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Root system development in naturally regenerated Douglas-fir saplings as influenced by canopy closure and crowding

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ABSTRACT: Documented information on the growth dynamics and related silvicultural manipulation of naturally regenerated Douglas-fir beneath a canopy shelter is scarce. We hypothesized that long regeneration phases creating dense cohorts of Douglas-fir advanced regeneration beneath a closed canopy of mature trees have a negative impact on the formation of a stable root system. We therefore studied the influence of shading and competition on root system characteristics of 28 naturally regenerated, ca 3 m tall Douglas-fir saplings growing either without immediate competitors or in dense neighbourhoods, and these situations were located either beneath a closed canopy or in large canopy openings. Both canopy shelter and neighbourhood crowding limited sapling growth and root system development. Saplings from groups located beneath the canopy, although significantly older than the saplings growing in the open, exhibited lower root-to-shoot ratios. When growing in the open, maximum width, total length, and total biomass of root systems was much lower for saplings with than without competitors. In contrast, reductions in root development owing to competition within the sapling cohort were less pronounced under closed canopy conditions. Our results suggest that irrespective of the level of canopy closure, high sapling densities in naturally regenerated young Douglas-fir stands should be reduced early to improve root system development and hence physical stability.

Keywords: natural regeneration; competition; shading; physical tree stability; carbon allocation; root-to-shoot ratio

During the past three decades, management of public forests in Central Europe has undergone a paradigm shift from traditionally even-aged management to close-to-nature forestry characterized by more irregular uneven-aged regimes (Diaci 2006). In place of large-scale clearcut and planting operations, close-to-nature forest management relies on successful natural regeneration that commonly establishes beneath existing mature forest canopies over long regeneration phases (Bauhus et al. 2013). Advance natural regeneration has been practiced in forests of native species and has also gained in importance in stands comprising Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which is an introduced species in Europe. Consequently, abundant advanced natural regeneration has been establishing in the understorey of cone-bearing Douglas-fir stands (Thünen Institute 2014). In the context of adapting forests to climate change by increasing the share of more drought-tolerant species such as Douglas-fir, there is considerable interest to use this natural regeneration for the next forest generation (Eisenhauer, Sonnemann 2009; Reif et al. 2010). Moreover, regenerating Douglas-fir beneath mature overstorey trees lowers the risks of frost damage, drought-related mortality, reduces the juvenile wood fraction and reduces the branch size (Otto 1987; Wobst, Becker 1997).

Within its natural range, the Pacific Northwest of North America, Douglas-fir regenerates naturally in open conditions following stand-replacing fires (Hermann, Lavender 1990). Furthermore, the majority of existing secondary Douglas-fir forests in North America and Europe have been established by low density plantings after clearcutting (Schülli 1984; Talbert, Marshall 2005). Thus, documented information on the growth and silvicultural management of naturally regenerated Douglas-fir beneath a canopy shelter is scarce (Tesch, Mann 1991; Curtis 1998; Buermeyer, Harrington 2002; Emmingham 2002). The challenge to develop appropriate silvicultural practices and techniques to integrate Douglas-fir as an element in close-to-nature management regimes over longer regeneration periods is, therefore, an emerging focus in Europe and North America (Kuehne, Puettmann 2008; Kühne et al. 2011).

The long-term growth and stability of individuals from advance regeneration will depend heavily on how well the saplings develop under the mature overstorey as well as their potential growth response after release from that overstorey competition (Maranto et al. 2008; Briggs et al. 2012). Non-systematic, empirical observations in experimental stands as well as by forest practitioners indicate that understorey Douglas-fir in two-layered mixed-species forests suffers from high risks of uprooting through strong storm events or high snow loads. This susceptibility may well be a result of an inadequate structural root system resulting from light limitation and overstorey competition. Partitioning of growth to roots tends to decline as light availability is reduced (Poorter et al. 2012). Resulting physical instability may develop, in particular, in tree species with intermediate shade-tolerance such as Douglas-fir, which can survive long periods of shading, and even exhibit considerable height growth, but simultaneously sacrifice root growth and hence develop unfavourable root-to-shoot ratios (Devine, Harrington 2008).

Moreover, recent findings on the susceptibility to uprooting of mature trees clearly indicated that the vulnerability of up to ca 100-year-old planted Douglas-fir trees to storm risk in Germany appears to be equivalent to that of Norway spruce (*Picea abies* [L.] H.Karst), which is a European tree species known for its compromised root anchorage and hence poor wind stability (Albrecht et al. 2012). However, there is no information about whether this higher susceptibility of Douglas-fir to wind damage is partially attributable to growing conditions in the sapling stage. Current silvicultural management guidelines in German public forests call for mixed-species stands (e.g. Landesbetrieb Forst Baden-Württemberg 2014), preferentially mixing Douglas-fir with group-sized portions of mostly hardwoods such as European beech (*Fagus sylvatica* L.). Owing to its superior height growth, crowns of Douglas-fir are particularly exposed to winds in such stand structures and hence trees are likely to be at a higher risk of uprooting than in pure stands. In particular in mixed-species stands, early facilitation of adequate root development appears to be imperative.

In this study, we investigated the extent to what the root system development of Douglas-fir saplings may be impeded by intense neighbourhood and overstorey competition. We hypothesized that long regeneration phases creating dense cohorts of Douglas-fir advanced regeneration underneath a closed canopy of mature trees may have a negative impact on the formation of a stable root system. Furthermore, we hypothesized that in comparison with small seedlings (Kühne et al. 2011), the negative effects of neighbourhood crowding and canopy closure on root development and plant growth would intensify with ontogenetic development and hence may be more pronounced in larger saplings.

MATERIAL AND METHODS

Study area and site characteristics. The saplings analysed in this study came from two mountain forest sites situated in close proximity on the western slope of the southern Black Forest at circa 500 m a.s.l. near Freiburg, southwestern Germany (Merkel 2009). The Atlantic climate of the study area is characterized by a mean annual temperature of approximately 9°C and mean annual precipitation of about 1000 mm, with the majority of precipitation occurring during the growing season between May and September (Gauer, Aldinger 2005). The soils are deep, loamy, well-drained and acidic Cambisols superficially influenced by a layer of loess developed from gneiss and granite bedrock materials. Soil samples collected randomly at either study site revealed no significant differences in bulk density. Root development might have been slightly impeded at both study sites by the high content of soil skeleton (coarse fraction > 5 mm), which was up to 25% of the total soil volume (Kühne et al. 2011).

The 75-year old Douglas-fir plantation at the first site (47°58'43''N, 7°52'10''E) was last thinned in 2000. The natural regeneration varied in height and density and consisted mostly of Douglas-fir, scattered silver fir (*Abies alba* Mill.), and European beech seedlings and saplings. Ground vegetation was scarce. As a result of the closed overstorey canopy, light availability, quantified as total site factor (TSF, percentage of photosynthetically active radiation of open-field light conditions), was about 12% (Table 1). Light was measured using hemispherical

Table 1. Mean and standard deviation of selected plant characteristics of the studied Douglas-fir saplings (classes that do not share the same letter are significantly different; n = 7 per sampling group)

Characteristic	Closed canopy		Large canopy opening		P
	neighbourhood competition				
	with	without	with	without	
Age (years)	21 ± 2.9[b]	18 ± 1.1[b]	10 ± 1.7[a]	10 ± 1.1[a]	< 0.001
Total site factor (%)[1]	12 ± 5.4[a]	12 ± 2.9[a]	34 ± 15[b]	29 ± 9.7[b]	< 0.001
Competition index[2]	10 ± 3.8[b]	4.2 ± 2.3[a]	13 ± 4.1[b]	2.2 ± 1.4[a]	< 0.001
Height (cm)	271 ± 24	258 ± 22	273 ± 59	277 ± 29	0.464
Crown length (cm)	157 ± 42[a]	187 ± 18[a]	226 ± 69[ab]	235 ± 14[b]	0.005
Crown width (cm)	159 ± 31[b]	193 ± 28[b]	102 ± 16[a]	166 ± 26[b]	< 0.001
Vertical crown area (m^2)[3]	1.3 ± 0.4[a]	1.9 ± 0.4[b]	1.2 ± 0.4[a]	2.0 ± 0.3[b]	0.006
Root collar diameter (mm)	27 ± 4.5[a]	35 ± 5.4[b]	29 ± 3.9[a]	47 ± 4.6[c]	< 0.001
HDR ($mm \cdot mm^{-1}$)[4]	105 ± 20[c]	75 ± 13[b]	95 ± 14[c]	60 ± 7[a]	< 0.001

[1]percentage of open field photosynthetically active radiation, [2]Hegyi (1974), [3]crown length × crown width (reversed deltoid), [4]height to root collar diameter ratio

photos taken immediately above the regeneration layer in July 2012 and analysed with the WinScanopy software (Régent Instruments Inc., Canada).

The mixed conifer forest at the second site (47°58'02''N, 7°50'41''E) had been partially disturbed by the storm Lothar in 1999 resulting in a few remaining scattered overstorey trees and areas where the original mature Douglas-fir-silver fir stand remained intact. Investigated saplings were selected in large openings east of one of the undisturbed forest patches, a situation comparable to a strip clearcut. Naturally established Douglas-fir and silver fir seedlings and saplings formed the regeneration layer. Areas without woody regeneration were covered by grass (*Luzula* sp.) and black berry (*Rubus* sp.). TSF averaged 32% for saplings in the canopy opening (Table 1).

Data collection and analysis. A total of 28 Douglas-fir saplings, 14 from each site, ranging in height from approximately 2.5 to 3.5 m were analysed in this study (Table 1). Tree height and not tree age was deliberately chosen as the major selection criterion as we aimed to study differences in growth and development among the same-sized individuals. Based on the tree neighbourhood, seven saplings growing with or without mostly conspecific neighbouring competitors, respectively, were selected at either study site, yielding four sapling classes differing with regard to light availability (canopy closure) and neighbourhood competition (crowding). All 28 intensively studied saplings, hereinafter referred to as focal saplings, were healthy and vigorous and randomly distributed across their respective study site. Focal saplings taken from dense groups were dominant or co-dominant relative to their regeneration neighbourhood. Root collar diameter, total height, height to the first live branch, crown radii (four measurements at the height of maximum crown width) and TSF were measured for each of the 28 focal saplings. As a measure of total plant photosynthetic potential, vertical crown area was calculated by multiplying the mean crown radius and the crown length of each focal sapling (Table 1).

To quantify the competitive impact of neighbouring seedlings and saplings on the focal saplings, we recorded species, distance and angle relative to the focal sapling, root collar diameter, and total height of each competitor within a search radius of 2 m around each focal sapling.

To quantify crowding and thus the competitive influence of neighbouring saplings on each focal sapling, we calculated the Hegyi index (1974) – Eq. (1):

$$CI = \sum_{j=1}^{n} \frac{RCD_j}{RCD_i} \frac{1}{Dist_{ij}} \tag{1}$$

where:

CI – competition from all neighbouring trees experienced by the focal sapling i, from n neighbours (j),

RCD – root collar diameter,

$Dist_{ij}$ – distance between the focal sapling and the competitor.

Optimum neighbourhood radius analysis was conducted for the selection of competing neighbours using a software based procedure (Simile v4.7, Simulistics Ltd, Midlothian, United Kingdom) described previously (Forrester et al. 2011). The optimal radius r was determined using least squares, where the coefficient of determination (R^2) of the relationship between focal sapling mean annual radial increment (root collar diameter divided by age) and competition was plotted against r. To create this plot the competition was recalculated along a continuous range of r (0.1 m intervals) so that the maximum R^2 could be found and hence appropriate values of r

could be determined. Given the results of the least square analyses a fixed search radius of 1.5 m was finally used.

Following measurements of aboveground sapling characteristics, North direction and stem base were marked for each focal sapling. The stem was then separated from the root system and brought to the laboratory. To determine leaf mass area, a previously described sampling procedure was followed for 5 randomly selected saplings of each sapling class (Gower, Norman 1991). The live crown was divided along the stem axis into three same-sized segments. One branch representative of the average branch size (diameter and length) of each segment was cut and separately stored in a bag. A total of 60 needles, obtained in equal proportions from the last three annual shoots (2009–2011), was harvested from each branch and the one-sided surface area of the sampled needles was determined using WinRhizo (Régent Instruments Inc., Canada). Finally, the needle samples as well as the rest of the aboveground biomass of each sapling (stem, branches, remaining needles) were dried at 40°C to constant weight before weighing. A disk removed at 10 cm stem height was sanded with progressively finer sandpaper (100 to 400 grit) until all growth rings were discernible. Disk aging was conducted along 4 radii using WinDendro (Régent Instruments Inc., Canada).

Root systems of the focal saplings were excavated with hand tools as carefully as possible. Despite the very cautious procedure, it was not possible to retrieve every fine root (root diameter < 2 mm), particularly the vertical and lateral roots growing into the weathered bedrock. Maximum horizontal root extension within four 90-degree sections (i.e. north-east, south-east, south-west and north-west quadrant) as well as maximum root depth (= excavation pit depth) were measured in the field. The excavated root systems were brought to the laboratory, washed and further measured and processed. First, all fine roots (root diameter < 2 mm) were severed and stored separately. Maximum extension in the four 90-degree sections (see above), maximum depth, taproot depth and the number of root ramifications of the remaining structural coarse root system (root diameter ≥ 2 mm) were recorded. The root system was then dissected. The remaining lateral and vertical roots were cut into more manageable, shorter sections if necessary. To assess total length and volume each dissected root system was then scanned root by root using WinRhizo (Régent Instruments Inc., Canada). Large and very unshapely sections were measured by hand using a calliper and a water-filled measuring cylinder to determine volume by liquid displacement. All root compartments (taproot stock, lateral roots, fine roots, 10 cm sections) were dried at 40°C to constant weight.

Area and space occupied by each focal sapling's root system was calculated based on the root extension measurements using ellipse and ellipsoid formulas, respectively.

All statistical tests and analyses were executed using R 3.1.1 (R Development Core Team 2014). Because of the small sample size the non-parametric Kruskal-Wallis ANOVA was used to test for differences among the four sapling classes followed by a pairwise Mann-Whitney post-hoc test to identify significant differences among classes. Owing to strong collinearity between the potential predictor variables light availability (*TSF* – total site factor) and age ($r = -0.62$), as well as crowding (*CI* – competition index) and vertical crown area ($r = -0.71$), linear models to detect factors influencing plant and root system characteristics of the focal saplings were thus limited to the following Eq. (2):

$$Y = a_0 + a_1 \times TSF + a_2 \times \log(CI) + a_3 \times \mathrm{TSF} \times \log(CI) \quad (2)$$

where:

Y – above- or belowground sapling characteristic,

a_0–a_3 – model parameters,

$\mathrm{TSF} \times \log(CI)$ – interaction term of light availability (*TSF*) and log-transformed crowding (*CI*).

With the exception of root collar diameter, height-to-root collar diameter ratio, root-to-shoot ratio, and all crown parameters, sapling characteristics were log-transformed in this analysis to achieve a normal distribution of the dependent variable *Y*.

RESULTS

Saplings sampled underneath the closed canopy were on average twice as old as the saplings from the large openings (Table 1). As intended by the study design, there were no statistically significant differences in mean sapling height, whereas *TSF* and *CI* significantly differed among the respective sapling classes.

Aboveground plant characteristics

Individuals growing in the canopy opening without neighbourhood competition had the largest average root collar diameter, root-to-shoot ratio, crown length, and dry mass in all studied plant compartments as well as the lowest mean height-to-root col-

Table 2. Mean and standard deviation of absolute dry mass and relative proportion of total sapling biomass for individual plant compartments of the studied Douglas-fir saplings (classes that do not share the same letter are significantly different; n = 7 per sampling group)

Characteristic	Closed canopy		Large canopy opening		P
	neighbourhood competition				
	with	without	with	without	
Biomass (g)[1]					
Total	644 ± 279^a	998 ± 417^a	736 ± 223^a	2,240 ± 581^b	< 0.001
Shoot	484 ± 205^a	709 ± 275^a	490 ± 186^a	1,358 ± 325^b	0.001
Needles	81 ± 37^a	159 ± 117^b	156 ± 34^b	541 ± 168^c	< 0.001
Roots	79 ± 48^a	130 ± 48^a	90 ± 24^a	342 ± 103^b	< 0.001
Coarse roots	67 ± 44^a	113 ± 43^a	74 ± 21^a	290 ± 77^b	< 0.001
Fine roots	12 ± 4.3^a	17 ± 5.7^a	16 ± 3.8^a	52 ± 31^b	0.002
Root-to-shoot ratio[2]	0.13 ± 0.03	0.15 ± 0.04	0.15 ± 0.03	0.18 ± 0.02	0.088
Percentage (%)[3]					
Shoot	75 ± 2.9^b	72 ± 6.2^b	66 ± 5.3^{ab}	61 ± 2.6^a	< 0.001
Needles	13 ± 4.1^a	15 ± 4.8^{ab}	22 ± 3.3^{bc}	24 ± 2.2^c	< 0.001
Roots	12 ± 2.7	13 ± 1.4	13 ± 2.8	15 ± 1.6	0.102

[1]dry weight, [2]belowground biomass/aboveground biomass ($g \cdot g^{-1}$), [3]percentage of total sapling biomass

lar diameter ratio (Tables 1 and 2). Each variable also differed among each sapling class with the exception of crown width. In contrast, saplings sampled from dense neighbourhoods underneath the closed canopy showed the poorest growth. However, differences between closed canopy saplings without competition and saplings of the opening with neighbouring competitors were rarely significant. While averages differed in absolute terms, statistically significant differences were only observed for root collar diameter and hence height-to-root collar diameter ratio and needle biomass. Based on the derived average plant characteristics, aboveground development of individuals from dense groups in the opening were quite comparable to the saplings growing with high levels of competition underneath the closed canopy.

Biomass allocation also differed among the studied sapling classes (Table 2). Shoot proportion was significantly higher and relative needle biomass lower in saplings from the closed canopy site when compared to saplings from the opening without competing neighbours.

Leaf mass area differed only marginally among the various crown segments of each sapling class (data not shown). The observed slight increase from the top of the crown to the bottom was most pronounced in saplings growing in the large opening. While there were statistically significant differences in leaf mass area between the saplings of the two study sites (averages of 111 vs. 88 $g \cdot cm^{-2}$ for closed canopy and canopy opening, respectively), differences between saplings of the same site growing with or without competitors were not significant.

Root system characteristics

Root system size and biomass were largest in saplings growing in the canopy opening and without competing neighbours (Tables 2 and 3). The number of ramifications, horizontal extension, total length, and occupied space were also highest in these individuals, though differences with saplings from the same site but with close-by neighbours were seldom statistically significant (Table 3). Irrespective of the study site, vertical roots of saplings growing in dense groups appeared to reach greater depths when compared to the respective counterparts growing freely without neighbourhood competitors. With the exception of total root length, root system characteristics of the two sapling classes – either with intense or with little neighbourhood competition – from the site with the closed canopy did not differ significantly among each other. However, root characteristics of saplings from dense neighbourhoods in the canopy opening were different from the crowded saplings at the closed canopy site. The latter group of saplings differed also with respect to the number of ramifications and total root system length from their counterparts at the site growing without immediate competitors.

Linear modelling

Many of the analysed above- and belowground sapling characteristics were significantly affected by light availability and crowding (Table 4). Only taproot

Table 3. Mean and standard deviation of selected root characteristics of the studied Douglas-fir saplings (classes that do not share the same letter are significantly different; n = 7 per sampling group)

Characteristic	Closed canopy		Large canopy opening		P
	neighbourhood competition				
	with	without	with	without	
Fine roots[1]					
Deepest root (cm)[2]	76 ± 44	54 ± 15	99 ± 47	70 ± 9	0.140
Max. extension (cm)	60 ± 18[a]	60 ± 14[a]	124 ± 44[b]	184 ± 31[b]	0.002
Coarse roots[2]					
Root ramifications	19 ± 5.5[a]	20 ± 2.3[a]	21 ± 3.5[a]	53 ± 13[b]	0.010
Taproot depth (cm)	47 ± 31	41 ± 11	66 ± 33	46 ± 19	0.434
Max. extension (cm)[3]	18 ± 6.4[a]	22 ± 3.9[a]	59 ± 41[b]	97 ± 39[b]	< 0.001
Total length (cm)	249 ± 93[a]	383 ± 76[b]	535 ± 258[b]	1.798 ± 730[c]	< 0.001
Root plate area (m^2)	0.1 ± 0.1[a]	0.2 ± 0.1[a]	1.4 ± 1.7[b]	3.3 ± 2.1[b]	< 0.001
Occupied space (l)[4]	18 ± 17[a]	20 ± 10[a]	367 ± 569[b]	473 ± 383[b]	< 0.001

[1]root diameter < 2 mm, [2]root diameter ≥ 2 mm, [3]mean maximum length of horizontal roots (4 quadrants), [4]calculated with taproot depth

depth and root-to-shoot ratio were not influenced by either of the two predictor variables. Based on the *F*- and respective *P*-values, competition within the sapling cohort appeared to have a stronger effect on aboveground sapling characteristics than light availability. A similarly clear pattern was not evident in root system characteristics, where depending on the trait either light or competition was the more influential factor. Significant interactions between light availability and competition index were not found for any model. The effect of competing neighbours or light availability, respectively, therefore did not change with the level of the other predictor variable. Or put another way, a significant impact of crowding on any sapling characteristic was evident in the canopy opening as well as under the closed canopy (Fig. 1).

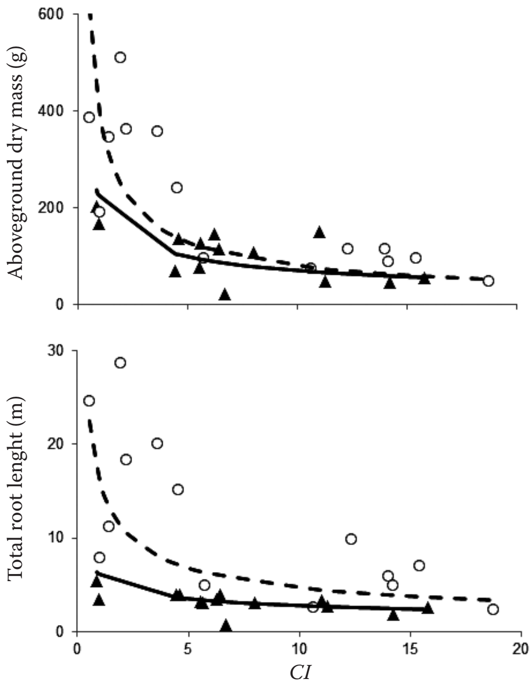

Fig. 1. Influence of crowding quantified using Hegyi's competition index *CI* on aboveground total dry mass and total length of the coarse root system (root diameter ≥ 2 mm, m) in Douglas-fir saplings growing beneath a closed canopy (filled triangles and solid line) and in large canopy openings (open circles and dashed line)

to derive model curves light availability (TSF) was held fixed at its site-specific sub-sample mean (closed canopy: 12%, large opening: 32%), see Table 4 for model statistics and parameters

DISCUSSION

This study showed that both canopy closure and neighbourhood crowding within the advance regeneration cohort restricted growth and development of Douglas-fir saplings. In comparison, neighbourhood competition had a stronger impact on saplings growing in the opening and seemingly influenced shoot growth to a higher degree than root growth. However, the combination of reduced light levels and competition appeared to have a more detrimental effect on root formation.

Average light values in the large opening of this study were close to 35% of open-field light conditions, a threshold below which Douglas-fir growth is substantially inhibited (Mason et al. 2004; Harrington 2006). Hence, it was concluded that light availability should be a major growth limiting factor only in cases when light levels drop below this threshold (Carter, Klinka 1992) and that under a moderate temperature regime with a steady

Table 4. Fit and prediction statistics for linear models evaluating the influence of light availability (*TSF* – total site factor), crowding (*CI* – competition index), and the interaction of *TSF* and *CI* on selected above- and belowground characteristics of excavated Douglas-fir saplings (n = 28)

Characteristic	Statistic	Parameter			
		a_0	a_1	a_2	a_3
Root collar diameter	Adjusted R^2	0.74			
	F		9.9**	76.6***	2.9
	Estimate	34.40	0.46	–0.87	–0.02
Height-to-root collar diameter	Adjusted R^2	0.50			
	F		0.1	29.9***	0.2
	Estimate	69.91	–0.41	2.53	0.02
Vertical crown area	Adjusted R^2	0.51			
	F		0.8	30.0***	0.2
	Estimate	2.03	0.01	–0.08	0.001
Log (needle biomass)	Adjusted R^2	0.68			
	F		18.5***	40.7***	0.48
	Estimate	5.23	0.04	–0.46	–0.004
Log (stem biomass)	Adjusted R^2	0.58			
	F		6.3*	33.7***	0.4
	Estimate	6.71	0.02	–0.33	–0.003
Log (above-ground biomass)	Adjusted R^2	0.65			
	F		10.1**	41.4***	0.6
	Estimate	6.92	0.02	–0.34	–0.01
Log (coarse root biomass)[1]	Adjusted R^2	0.51			
	F		4.2	26.3***	0.4
	Estimate	4.95	0.03	–0.43	–0.005
Log (below-ground biomass)	Adjusted R^2	0.54			
	F		5.2*	28.2***	0.4
	Estimate	5.04	0.03	–0.38	–0.01
Root-to-shoot ratio	Adjusted R^2	0.01			
	F		0.1	2.7	0.4
	Estimate	0.15	0.001	–0.001	–0.001
Log (total root length)[1]	Adjusted R^2	0.57			
	F		19.5***	17.3***	1.3
	Estimate	5.81	0.05	–0.22	–0.01
Log (taproot depth)[1]	Adjusted R^2	0.00			
	F		0.1	0.8	0.1
	Estimate	3.64	0.001	0.07	0.001
Log (root area)[1]	Adjusted R^2	0.50			
	F		24.7***	4.2	0.6
	Estimate	–2.66	0.11	–0.15	–0.01

asterisks denote significant effects of the explanatory variables *TSF*, log(*CI*), and *TSF* × log(*CI*): *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, [1]root diameter ≥ 2 mm

water supply, young Douglas-fir grow best in full light (Mailly, Kimmins 1997; Chan et al. 2003). Therefore, while the large openings provided the best growing conditions in this study, they were not optimal for the investigated saplings. Light levels underneath the closed canopy constituted poorer growing conditions with only 12% of open-field light availability. The observed significant differences in above- and belowground growth between saplings growing without nearby neighbours in the opening and under the closed canopy confirm previous findings from shading experiments (Fairbairn, Neustein 1970; Drew, Ferrell 1977). The contrasting ages of the saplings of the different sites, despite similar heights emphasize how overstorey competition can restrict tree development and especially root system formation (Chen 1997) and also verify the ability of Douglas-fir advanced regeneration to persist in comparatively deep shade over a prolonged period of time (Churchill 2005).

Overall, reduced light availability beneath the canopy limited root system formation more strongly than stem development. This is a common pattern found for intermediate shade-tolerant, mid-successional species such as Douglas-fir (Williamson, Twombly 1983; Drever, Lertzman 2001). In contrast to more shade tolerant late-successional species, Douglas-fir reduces shoot growth to a lesser extent under unfavourable light regimes (Chan et al. 2003; Petritan et al. 2010, Petritan et al. 2011). Hence, instead of lingering in the shade "waiting" for a canopy gap to emerge, Douglas-fir regeneration obviously tends to allocate limited growth resources preferably to stem height growth towards the light (Beaudet, Messier 1998). This dynamics often leads to an imbalance between aboveground and belowground biomass and lowers individual tree stability (Churchill 2005).

Under both light regimes investigated, intraspecific competition within the advance regeneration cohort caused substantial changes in sapling growth and morphology, further reducing stability and vigour. Slenderness, measured as height-to-root collar diameter ratio, increased significantly for saplings of dense groups to average values exceeding 90. In previous studies height to diameter-at-breast-height (DBH) ratios of advanced Douglas-fir regeneration in excess to 90 were associated with compromised stability and strongly limited viability (Cole, Newton 1987; Emmingham et al. 2000). Slenderness must have been even more unfavourable for saplings in our study because the height-to-diameter ratio was calculated with the diameter at the stem base instead of DBH.

Although competition inhibited the development of saplings growing under a closed canopy to a smaller extent than of saplings growing in the opening, the impact of neighbourhood competition was still evident for some of the studied plant and root characteristics. This is at least partially in contrast to a previous study that found no crowding effect on various above- and belowground characteristics of Douglas-fir seedlings smaller than 1 m also growing beneath a closed canopy (Kühne et al. 2011).

We assume that this difference between seedlings and saplings may be attributable to increased plant size. A larger proportion of non-photosynthetically active tissue in larger plants in comparison with smaller conspecifics is usually associated with increased individual light demand, or light compensation points, and lower shade tolerance (Williams et al. 1999). Thus for a given light availability, the effects of crowding, and competition for light, may be more evident for larger plants than for smaller ones. However, other studies found no additional growth restriction as a result of strong intraspecific competition in advanced Douglas-fir regeneration growing beneath a mature overstorey (Gürth 1987; Churchill 2005).

Management implications

Physical instability of individual trees as a result of very high population densities is a well-known phenomenon in conifer stands. In this situation, substantial tree damage and mortality may result from heavy snow and ice loads during early stand development phases (Spellmann et al. 1984). If the necessary pre-commercial thinning operations are not conducted at appropriate times, windthrow can cause further losses during later phases of stand development (Gardiner et al. 1997). This also applies to Douglas-fir plantations and naturally regenerated stands (Groth 1927; Kramer, Smith 1983). Retarded self-thinning in overly dense young Douglas-fir stands has been described previously and attributed to the comparatively high shade tolerance of the species at an early development stage (Chen 1997; Harrington et al. 2009). Our results confirm earlier assessments of crowded young stands under full canopy shelter for which early release operations were recommended to lower stand density and thus promote the growth of a limited number of vigorous individuals necessary for increasing long-term stability on the tree- as well as the stand-level (Gürth 1987). Our study therefore suggests that timely spacing interventions are also beneficial in young densely stocked Douglas-fir cohorts growing in partial shade. Furthermore, the detrimental effects on physical tree stability caused by the persistence of Douglas-fir saplings in deep shade suggests that prolonged phases with regeneration growing under canopy shelter should be avoided.

References

Albrecht A., Kohnle A., Hanewinkel M., Bauhus J. (2013): Storm damage of Douglas-fir unexpectedly high compared to Norway spruce. Annals of Forest Science, 70: 195–207.

Bauhus J., Puettmann K.J., Kühne C. (2013): Is close-to-nature forest management in Europe compatible with managing forests as complex ecosystems? In: Messier C., Puettmann K., Coates K.D. (eds): Managing Forests as Complex Adaptive Systems. Building resilience to the challenge of global change. Oxon, Routledge: 187–213.

Beaudet M., Messier C. (1998) Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. Canadian Journal of Forest Research, 28: 1007–1015.

Briggs N., Kuehne C., Kohnle, U., Bauhus J. (2012): Root system response of naturally regenerated Douglas-fir (*Pseudotsuga menziesii*) after complete overstory removal. Canadian Journal of Forest Research, 42: 1858–1864.

Buermeyer K.R., Harrington C.A. (2002): Fate of overstory trees and patterns of regeneration 12 years after clearcutting with reserve trees in southwest Washington. Western Journal of Applied Forestry, 17: 78–85.

Carter R.E., Klinka K. (1992): Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. Forest Ecology and Management 55: 87–105.

Chan S.S., Radosevich S.R., Grotta A.T. (2003): Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. Canadian Journal of Forest Research, 33: 106–117.

Chen H.Y.H. (1997): Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Canadian Journal of Forest Research, 27: 1383–1393.

Churchill D.J. (2005): Factors Influencing Understory Douglas-fir Vigor in Multi-cohort Prairie Colonization Stands at Fort Lewis, Washington. [MSc Thesis.] Washington, University of Washington: 70.

Cole E.C., Newton M. (1987): Fifth-year responses of Douglas-fir to crowding and nonconiferous competition. Canadian Journal of Forest Research, 17: 181–186.

Curtis R.O. (1998): Selective cutting in Douglas-fir. Journal of Forestry, 96: 40–46.

Devine W.D., Harrington T.B. (2008): Belowground competition influences growth of natural regeneration in thinned Douglas-fir stands. Canadian Journal of Forest Research, 38, 3085–3097.

Diaci J. (ed.) (2006): Nature-based Forestry in Central Europe: Alternatives to Industrial Forestry and Strict Preservation. Studia Forestalia Slovenica 126. Ljubljana, University of Ljubljana: 178.

Drever C.R., Lertzman K.P. (2003): Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research, 33: 137–146.

Drew A.P., Ferrell W.K. (1977): Morphological acclimation to light intensity in Douglas-fir seedlings. Canadian Joural of Botany, 55: 2033–2042.

Eisenhauer D.R., Sonnemann S. (2009): Waldbaustrategien unter sich ändernden Umweltbedingungen – Leitbilder, Zielsystem und Waldentwicklungstypen. Waldökologie, Landschaftsforschung und Naturschutz, 8: 71–88.

Emmingham W.H. (2002): Status of uneven-aged management in the Pacific Northwest, USA. Forestry, 75: 433–436.

Emmingham B., Chan S., Mikowski D., Owston P., Bishaw B. (2000): Silviculture practices for riparian forests in the Oregon coast range. Research Contribution 24. Corvallis, Forest Research Laboratory, Oregon State University: 34.

Fairbairn W.A., Neustein S.A. (1970): Study of response of certain coniferous species to light intensity. Forestry, 43: 57–71.

Forrester D., Vanclay J., Forrester R. (2011): The balance between facilitation and competition in mixtures of *Eucalyptus* and *Acacia* changes as stands develop. Oecologia, 166: 265–272.

Gardiner B.A., Stacey G.R., Belcher R.E., Wood C.J. (1997): Field and wind-tunnel assessment of the implications of respacing and thinning on tree stability. Forestry, 70: 33–252.

Gauer J., Aldinger E. (2005): Waldökologische Naturräume Deutschlands. Braunschweig, Bundesforschungsinstitut für Ländliche Räume, Wald und Fischerei: 48.

Gower S.T., Norman J.M. (1991): Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology, 72: 1896–1900.

Groth O. (1927): Die Wurzelbildung der Douglasie und ihr Einfluss auf die Strum- und Schneefestigkeit dieser Holzart. Allgemeine Forst- und Jagdzeitung, 103: 186–205, 268–285.

Gürth P. (1987): Zur Naturverjüngung der Douglasie im Südwest-Schwarzwald. Der Forst- und Holzwirt, 42: 59–63.

Harrington T.B. (2006): Five-year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. Canadian Journal of Forest Research, 36: 2439–2453.

Harrington T.B., Harrington C.A., DeBell D.S. (2009): Effects of planting spacing and site quality on 25-year growth and mortality relationships of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Forest Ecology and Management, 258: 18–25.

Hegyi F. (1974): A simulation model for managing jack pine stands. In: Fries J. (ed.): Growth models for tree and stand simulation. Royal College of Forestry, Research Note 30: 74–90.

Herman R., Lavender D. (1990): *Pseudotsuga menziesii* (Mirb.) Franco, Douglas-fir. In: Burns R., Honkala B. (eds): Silvics of North America. Vol. 1. Conifers. USDA Agricultural Handbook 654. Washington, DC, United States Department of Agriculture: 527–540.

Kramer H., Smith J.H.G. (1985): Bestandesbegründung der Douglas-fir in Britisch-Kolumbien, Kanada. Forstarchiv, 56: 9–13.

Kuehne C., Puettmann K.J. (2008): Natural regeneration in thinned Douglas-fir stands in western Oregon. Journal of Sustainable Forestry, 27: 246–274.

Kühne C., Bauhus J., Hörnig T., Oh S. (2011): Einfluss von Überschirmung, Dichtstand und Pflanzengröße auf die Wurzelentwicklung natürlich verjüngter Douglasien. Forstarchiv, 82: 184–194.

Landesbetrieb Forst Baden-Württemberg (2014): Richtlinie landesweiter Waldentwicklungstypen. Stuttgart, Landesbetrieb Forst Baden-Württemberg: 118. Available at http://forstbw.de/fileadmin/forstbw_mediathek/forstbw_praxis/wet/ForstBW_Waldentwicklung_web.pdf

Mailly D., Kimmins J.P. (1997): Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. Canadian Journal of Botany, 75: 1424–1435.

Maranto J.C., Ferguson D.E., Adams D.L. (2008): Response of Douglas-fir advance regeneration to overstory removal. Research Paper RMRS-RP-73. Fort Collins, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 17.

Mason W.L., Edwards C., Hale S.E. (2004): Survival and early seedling growth of conifers with different shade tolerance in a Sitka spruce spacing trial and relationship to understorey light climate. Silva Fennica, 38: 357–370.

Merkel E. (2009): Zur Ästigkeit von Douglasien unter Schirm. [Diploma Thesis.] Rottenburg University of Applied Forest Sciences: 55.

Otto H.J. (1987): Skizze eines optimalen Douglasienanbaues in Nordwestdeutschland. Der Forst- und Holzwirt, 42: 515–522

Petritan I.C., Lüpke v.B., Petritan A.M. (2010): Einfluss unterschiedlicher Hiebsformen auf das Wachstum junger Buchen und Douglasien aus Pflanzung. Forstarchiv, 81: 40–52.

Petrițan I.C., von Lüpke B., Petrițan A.M. (2011): Effects of root trenching of overstorey Norway spruce (*Picea abies*) on growth and biomass of underplanted beech (*Fagus sylvatica*) and Douglas fir (*Pseudotsuga menziesii*) saplings. European Journal of Forest Research, 130: 813–828.

Poorter H., Niklas K.J., Reich P.B., Oleksyn J., Poot P., Mommer L. (2012): Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist, 193: 30–50.

R Development Core Team (2014): An introduction to R. Available at https://cran.r-project.org/doc/manuals/R-intro.pdf

Reif A., Brucker U., Kratzer R., Schmiedinger A., Bauhus J. (2010): Waldbau und Baumartenwahl in Zeiten des Klimawandels aus Sicht des Naturschutzes. Bonn, Bundesamt für Naturschutz: 272

Schülli L. (1984): Erfahrungen mit der Douglasie zwischen Oberrhein und Bodensee. Allgemeine Forstzeitung, 39: 436–437.

Spellmann H., Caspari C.O., Michalewski R. (1984): Analyse von Schneeschäden in Kiefernbeständen unter besonderer Berücksichtigung der Bestandesstruktur. Allgemeine Forst- und Jagdzeitung, 155: 146–164.

Talbert C., Marshall D. (2005): Plantation productivity in the Douglas-fir region under intensive silvicultural practices: Results from research and operations. Journal of Forestry, 103: 65–70.

Tesch S.D., Mann J.W. (1991): Clearcut and Shelterwood Reproduction Methods for Regenerating Southwest Oregon Forests. Forest Research Lab Research Bulletin 72. Corvallis, Oregon State University: 45.

Teuffel K.Frhr.v., Kastrup M. (1998): Die Douglasie in Baden-Württemberg. AFZ/Der Wald, 53: 283–287.

Thünen-Institute (2014): Third National Forest Inventory – Results database. Available at: https://bwi.info/start.aspx

Williams H., Messier C., Kneeshaw D.D. (1999): Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Canadian Journal of Forest Research, 29: 222–231.

Wobst J., Becker G. (1997): Möglichkeiten zur Erweiterung des waldbaulichen Einflusses auf die Holzqualität der Douglasie. Forst und Holz, 52: 555–563.

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