnish thinning models (Anonymous 2001; see Table 1). Furthermore, the method we used for selecting the competitor trees may have excluded some of the competitive crown effect from the study, for many previous results using the radius length employed here to measure tree competition have been inconsistent (e.g. Lorimer 1983; Mitsuda et al. 2002). It should also be noted that although our usage of current competition to explain past growth may seem inadequate, the present values of the CIs very likely correlated with their former values since all the study species are fast-growing pioneer trees and no recent management operations had been implemented in the stands. However, if the former growth rates clearly differed between species, it is possible that this partly explained the interaction between neighbouring species and CI in the case of branch number and angle which both represented long-term responses.

Similarly, Umeki and Kikuzawa (2000) reported a negative effect of aboveground competition on the number of first-order branches in Asian white birch *Betula platyphylla* Suk. and Jones and Harper (1987a) on branch length in *B. pendula*. Jones and Harper (1987b) also found that the proportion of developing long shoots and their survival in *B. pendula* were lower in the presence of aboveground competition while the proportion of short shoots increased with competition. The former did not apply in our study whereas the latter applied only with certain neighbouring trees.

Shoots and branches

Inside the crown, the number of long shoots as well as the mean and maximum length of long shoots in *B. pendula* increased towards the crown top. Generally the formation and growth of long shoots in the top of the crown are positively associated with better light conditions in addition to hormonal regulation (e.g. Goulet et al. 2000; Takenaka 2000; Sachs 2004). Goulet et al. (2000) identified a clear effect of vertical branch position on long shoot growth in yellow birch *Betula alleghaniensis* Britton. Maillette (1982) was one of the first to study the crown structure of *B. pendula*, obtaining results comparable to ours which support the observations of relatively more and lengthier long shoots and apical dominance resulting in lengthier leader shoots in the crown top.

Despite the observed trend towards increase in long shoot length with RHC, wide variation occurred in long shoot growth throughout the crown. As many as 70% of the long shoots observed were shorter than the mean within each 10% interval of RHC. This resembled the pattern of variation also observed in *B. pubescens ssp. czerepanovii* (Orlova) Hämet-Ahti (Kaitaniemi and Ruohomäki 2003). Intraplant signalling may cause variation in shoot growth, for it could potentially result in efficient resource allocation to the few, best long shoot individuals in order for them to lengthen and reach for light (Trewavas 2005). The best growing individuals are usually situated under better light conditions which increase the production effectiveness of the shoot and its lifespan. The GO affected long shoot growth in interaction with RHC. The decrease in shoot growth in relation to increased GO was also reported by Maillette (1982) in *B. pendula*. "Undemocratic" long shoot systems are crucial in birch, for the leader shoot is the keystone to the structure, size and shape of the entire tree (Maillette 1982).

The branch angle and length decreased from the bottom to the top of the crown, but at fixed relative height, decreasing branch angle was surprisingly related to increasing branch length. Sumida et al. (2001) also found that longer branches of Japanese chestnut *Castanea crenata* Siebold & Zucc. had a relatively small branch angle, and they concluded that by doing so the tree avoids being overtopped by neighbouring branches. Due to smaller branch angles, longer branches do not necessarily lead to horizontal expansion of the crown.

The fact that all crown variables except branch angle were dependent on tree height or age suggests the importance of the ontogenetic stage of the tree in shaping the tree responses (Weiner 2004). During ontogeny, trees of differing height (or age) posses various physiological traits to maximize their photosynthetic efficiency (e.g. Osada et al. 2002, 2004) as was also shown here. Growth vigour and number of long shoots were lower in more mature trees than in younger trees; whereas the number of short shoots and branches as well as the length of branches were higher in more mature trees. The length of long shoots was higher in younger trees in case of no actual competition but when the amount of competition increased, long shoot length was higher in more mature trees.

Conclusions

We studied the crown architecture of *B. pendula* in great detail and brought new insights into its crown development owing to competition by neighbouring trees of varying species. *B. pendula* was able to modify its crown architecture in a manner that depended not only on the amount of competition, but also on the main tree species in the neighbourhood. In general, *B. pendula,* growing with intraspecific neighbours or with *P. sylvestris,* invested in shoots by growing them rather densely in limited numbers and sizes of branches. In contrast with *L. sibirica*, the high number and length of branches contributed to high growth rates in the past and more investments were made in woody structures. Moreover, tree ontogeny played a significant role in shaping the tree crowns.

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