

# Tree allometry of Douglas fir and Norway spruce on a nutrient-poor and a nutrient-rich site

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**Abstract** Research related to the allometric relationships of tree height and projected tree crown area to diameter at breast height was conducted to look at the biological suitability and timber production potential of Douglas fir under the conditions present in central Europe. The dependence of allometric relationships on soil nutrient conditions were described in forest stands of Douglas fir and Norway spruce. The studied sites were climatically similar but differed in soil nutrient availability. A significant difference was found in the allometric relationships of Norway spruce trees from the nutrient poor and nutrient rich site. In contrast to the Norway spruce, there was no significant effect of site fertility on allometric relationships for Douglas fir suggesting that its allocation patterns were less sensitive to site nutrient conditions. Stem growth increment, which was measured weekly during two consecutive seasons for both species, was related to the weather conditions and available soil moisture. Stem growth of Douglas fir began about 2 weeks earlier than in the Norway spruce at both sites. At the nutrient rich site, most of the stem growth of both species occurred at the beginning of the season, while growth at the other site was more evenly distributed throughout the season. Data obtained in this study will be useful for modeling stem growth and analysis of water use efficiency of these two tree species.

**Keywords** Allometry · Biometry · Douglas fir · Norway spruce · Stem increment

## Introduction

Allometry has a long history in plant studies, as scientists searched for interdependence among tree morphological characteristics. Allometry, in its broader sense, as will be considered in this study, is concerned with the size of organisms and its consequences for their shape and function (Niklas 1994; Pretzsch 2010). For this reason we decided to use tree allometry to describe differences among the tree species from two climatically similar sites which differed in soil nutrient availability. Tree biometric relationships vary considerably not only with species and geographic location but also with stand age, site quality, climate and stocking density of stands (Cannell 1982; Bartelink 1997; Poorter et al. 2012). In theory, allometric equations describing tree dimensions are affected by the physiological requirements of the tree; that is, form and function are related. The most important of these requirements are water transport, light interception, and mechanical support against gravity or wind (Niklas 1994). Consequently, allometry is an effective tool for evaluating differential plant responses to site conditions (Pretzsch 2010; Poorter et al. 2012).

This allometric study will serve as a background for more detailed work on water relations of Douglas fir and Norway spruce. From the hydraulic point of view, a tree may be viewed as a network of interconnected pipes (Zimmerman 1983). According to the “pipe model theory” (Shinozaki et al. 1964), the quantity of absorbing roots should be proportional to the sapwood area of a tree and the sapwood area should be proportional to the quantity of foliage, although we should remember, such relationships could be non-linear, when sap flow density is usually very different in different sapwood depths—Čermák and Nadezhdina 1998; Čermák et al. 2004. Therefore, any disproportion in this balance should be projected into tree

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function. For example, larger crowns relative to the stem diameter would (if other tree parameters remain unchanged) result in higher stem sap flow rates, or lower needle water potentials would be needed in taller trees to manage higher flow pathway resistances and to maintain the same transpiration rate (Ryan and Yoder 1997). Therefore, knowledge on the tree structure is necessary for the correct investigation of a particular tree function.

Norway spruce is one of the most important commercial forest tree species in Europe (Michalak 2011). Global change, bringing increased temperatures and lack of precipitation, may be a significant threat to commercial plantations of Norway spruce (Mäkinen et al. 2001; Jönsson et al. 2007; Rötzer et al. 2008; Lindner et al. 2010). One possible substitute for Norway spruce may be Douglas fir, especially at lower altitudes. Better growth on some sites and lower vulnerability to drought favors Douglas fir over Norway spruce (Šika and Vinš 1980; Keyes and Grier 1981; Kantor 2008). The timber production potential of Douglas fir is often superior to that of Norway spruce. Better use of available soil nutrients (Ranger et al. 1995) favors Douglas fir especially on nutrient-poor sites, where its productivity may be several times higher (Peric et al. 2006; Mäkinen and Hein 2006; Hein et al. 2008; Bartoš and Kacálek 2011).

To further understand differences between these two conifers, we analyzed the rate of stem growth, ecological site conditions and their impact on allometric relationships of Douglas fir and Norway spruce on two sites with similar climatic conditions but differing in nutrient availability. Our hypotheses state: (1) size relationships between a tree's aboveground biometric parameters (i.e. tree height, crown projected area) to diameter at breast height (DBH or at 130 cm aboveground) differ between Norway spruce and Douglas fir as well as between sites of contrasting soil quality and (2) relative patterns of a radial stem growth increment of the two species react differently to weather conditions. The information related to tree allometry will also be used as a background for assessment of a hydraulic architecture and water use of the trees. Information about sensitivity of the radial stem increment to different environmental conditions is necessary for tree growth modeling as well as for understanding how these two species grow in different ways.

## Materials and methods

### Research plots

Research plots were located in two different forest stands. The nutrient poor stand (2,780 m<sup>2</sup>), referred to here as the “poor site,” was situated at a forest site named ‘15 E 9’ and was part of the Hürky Forest Training Enterprise managed

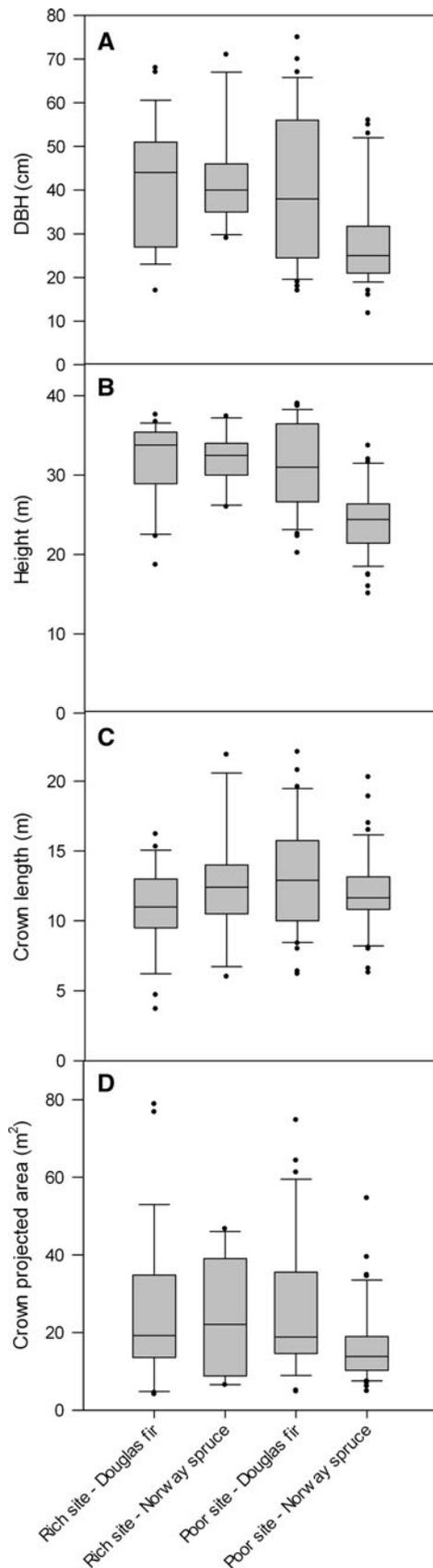
by the Forest Technical School in Písek, Czech Republic (49°15'28"N, 14°09'43"E, altitude 472 m). Mean annual precipitation was 575 mm and mean air temperature was 7.3–7.5 °C (Bušina 2007). The forest study site was classified according to the Czech forest type classification (Plíva 1991) as the type 3K-Querceto-Fagetum acidophilum. This 89-year old mixed forest stand (in 2008) was composed of Scots pine (*Pinus sylvestris*, 30 %), Norway spruce (*Picea abies*, 29 %), Douglas fir (*Pseudotsuga menziesii*, 25 %), with some European beech (*Fagus sylvatica*) and sessile oak (*Quercus petraea*). The total stem basal area for all tree species at the site, as calculated from the stem DBH, was 45 m<sup>2</sup> ha<sup>-1</sup>.

The nutrient rich research stand (2,220 m<sup>2</sup>), referred to as here as the “rich site,” was situated at a forest site named ‘130 B 10’ and was part of the Training Forest Enterprise in Křtiny of the Mendel University in Brno (49°19'12"N, 16°40'16"E, altitude 480 m). Mean annual precipitation was 634 mm and mean air temperature was 7.4 °C (Vyskot 1975). This 97-year old mixed forest was classified as type 3H-Querceto-Fagetum illimerosum mesotrophicum. The main tree species were European larch (*Larix decidua*, 33 %), Douglas fir (*Pseudotsuga menziesii*, 25 %), European beech (*Fagus sylvatica*, 20 %) and Norway spruce (*Picea abies*, 10 %), with some silver fir (*Abies alba*) and Scots pine (*Pinus sylvestris*). The total basal area of all tree species was 54 m<sup>2</sup> ha<sup>-1</sup>. While the sites were climatically similar they differed in soil nutrient availability. Biometrical parameters were collected for tree species from both plots (Fig. 1) and maps show tree distribution (Fig. 2).

### Soil analyses

Humus forms were determined following Green et al. (1993) and Delft et al. (2006). Ten samples of each of the humus layers (L, F and H) and five samples of the organomineral Ah horizon were collected after leaf fall in autumn 2006 (Menšík et al. 2009). Samples were dried at 60 °C to a constant weight. Values of active and exchangeable soil acidity were determined by a potentiometric method (Zbiral et al. 1997) using a digital pH-meter OP-208/1 (Radelkis Budapest, Hungary). Carbon and nitrogen content were determined from samples devoid of coarse particles after fine grinding or comminution on a LECO TruSpec analyzer (Leco Corp., St. Joseph, MI, USA) following Zbiral et al. (1997).

Based on the soil nutrient analyses we selected a nutrient-poor (“poor site”) forested site named “15 E 9” which was part of the Forest Training Enterprise Hürky (49°15'28"N, 14°09'43"E) and nutrient-rich forest site (“rich site”) named “130 B 10” which was part of the Training Forest Enterprise in Křtiny (49°19'12"N, 16°40'16"E). The humus form “moder” was typical at the poor site while the

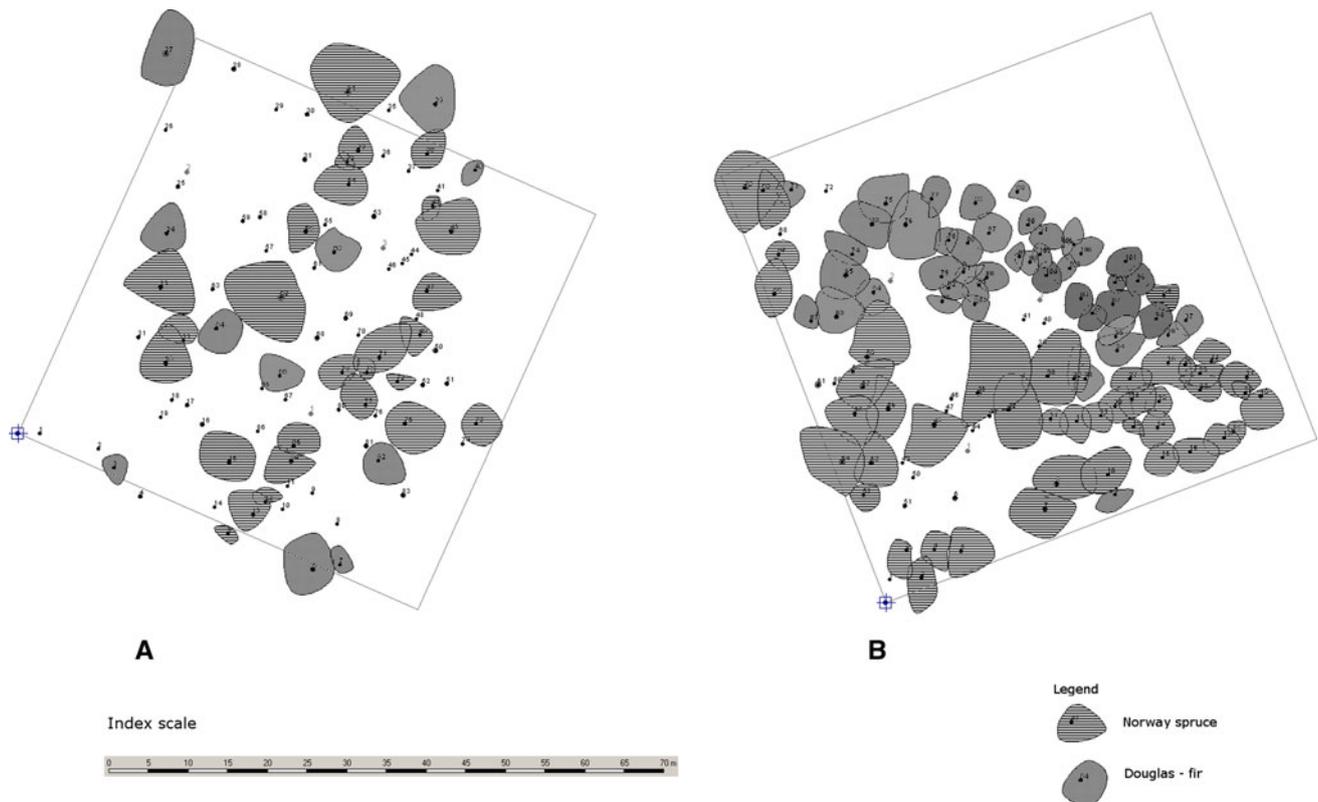


◀ **Fig. 1** Biometric parameters of sample trees in the research stands. Bars inside the boxes are the median response, 75 % (edges of the boxes) and 90 % (the bars) percentiles of breast height diameter (a), height (b), crown length (c) and crown projected area (d). Table 1 gives the assigned number for each tree studied

“mull-moder” form was present at the rich site. A Cambisol oligotrophic soil type was typical at the poor site and a Cambisol mesotrophic soil type was found at the rich site. Both actual and exchangeable pH decreased with soil depth and the pH values of both were lower at the poor than at the rich site (Table 1). Nitrogen content in the organic soil layers (L, F) was higher at the rich compared with the poor site by 43–75 % and by 16 % in organomineral soil horizon (Ah). The carbon to nitrogen (C/N) ratio was also more favorable for tree growth at the rich site (Table 1). Analyses of the other available soil nutrients (P, Mg, Ca, K) were done in the Ah soil horizons in neighboring forest stands with similar tree species composition on a same soil type (Kantor et al. 2009); the concentration was usually by about 20–30 % higher at the rich site. Specifically: phosphorus was  $52 \text{ mg kg}^{-1}$  versus  $34 \text{ mg kg}^{-1}$ ; magnesium was 144 versus  $140 \text{ mg kg}^{-1}$ ; calcium was 1,476 versus  $1,029 \text{ mg kg}^{-1}$ , potassium was  $114 \text{ mg kg}^{-1}$  versus  $85 \text{ mg kg}^{-1}$  at rich and poor site, respectively. The soil base saturation was 60 % at the rich site while only 20 % at the poor site (Kantor et al. 2009).

#### Tree biometric measurements

The aboveground structure of each forest stand was measured using the Field-Map measuring system which contains both hardware and software tools for mapping forest stand structure (IFER Inc., Jílové u Prahy, Czech Republic). This measuring system consists of an Impulse 200LR laser distance meter with a resolution of 1 cm (Laser Technology Inc., Englewood, CO, USA), a MapStar Module II electronic compass (Laser Technology Inc.), a Hammerhead laptop and range poles with reflecting glass. The software allows in-field map view of the measured parameters and export to GIS software (i.e. Arc View). GPS coordinates were measured with a Trimble Pro XH device (Trimble Navigation Ltd., Sunnyvale, CA, USA). Tree diameters were measured with calipers with a resolution of 1 cm from two perpendicular sides of each tree. Height was measured with a Vertex IV meter (Haglof, Sweden) with a resolution of 0.25 m. At the plot, we measured the number and position (with an accuracy of 3 cm) of each tree larger than 10 cm, as well as its DBH (with accuracy of 1 cm), projected crown area ( $A_{\text{pro}}$ ), and heights to treetop and crown base (with resolution of 0.25 m). Crown base was defined as a height of the lowest living branch. Crown length (crown



**Fig. 2** Map of tree positions at the study site. Crown projected areas are provided for Douglas fir and Norway spruce; only the stump position is drawn for other species. **a** nutrient rich site, **b** nutrient poor site

**Table 1** Soil properties within the stands

Site	Soil horizon	C (%)	N (%)	C/N ratio	pH	
					nH <sub>2</sub> O	nKCl
Poor site	L	47.4	1.54	31	5.0	4.6
	F	27.6	1.20	23	4.5	4.1
	H	17.8	0.85	21	4.0	3.3
	Ah	7.5	0.33	23	3.9	3.1
Rich site	L	43.4	2.20	20	5.4	5.2
	F	31.9	2.10	15	5.5	5.2
	H	15.1	0.92	16	4.7	4.2
	Ah	6.6	0.38	17	4.3	3.6

depth) was defined as difference between the tree height and height of the crown base. Data were exported in the form of maps in a dBase format. Parameters of trees were then exported to a MS Access file.

#### Stem increment measurements

We measured stem increment on the same sites as the biometry using Vernier band dendrometers (EMS Brno, Inc., Brno, Czech Republic) with a resolution of 0.1 mm. Readings were taken weekly from 15 April 2008 to 15

October 2008 and from 12 April 2009 to 29 October 2009 on 12 trees—six Douglas fir and six Norway spruce—at each of the sites. Sample trees covering the entire range of DBH (Table 2) were selected so that each could represent approximately the same fraction of stand basal area based on the quantile of the total statistical procedure (Čermák and Michálek 1991). The relative week increment (RWI, %) was calculated according to the equation:

$$\text{RWI} = \frac{C_n - C_{n-1}}{C_e} \times 100,$$

where  $C_n$  and  $C_{n-1}$  (mm) are stem circumference of a given tree in the current week and in the previous reading, respectively;  $C_e$  is the circumference at the end of the growing season.

#### Meteorological measurements

Minikin therm-hygro and global radiation meters with radiation shelters (EMS Brno, Czech Republic) were situated 150 m from the experimental plot in a rich site and 800 m from the poor site. Data were measured every minute and stored as 10-min averages. Soil water potential (SWP) was measured at three depths with three replications at each depth using calibrated gypsum blocks (Delmhorst Inc., USA;

**Table 2** Biometric parameters of 12 Norway spruce (SM) and 12 Douglas fir (DG) trees selected for analysis of stem growth increment in the years 2008 and 2009 (Figs. 6, 7)

	Rich site				Poor site			
	DBH (cm)	Height (m)	$A_{pro}$ (m <sup>2</sup> )	Map no.	DBH (cm)	Height (m)	$A_{pro}$ (m <sup>2</sup> )	Map no.
DG	66	36.5	77	62	70	38.9	75	70
	51	35.4	33	20	61	37.5	51	48
	45	34.4	21	47	54	32.2	26	19
	41	35.2	27	54	39	34.4	34	10
	40	33.6	19	77	30	27.5	17	28
	30	29.7	16	79	17	22.3	12	31
SM	67	36.4	47	27	48	32.0	39	75
	51	37.4	39	6	39	26.0	28	97
	44	34.0	23	64	34	26.4	24	87
	40	33.0	22	82	28	23.7	15	86
	31	32.0	7	40	25	26.2	12	37
	25	27.0	7	7	16	15.1	10	78

Column “Map No.” refers to the tree number in Fig. 2

DBH breast height diameter,  $A_{pro}$  crown projected area

datalogger SP3, EMS Brno, Czech Republic). Soil temperature was measured by Pt 100 soil temperature sensors (Delta-T Devices Ltd., Cambridge, UK) at 30 and 60 cm deep, and stored every hour. Daily means of SWP, air temperature, and global radiation were calculated for increment data analysis.

Mean air temperature in the period 1 May to 30 September 2008 was 15.6 and 15.5 °C at the rich and poor site, respectively, and 15.8 °C at both sites in the same period of 2009. Mean air temperature in 2009 was 8.0 °C at the rich site and 8.1 °C at the poor site, which was more than 0.5 °C above the long term average. Temperature of the year 2008 was apparently closer to the historic mean (given lower summer temperatures); however, no winter data were available. In both years, two or three periods of low temperatures occurred in the spring, the first of them in the middle of May. Soil water was less available in the 2008 growing season, when periods of severe drought started in the end of June, while in 2009 drought appeared in late August.

### Statistical analysis

Statistical analysis was performed using Statistica 8.0 software (StatSoft, Inc., Tulsa, OK, USA). Graphs were created in SigmaPlot software (Systat Software Inc., Chicago, IL, USA). To test the hypothesis and scale-up parameters at the stand-level, we used linear and non-linear regression analysis and analysis of variance (ANOVA). To estimate allometric relationships of tree height, length of crown and  $A_{pro}$  to DBH, we used a one-dimensional, mostly non-linear regression analysis. Specifically for the calculation of allometric relationships of tree height, we used the Näslund equation (Näslund 1936):

$$h = 1.3 + \frac{DBH^2}{(a + bDBH)^2},$$

where  $h$  is tree height (m), DBH (cm) and  $a$ ,  $b$  are parameters in the equation. From the linear and several non-linear regression models we chose the one with the greatest  $r^2$ . This gave a logarithmical equation for crown length ( $y = a \times \ln(DBH) + y_0$ ), and a linear ( $y = a \times DBH + y_0$ ) or a power equation ( $y = a \times DBH^b$ ) for projected crown area.

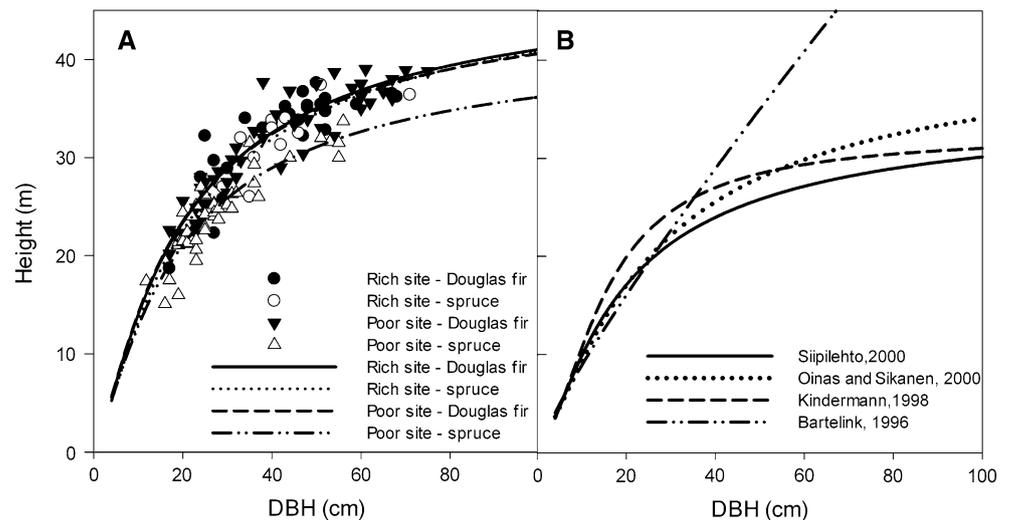
All statistical tests were done at the 95 % confidence level. The significance of the  $r^2$  and of the model was tested by ANOVA ( $\alpha = 0.05$ ). If the calculated  $F$  value was greater than the threshold for  $F_{0.05, n-2}$  we considered the proposed model significant. In linear models we also tested the significance of the absolute coefficient by a  $t$  test for  $t_{0.025, n-2}$ ; if the calculated value was lower than the threshold value the coefficient was excluded from the equation. To test the difference between individual parameters of selected plots, we used a one-way ANOVA. The  $\alpha$  value was set to 0.05 and the  $P$  value to 95 %. A  $t$  test was used to test for significant differences between RWI of the tree species within the same weeks. ANCOVA was used to compare the regression slopes of the models.

### Results

Aboveground tree size relations and its dependence on site fertility

There was significant difference between allometric relationships of Norway spruce and Douglas fir at the poor site.

**Fig. 3** **a** Allometric relationships for tree height. Symbols represent individual trees (full symbols for Douglas fir, open symbols for Norway spruce) from “rich” (circles) and “poor” (triangles) sites. Lines represent our models of the Näslund height curves for both species at both localities. **b** Allometric models for tree height from the literature

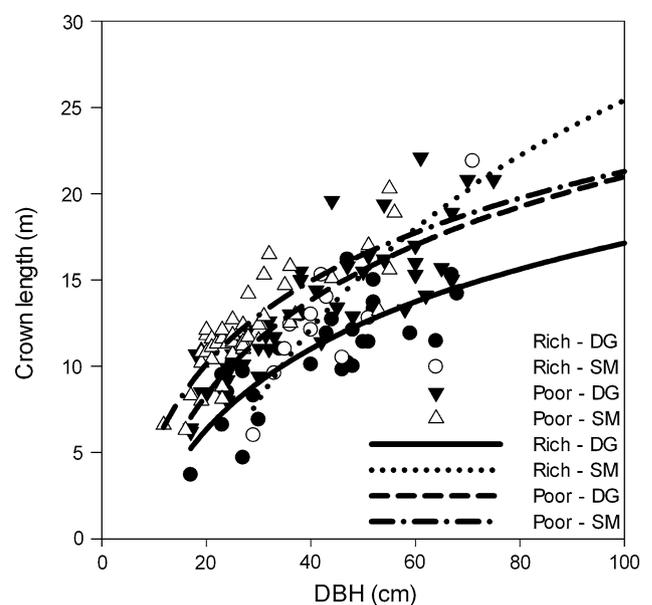


Therefore, we accepted the first hypothesis that the tree species affects aboveground tree size relationships. Allometric relationships of the Norway spruce also were affected by site nutrient availability. Therefore, we also accepted this point of the first hypothesis. However, there was no effect of the nutrient availability on the Douglas fir biometry (for the investigated nutrient range); therefore, this part of the first hypothesis was rejected.

Biometrical parameters, DBH, mean height, and crown projected area of the Norway spruce trees from the nutrient poor stand were significantly lower than those from the nutrient rich stand (Fig. 1a, b, d). In contrast, site fertility had little effect on the biometry of Douglas fir, where the mean crown length (as defined above) was significantly shorter in the nutrient-rich site (Fig. 1c). Biometry of the Douglas fir and Norway spruce trees was rather similar at the nutrient rich site but there was a difference between the DBH, mean height, and crown-projected area between the two species at the poor site.

Correlations between DBH and tree height were performed separately for each tree species and the location. Coefficients of the Näslund height equations for Douglas fir were statistically similar for both localities. In addition, equations for Norway spruce growing on the fertile forest site were similar to those for Douglas fir. However, there was a statistically significant difference between the height curve of Norway spruce at the poor site and at the rich site for  $DBH > 31$  cm and between Norway spruce from the poor site and Douglas firs at the both localities for  $DBH > 20$  cm ( $P < 0.05$ ; Fig. 3).

Crowns of trees of the same size were longer at the poor site than those at the nutrient rich site. Crowns of Norway spruce in both localities were longer than those of Douglas fir, though not significantly (Fig. 4). Crown projected area ( $A_{pro}$ ) of Douglas fir was best approximated by a power function, whereas  $A_{pro}$  of Norway spruce was best



**Fig. 4** Allometric relationships between crown length and DBH. Crown length (crown depth) is defined as difference between tree height and height of the crown base (height of the lowest living branch). Full and open symbols represent individual Douglas fir and Norway spruce trees, respectively, from “rich” (circles) and “poor” (triangles) sites

estimated by a linear function (Table 3; Fig. 5). While  $A_{pro}$  models for Douglas fir did not differ significantly between the two stands, the models for Norway spruce differed between the two sites in both absolute parameter and slope.

#### Stem growth increment

Douglas fir started to grow when soil temperature was 6 °C at 30 cm deep, earlier than Norway spruce. Norway spruce started growing about 2 weeks later when the soil warmed

**Table 3** Allometric equations of DBH and tree height, and crown properties of Norway spruce (SM) and Douglas fir (DG) at two study sites, listing the corresponding coefficients of determination, numberof investigated trees (*n*), standard errors (SE) of the parameter estimates, and *P* values of the parameters

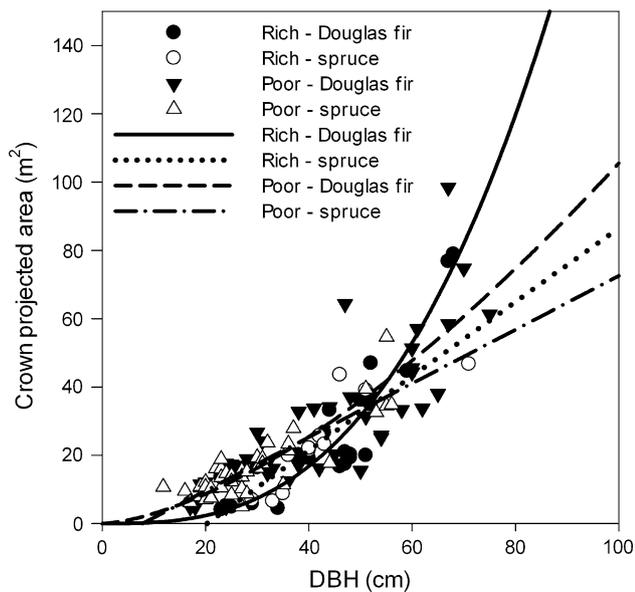
Site	Species	$R^2$	<i>n</i>	Coef.	Coef. value	SE	<i>P</i>
Height (m)							
Rich	DG	0.79	27	a	1.35	0.160	<0.0001
				b	0.15	0.004	<0.0001
	SM	0.64	11	a	1.44	0.358	0.003
				b	0.14	0.009	<0.0001
Poor	DG	0.87	45	a	1.32	0.084	<0.0001
				b	0.15	0.002	<0.0001
	SM	0.83	44	a	1.39	0.100	<0.0001
				b	0.16	0.004	<0.0001
Crown length (m)							
Rich	DG	0.65	27	$y_0$	13.85	3.646	0.0008
				a	6.74	0.992	<0.0001
	SM	0.76	11	$y_0$	40.79	9.984	0.0027
				a	14.36	2.680	0.0005
Poor	DG	0.77	45	$y_0$	15.40	2.410	<0.0001
				a	7.92	0.663	<0.0001
	SM	0.73	44	$y_0$	10.70	2.184	<0.0001
				a	6.95	0.660	<0.0001
Crown projected area (m <sup>2</sup> )							
Poor	DG	0.86	27	a	0.0005	0.005	0.35
				b	2.83	0.260	<0.0001
	SM	0.76	11	$y_0$	22.01	8.861	0.0348
				a	1.09	0.203	0.0005
Rich	DG	0.69	45	a	0.083	0.065	0.20
				b	1.55	0.19	<0.0001
	SM	0.76	44	$y_0$	-6.13	2.093	0.0055
				a	0.79	0.068	<0.0001

Model equations are: (1) height  $h = 1.3 + \frac{DBH^2}{(a+bDBH)^2}$ , (2) crown length  $y = a \times \ln(DBH) + y_0$ , (3) crown projected area  $y = a \times DBH + y_0$  for Norway spruce and  $y = a \times DBH^b$  for Douglas fir

to about 7 °C. At the beginning of the season, until June, Douglas fir grew faster than the Norway spruce (Figs. 6, 7). The period of faster growth of Douglas fir was also longer at the nutrient poor site. Douglas fir seemed to grow better in cold or unfavorable weather conditions; however, the difference in the relative growth rate was significant ( $P < 0.05$ ) only at the rich site on weeks preceding May 28 and July 26 in 2008 and preceding May 13 and June 6 in 2009. These data confirm the validity of the second hypothesis that there were significant differences in the relative growth rates of Douglas fir and Norway spruce within the year.

Spring of 2008 (Fig. 6), had two periods of unfavorable (i.e. cold) weather conditions (Fig. 6c, d). Three consecutive cloudy and rainy days around May 20, with air temperature around 7 °C and mean global radiation less than

100 W m<sup>-2</sup> suppressed a week of growth (Fig. 6e, f). The second cold period in mid-June lasted for almost 2 weeks and suppressed growth for three-weeks. This second period of growth suppression was prolonged into the beginning of July by a short episode of drought which was stronger at the poor site. Two longer episodes of drought at the beginning of both August and September (Fig. 6a, b) resulted in the cessation of growth and stem shrinkage (Fig. 6e, f). In 2009, we identified five periods of unfavorable weather at each of the sites (Fig. 7). Four of them (three at the poor site) were related to air temperature and the availability of solar radiation and lasted from May until the end of June (mid July at the rich site), when soil water was not a limiting factor (Fig. 7c, d). Soil water availability became a limiting factor to growth in August (Fig. 7a, b). Similar to 2008 conditions, the poor site was more drought



**Fig. 5** Allometric relationship for crown projected area to DBH in sample trees. *Full and open symbols* represent individual Douglas fir and Norway spruce trees, respectively, from “rich” (*circles*) and “poor” (*triangles*) sites

stressed. A short rain event at the end of August was reflected in a relatively high stem increment at this site, even though soil water potential was still quite low. At both sites in 2009, the end of the vegetative growing season was extremely dry, which resulted in an earlier cessation of growth than in 2008.

Absolute values of the stem growth increment were positively correlated with a tree diameter; this dependence was linear and no significant intercept of the regression was found ( $P < 0.05$  %; Fig. 8). Regression slopes were statistically similar for both tree species on the rich site, as well as for Douglas fir at the poor site. However, the coefficient of the regression was significantly smaller for Norway spruce at the poor site.

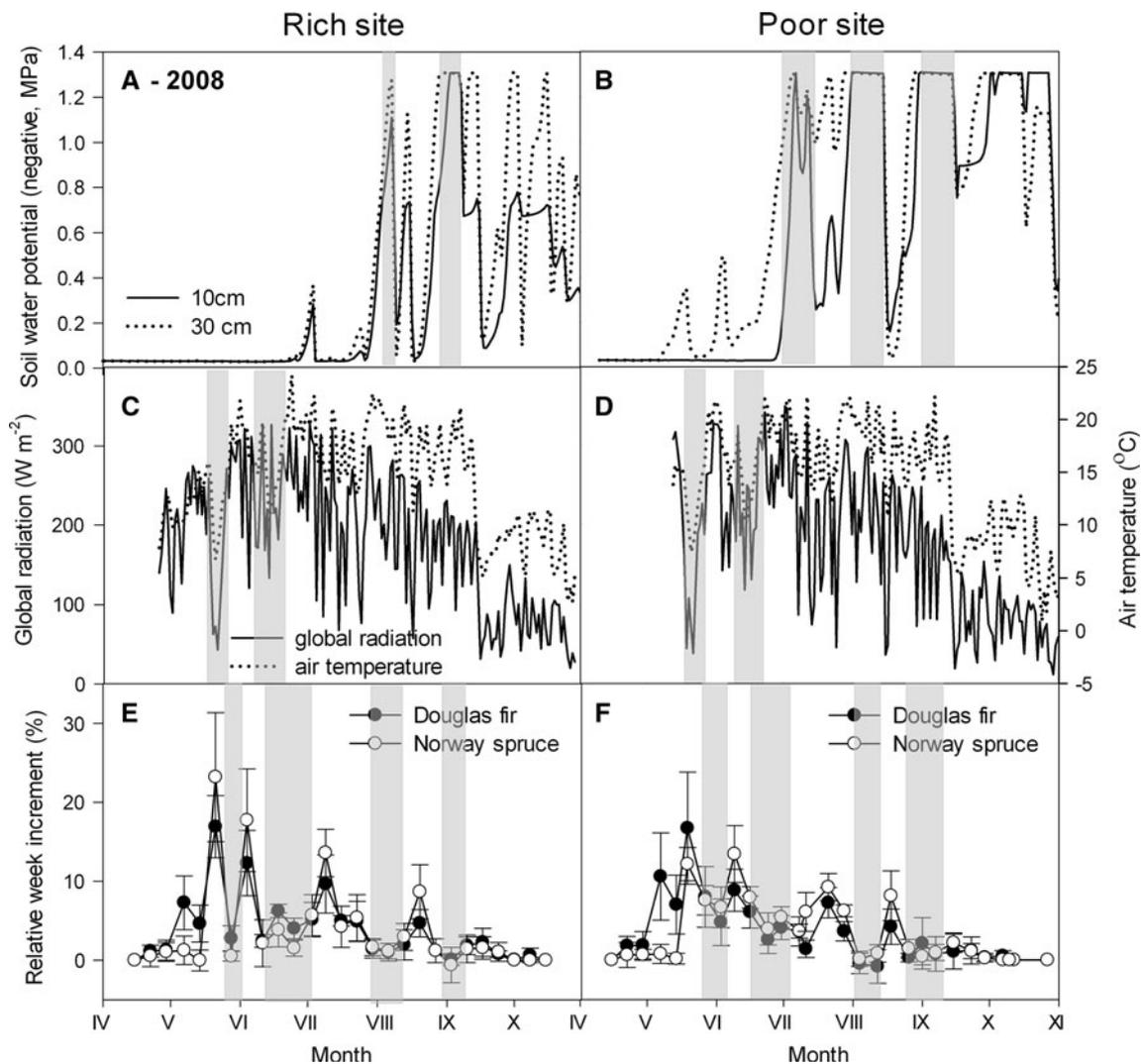
## Discussion

Effects of site fertility on aboveground biometric relations

As the introduction stated the absolute growth rate is strongly affected by availability of a particular environmental limiting factor. Optimal site conditions ensure optimal growth of a certain tree species and deviation on either side of the optimum results in a decrease in the absolute growth rate. Growth of an organism follows a unimodal dose–effect-curve in response to an increase in a particular growth factor. Both high and low levels of a

certain factor may limit tree growth (Loehle 1998, 2000; Mäkipää 1999; Pretzsch 2009). Optimal dose of the growth factor differs not only among species but also within a certain species for the different plant organs. Trees appear to allocate resources preferentially to the organs functionally connected with the deficient growth factor. For example, as levels of soil nutrients decrease the proportion of roots to the aboveground mass of a tree increases (Keyes and Grier 1981; Reich 2002; Leuschner et al. 2004; Tatarinov et al. 2008). There are even changes in allocation patterns within the aboveground part itself; leaf mass increases at a different rate than tree structural components if the nutrients become more readily available (King et al. 1999; Poorter et al. 2012). However, there is no simple objective way to characterize the level of the nutrient availability, since trees react to nutrients in complex ways (Poorter et al. 2012). Nutrient availability in forest trees is usually positively correlated with growth, although acidophilous species may have a unimodal growth pattern (Mäkipää 1999). In this study, stand fertility had a large impact on biometry, allometry and stem growth increment of Norway spruce (Figs. 1, 3, 4, 5, 8) while it had little effect on Douglas fir. Our results confirm previous research showing that Douglas fir exhibited a better use of soil-available nutrients than other tree species, especially on nutrient-poor sites (Ranger et al. 1995; Peric et al. 2006; Mäkinen and Hein 2006; Hein et al. 2008; Bartoš and Kacálek 2011), although saplings of Douglas fir in the experiment of Sicard et al. (2006) were more sensitive to initial fertilization than those of Norway spruce. However, the stage of a development may affect allometric responses; thus saplings can behave differently from mature trees.

Our allometric models of height growth yielded higher values than those found in the literature for both species (Fig. 3). Models calibrated for Norway spruce in Finland using Näslund’s height curves (Siipilehto 2000) were closest to ours. Smaller trees were observed in a 95-year-old spruce stand in Austria (Kindermann 1998). A possible reason for the lower growth in tree height in the literature might be that other models were generally obtained on extremely nutrient-poor sites, at higher altitudes, or high latitudes (i.e. podsollic soil—Bartelink 1996; Siipilehto 2000), that affected allocation patterns and, consequently, the DBH to height ratio (Urban et al. 2010). Both of our sites were closer to more favorable conditions—a combination of latitude 49° and an altitude of less than 500 m assured satisfactory growth of Norway spruce. The major limiting factor at our sites would be drought (Mäkinen et al. 2001; Jönsson et al. 2007; Lindner et al. 2010), which actually appeared at the end of both investigated growing seasons (Figs. 6, 7). Another possibility for the height differences might be that different forest management techniques used in the Czech Republic would theoretically



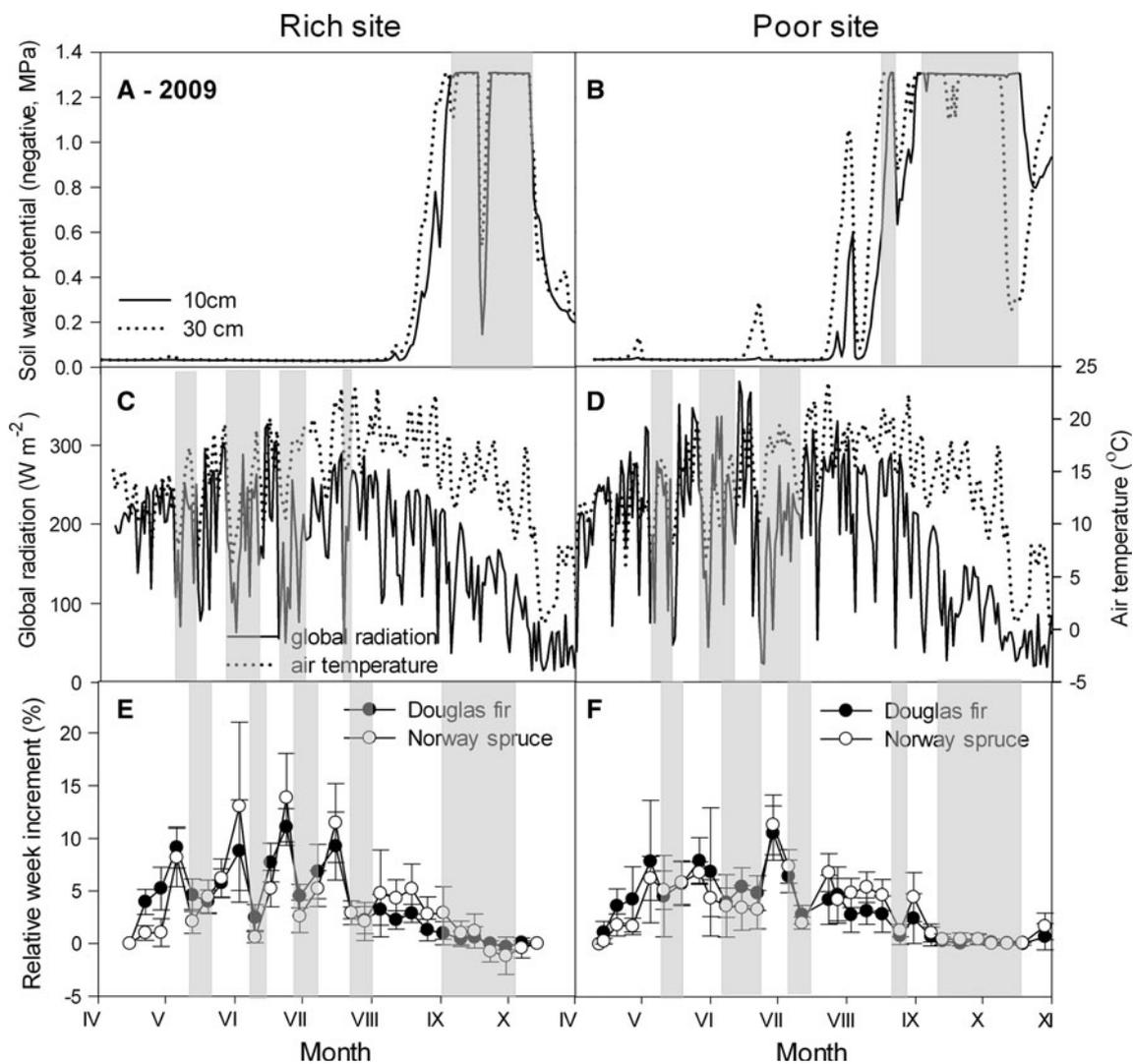
**Fig. 6** Seasonal course of soil water potential at two depths (**a**, **b**), daily means of a global radiation together with air temperature (**c**, **d**) and relative stem growth increment at individual weeks (**e**, **f**) during the growing season 2008 at the nutrient rich (**a**, **c**, **e**) and

nutrient poor sites (**b**, **d**, **f**). Symbols at **e** and **f** represent means of six trees per species (see Table 1)  $\pm$  standard deviation. Grey strips in the background highlight periods of unfavorable conditions

favor higher density forest stands; increased competition would induce faster height growth. But this seems unlikely, since Czech silviculture historically follows German and Austrian forestry schools; i.e. all three use a similar initial number of the trees in a forest stand, recommended stocking density and thinning intensity (including ways of selecting a certain tree for felling) for a stand of a particular age, and also use similar rotation periods for a given tree species). Therefore, at least Kindermann's (1998) relationships (Fig. 3b) should be similar. Another possibility is the age of the other stands was lower and perhaps allometry was affected by the stage of ontogeny, as was found for some biometrical parameters (i.e. crown biomass) in Douglas fir by Bartelink (1996). Nevertheless, given the similar tree age, Kindermann's (1998) model should have

produced similar results. Unlike Norway spruce, Douglas fir was insensitive to the relatively small differences in soil nutrient content in our study (still within the range of Cambisols); the allometry would have probably shifted only when soil changed to a podsol type (Bartelink 1996). This suggests a wider range of optimal soil nutrient conditions and a better use of available nutrients exist for Douglas fir than for Norway spruce (Ranger et al. 1995).

Crowns of same-sized Douglas fir on the nutrient-poor site were taller (i.e. the distance from the tree top to the lowest living branch was larger) than at the rich site (Fig. 4), similar to the findings of Spathelf (2003). Differences in crown height may be explained by a higher stand density at the rich site (stem basal area was  $54 \text{ m}^2 \text{ ha}^{-1}$  at the rich site vs.  $45 \text{ m}^2 \text{ ha}^{-1}$  at poor site)



**Fig. 7** Seasonal course of soil water potential at two depths (**a**, **b**), daily means of a global radiation together with air temperature (**c**, **d**) and relative stem growth increment at individual weeks (**e**, **f**) during the growing season 2009 at the nutrient rich (**a**, **c**, **e**) and

nutrient poor sites (**b**, **d**, **f**). Symbols at **e** and **f** represent means of six trees per species (see Table 1)  $\pm$  standard deviation. Grey strips in the background highlight periods of unfavorable conditions

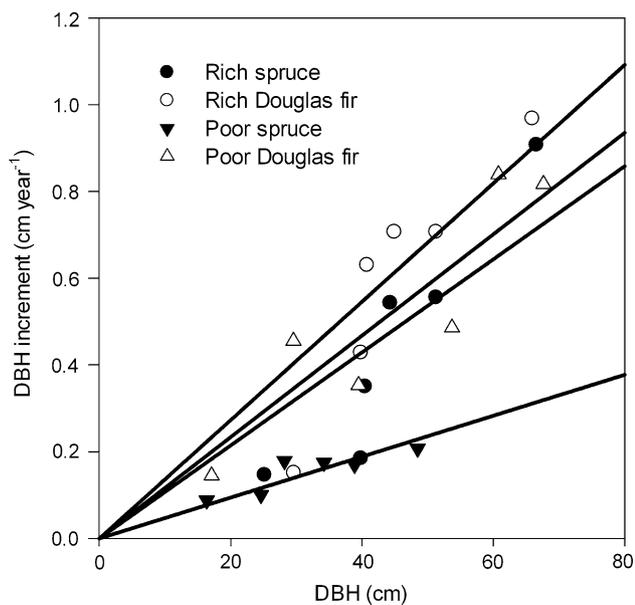
resulting in lower illumination in the lower branches, thus triggering the death of some trees (Mäkinen et al. 2003).

For both species  $A_{\text{pro}}$  was within the range given by Nagel et al. (2002) and Pretzsch et al. (2002). Best fitting models to DBH were a power function for Douglas fir and a linear function for Norway spruce (Fig. 5). The smallest crown projected areas were similar at both sites, about 5 m<sup>2</sup>. However, the size of the smallest tree was strongly site-dependent, especially for Norway spruce. While the smallest DBH of a Norway spruce was 29 cm at the rich site, there were many spruces with a diameter smaller than 20 cm at the poor site. Thus the slopes of the linear regressions between  $A_{\text{pro}}$  and DBH became different. One possible reason may be more solar radiation was available in the rather sparse and diverse canopy of the nutrient poor stand

which allowed for the survival of smaller trees. In other words, the point where the curve of the linear model crosses the  $x$  axis in Norway spruce may suggest a theoretical DBH of the smallest trees, which can survive in this forest stand, when reaching the light compensation point at the entire crown level (Čermák 1989, 1998; Lewis et al. 2000).

Sensitivity of stem growth increment to weather conditions and site fertility

On the rich site, most of the growth occurred at the beginning of the growing season while on the poor site, growth was more evenly distributed. This discrepancy between sites of contrasting fertility is normally reflected in a higher proportion of latewood to earlywood, and higher



**Fig. 8** Dependence of the mean DBH increment ( $\text{cm year}^{-1}$ ) on a tree diameter. Regression equations are: rich site, Norway spruce  $y = 0.0107\text{DBH}$  ( $R^2 = 0.69$ ); rich site, Douglas fir  $y = 0.0137\text{DBH}$  ( $R^2 = 0.75$ ); poor site, Norway spruce  $y = 0.0047\text{DBH}$  ( $R^2 = 0.71$ ); rich site, Douglas fir  $y = 0.0117\text{DBH}$  ( $R^2 = 0.82$ )

tree ring density at nutrient poor sites (Lindstrom 1997; Beets and Gilchrist 2001; Kantavichai et al. 2010). Dominant trees at both sites grew better than suppressed trees during periods of unfavorable weather (cold or drought); however, this difference was not statistically significant at either site.

In the spring, when soil water is not a limiting factor, tree growth is affected mostly by changes in temperature and the amount of photosynthetically active radiation (Tryon and Chapin 1983; Teskey et al. 1987; Briffa et al. 1998; Kirilyanov et al. 2003). It is still unclear to what extent soil and air temperature participate in triggering cambial activity. The classical approach favors the effect of the soil temperature (Van Cleve et al. 1990; Rossi et al. 2007), based on evidence that cambial reactivation and cell production would be inhibited at soil temperatures  $<6^\circ\text{C}$  (Alvarez-Uria and Körner 2007), although a recent manipulation experiment indicated the importance of air temperature (Lupi et al. 2012). Soil temperatures of 6 and  $7^\circ\text{C}$  initiated growth of Douglas fir and Norway spruce, respectively. This corresponded to the above mentioned minimal temperature of  $6^\circ\text{C}$  (Alvarez-Uria and Körner 2007). The relationship between soil temperature and the beginning of stem growth was the same in both years of our study. The earlier growth activation of the Douglas fir (Figs. 6, 7) may result in greater sensitivity of this tree species to late-spring frost than in Norway spruce (Day and Chrystal 1928; Vinš and Šika 1981; Timmis et al. 1994; Hawkins et al. 1995). Warm weather from March to May

usually enhances growth and positively affects xylogenesis in Douglas fir (Kantavichai et al. 2010). In our sites, no spring frost occurred, but the air temperatures dropped to  $5^\circ\text{C}$  in late May 2008 (Fig. 6c, d). Even though this temperature cannot damage non-acclimated newly grown cells, the low temperature coupled with lack of a solar radiation was sufficient to stop stem growth. Both spruce and Douglas fir responded to the low temperatures negatively (i.e. stem increment decreased), but spruce recovered faster and in the subsequent week yielded higher growth. Recovery with warmer temperatures occurred more quickly at the nutrient rich site than at the nutrient poor site for both species (Fig. 6e, f), confirming the results of Hawkins et al. (1995).

Decreasing soil water availability suppressed tree growth of both species at both sites (Figs. 6, 7). A small decline in soil water potential (i.e. to  $-0.5\text{ MPa}$ ) reduced the stem increment of both species (Fig. 6 in the beginning of July, especially at the poor site). Douglas fir grew better than Norway spruce during the mild drought; however the difference was not significant ( $P < 0.05$ ). However, whenever soil water potential approached the wilting point ( $-1.5\text{ MPa}$ ), stem growth ceased at both sites for both species and stems even shrank.

There are several reasons for this growth reduction and stem shrinkage. First, an initial response of trees to drought is to conserve water by closing stomata, which limits the uptake of atmospheric carbon dioxide and curtails photosynthesis and growth (Naidu and DeLucia 1997; Kobe 2006). Additionally, insufficient turgor of the living cambium cells cannot facilitate their enlargement during dry periods (Gryc et al. 2012). Stem shrinkage occurred when water for transpiration was supplied from internal storage in extensible stem tissues, i.e. living bark, phloem and cambium (Hinckley and Bruckerhoff 1975; Waring and Running 1978; Waring et al. 1979; Tyree and Zimmerman 2002; Čermák et al. 2007). Stem water storage plays an important role as an important source of water for both diurnal and longer-time tree transpiration (Goldstein et al. 1984, 1998; Zweifel et al. 2000; Čermák et al. 2007), when the daily change in stem radius can reach more than 0.1 mm depending on the size of the tree (Phillips et al. 2003) and sometimes even effects seasonal transpiration (Borchert 1994).

In summary, this paper presents a set of equations describing tree structure based on aboveground stem and crown biometrical parameters for two coniferous tree species at sites differing in nutrient availability. These biometric data provide a set of necessary tools for modeling tree biometry with respect to site conditions. Analysis of the stem growth increment related to weather conditions provides background data for modeling and for understanding of differences in the growth of those two

coniferous species. Climate change is a significant threat to current Norway spruce-based silviculture, especially at lower altitudes. Modeling of the differences in the allometric parameters, timber production and their dependence on climatic conditions provides a management tool for effective substitution of Norway spruce trees in the forest with a less vulnerable and still commercially viable alternative species.

## Conclusions

1. Significant differences were found in aboveground allocation patterns of Norway spruce trees growing at sites with different nutrient availability. Both tree height and crown projected area were affected.
2. Conversely, there were no significant effects of site fertility on allometric relationships of Douglas fir, suggesting a higher range of optimal soil-nutrient conditions exist for this species.
3. Growth increment in both species followed a unimodal lognormal curve with its peak at the beginning of the season. Douglas fir started its growth 2 weeks earlier and grew more intensively at the beginning of the season than Norway spruce.
4. Low spring temperatures and the limited amount of available solar radiation in spring stops the growth of both species in the field, even when temperatures are not low enough to damage living tissues. Norway spruce is more tolerant of unfavorable spring conditions than Douglas fir.
5. Mild drought suppresses stem growth increment while strong drought (i.e. less than  $-1.5$  MPa soil water potential) entirely stops incremental stem growth. While Douglas fir is better able to grow during mild drought conditions than Norway spruce; both species at both sites stopped growing during the episode of strong drought.
6. During dry periods trees used available water from the stem storage compartments for transpiration. There was no difference in the rate of stem shrinkage between tree species.

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