

Effect of wide spacing on tree growth, branch and sapwood properties of young Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] in south-western Germany

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Received: 26 February 2008 / Revised: 22 July 2008 / Accepted: 5 September 2008 / Published online: 25 September 2008
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Abstract The influence of stand density on Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is conceptually understood, but for wide spacings not well quantified, particularly in Europe. This study used 41 trees from 7 different locations in south-western Germany to compare important tree- and branch-level attributes across three different densities, namely 100, 200, and 1,200 stems ha⁻¹. In general, there were only a few tree and branch attributes that were significantly different between the 100 and 200 ha⁻¹ densities. Crown projection area and diameter of the thickest branches were the most important differences between the 100 and 200 ha⁻¹ densities. The most obvious and significant differences in this study were between 100 and 1,200 ha⁻¹ densities, where nearly every examined tree and branch attributes were statistically significant. However, relative sapwood area, the number of branches, branch angle, and the occurrence of spike knots were insensitive to stand density. Although the two lowest stand densities in this study represent rather extremely wide

spacings, these results still have important implications for the development of effective thinning regimes for Douglas-fir in south-western Germany. Important management recommendations from this study include thinned stands should be maintained to at least 200 stems ha⁻¹ to maintain high log quality and stand stability. Furthermore, even at stand densities exceeding more than 1,200 trees ha⁻¹ planted trees, artificial pruning may even be necessary to produce high quality logs.

Keywords Spacing · Branchiness · Sapwood · Douglas-fir · Timber quality · Open grown trees

Introduction

Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] continues to be an important and significant component of European forests. In the south-western region of Germany, Douglas-fir comprises nearly 3% of the current stocking volume (FVA-BW 2004) and this value is expected to increase in the upcoming years (Moosmayer 2002). Douglas-fir is a very valuable species in this region because it is adaptable to wide range of site conditions, maintains high growth rates, and produces high quality wood products (Kenk and Thren 1984a, b; Weise et al. 2001). In the context of climate change, Douglas-fir appears a particularly interesting commercial tree species for central Europe because the species' adaptive potential for warming might be superior to Norway spruce (*Picea abies* [L.] Karst.), which is currently the economically most important species in the region (Teuffel et al. 2004).

The European approach to Douglas-fir silviculture is well-established, but the long-term effects of very wide spacings on individual tree attributes have rarely been

Communicated by C. Ammer.

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quantified in the literature. Stand density is the most important factor influencing individual trees. In south-western Germany, Douglas-fir stands are generally planted with a maximum of 1,200 trees ha⁻¹, and density is routinely controlled by pre-commercial (if planting densities exceed >800 ha⁻¹) and commercial thinnings (MLR-BW 1997, 1999). Understanding the effects of these differing levels of stand density on individual tree attributes such as growth, branching, and sapwood is an important step for refining and predicting the response of future thinning activities.

Mäkinen and Hein (2006) recently evaluated the effects of wide spacings created by thinning on growth and branch properties of young Norway spruce. In their study, mean radial increment and branch properties were negatively influenced by decreased stand density, which have important implications for the final value of wood products yielded by these stands. For example, they found that all sample trees at the lower stand densities (700 stems ha⁻¹) had a maximum branch diameter that exceeded the quality class B (“regular quality”) in the European requirements for round wood.

The goal of this project was to examine the effects of various spacings on individual tree Douglas-fir growth, branch properties, and sapwood area. The spacings analysed covered very wide spacings (100 or 200 stems ha⁻¹) and fairly dense (1,200 stems ha⁻¹). The inclusion of sapwood area as a variant in this analysis provides interesting insights into the potential amount and distribution of leaf area in the stands. Sapwood also has important implications for several wood products. Specific objectives were to descriptively quantify the influence of stand density on: (1) individual tree dimensional and growth attributes such as radial and height increment, taper, and length of the live crown; (2) branch attributes such as size, frequency, and the occurrence of branches that might cause defects; and (3) the amount and relative proportion of sapwood.

Materials and methods

Experiments

The material was collected from three spacing experiments within the program “Solitary Trees” (“Solitärprogramm”) in south-western Germany. This program was established in the 1980s by Abetz (Abetz 1987; Abetz and Lässig 1989). The status of the program has lately been evaluated (Herbstritt and Kohnle 2006) and data obtained from plots of the program have been exploited in several analyses on growth and branch

characteristics (Mäkinen and Hein 2006; Hein et al. 2007; Hein et al. 2008). The principal and original aim of the experiments was to study the impact of environmental factors (e.g. weather conditions, air pollution, biotic pests) on tree growth without the confounding effects of inter-tree competition.

For Douglas-fir, the experiments were established in seven approximately 12-year-old single-species stands located in south-western Germany between 1989 and 1991. At each location, one to three plots were established, namely: (1) a plot with extremely widely spaced trees where the stands were thinned to a density of 100 stems ha⁻¹ at the establishment of the experiment (4 plots); (2) a plot with a wide spacing where the stands were thinned to an initial density of 200 stems ha⁻¹ at the beginning of the experiment (3 plots); and (3) a plot with an initial density of 1,200 stems ha⁻¹ (3 plots). The latter representing the recommended density of planted Douglas-fir in south-western Germany; this density also covers the recommendations for planting Douglas-fir in neighboring countries such as France (ONF-FR 1996). Square or rectangular plots (0.25 ha) were established at each location with evenly spaced stems (approximately 10 × 10, 7.1 × 7.1 m and 2.9 × 2.9 m, respectively). No thinnings have been carried out after the establishment of the experiments. In total, data from ten plots on seven different installations were available (Table 1).

The site index on the locations defined as the dominant height expected at the age of 100 years (Bösch 2001) ranged between 51.7 and 56.0 m, with no obvious differences between the three treatments (Table 1). The climatic and site conditions varied slightly among the seven locations. As an exception, the location “Kirchzarten” was situated at a relatively high altitude. The soil water holding capacity varied from moderately dry to moderately moist. Generally, the soils’ water availability was judged as sufficient with only one exception (location “Löwenstein”) with slightly restricted water availability. The different stands had been planted from 1977 to 1979 with plant material grown from seeds collected from approved local stands. Documentation on the age of the planting material was not available. However, considering the silvicultural guidelines recommending 2 + 1 nursery stock for Douglas-fir plantations (MLR-BW 1999), the trees were probably 3 years old. Furthermore, the provenance of the original North American seed source was not documented. Drawing from the introduction history of Douglas-fir to Baden-Württemberg in combination with the stands’ age and the observed satisfying growth characteristics, it appears reasonable to assume coastal provenances from low to medium altitudes of Oregon/Washington (Kenk and Thren 1984a, b).

Table 1 General information on the experiments from the seven installations

	Bad Herrenalb	Ellwangen	Emmendingen	Kirchzarten	Lörrach	Löwenstein	Walldürn
Longitude (E)	08°29'	10° 11'	07°51'	07°55'	07°41'	09°27'	09°19'
Latitude (N) (WGS84)	48°46'	49°01'	48°12'	47°53'	47°41'	49°05'	49°35'
Altitude (m a.s.l.)	700	500	400	1,100	550	550	400
Mean annual temperature (°C)	8	7.5	9	4.5	8.5	8	8
Annual total precipitation (mm)	1,200	800	1,000	1,500	950	900	700
Slope inclination (°)	25	12	26	32	20	14	13
Site unit	Podsollic loamy sand from red sandstone (Buntsandstein)	Loamy sand from sandstone with poor nutrient supply (Stubensandstein)	Loamy sand from red sandstone (Buntsandstein)	Stony loam from gneiss substrate (Gneis)	Loamy sand from red sandstone (Buntsandstein)	Loamy sand from red sandstone with poor nutrient supply (Stubensandstein)	Loamy sand from red sandstone (Buntsandstein)
Water holding capacity of the soil	Moderate dry	Moderate dry	Moderate dry	Moderate dry	Moderate moist	Moderate dry	Moderate moist
No of plots by experiment (<i>no. trees</i>)	A:1(5) C:1(9)	A:1(2)	B:1(5) C:1(5)	A:1(1)	C:1(1)	A:1(5) B:1(5)	B:1(3)
H_{100} (m) ^a	52.0	51.7	55.0	52.0	56.0	55.5	53.8
Age (years)	28.6	33.0	27.9	28	25	24.6	29.3

^a Height of dominant trees at age 100 years (site index)

Measurements and statistical analysis

In total, 41 trees were sampled from the 10 plots, with 13 trees from the lowest density, 13 trees from the intermediate, and 15 trees from the highest density. The sampling was targeted to dominant and co-dominant trees, which were randomly selected under the condition of having no visible signs of damage. As some of the plots had been discarded from the original study, they offered the opportunity to sample a larger number of trees without impairing the long-term monitoring program. The trees used in this study were harvested in 2004–2006 (i.e. 15–17 years after the beginning of the experiments). At the time of harvest, the trees were, on average, 27.6 years old counted on stem discs at 0.3 m stem height. Summary statistics of individual tree attributes are given in Table 2.

For each tree, tree height, stem diameter at breast height, height of the crown base (the height of the lowest living primary branch) and crown projection area were measured. The projected area of the crown was calculated using an eight-cornered polygon (Röhle and Huber 1985). Current basal area of a stem in relation to current crown projection area was used as a measure for the efficiency of stem wood production. For three trees from experiment B (location Walldürn), no measurement of crown projection area was available.

After felling the sample trees, the distance of whorls from the stem apex, branch status (living or dead), branch angle (in 5° increments) and diameter (on branch base after base swell) both in the horizontal and vertical directions of all branches above 1.3 m height were measured. The branch angle was defined as the vertical angle between the stem and the branch. The average branch diameter was calculated as the arithmetic mean of the horizontal and vertical diameters. In total, 6,409 branches were measured of which 5,857 (91.4%) were still alive.

Stem cross-sections were taken at 1.3 m height, then every 5.0 m thereafter. The number of annual rings was counted, and then compared with the number of whorls above the cross-section to assure the correct numbering of the whorls. The whole dataset covers a range of tree diameters between 27.2 and 48.1 cm and heights of 18.0–26.0 m measured at the time of felling.

Annual radial increment was measured on the 1.3 m cross section in eight directions (at 45° intervals beginning from north) and on the upper cross sections in four directions based on computer-aided tree-ring measurement equipment (Digitalpositionimeter K. Johann, Kutschenreiter, Vienna, Austria). On each radius of the cross section, we recorded the first year with no heartwood coloration as the first sapwood year. The sapwood area per cross section was calculated using an eight/four-cornered polygon by subtracting the heartwood area from the total area of the cross

Table 2 Summary statistics of the sample trees taken from stands with initial densities of 100, 200 and 1,200 Douglas-fir ha⁻¹

	100		200		1,200	
	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max
Stem characteristics						
Age (years)	28.5 ^a	24–34	26.4 ^a	24–30	28.1 ^a	25–31
$D_{1.3}$ (cm)	43.3 ^a	35.9–48.1	41.8 ^a	37.0–46.7	33.5 ^b	27.2–37.2
H (m)	21.6 ^a	18.0–25.8	22.8 ^{ab}	20.6–24.7	23.7 ^b	21.1–26.0
Volume (m ³)	1.28 ^a	0.82–1.74	1.25 ^a	0.95–1.65	0.87 ^b	0.61–1.05
$H/D_{1.3} \times 100$	49.9 ^a	40.8–56.7	54.8 ^a	48.9–60.0	71.4 ^b	56.6–88.3
Crown characteristics						
Crown diameter (m)	9.7 ^a	7.5–12.1	8.7 ^a	7.2–10.6	5.9 ^b	4.2–7.4
Crown projection area (m ²)	76.9 ^a	43.9–114.9	59.7 ^a	40.5–88.5	27.8 ^b	13.9–42.0
Crown ratio	0.89 ^a	0.82–0.96	0.88 ^a	0.79–0.97	0.70 ^b	0.58–0.93
Height to the lowest living branch (m)	2.3 ^a	0.7–3.7	2.7 ^a	0.6–5.3	7.0 ^b	1.8–10.4
Height to the lowest dead branch (m)	1.7 ^a	0.7–2.5	1.7 ^a	0.6–2.5	1.3 ^a	0.5–2.4
Branch characteristics						
Diameter of the thickest branch (cm)	7.8 ^a	6.1–9.6	6.8 ^b	5.9–9.4	5.4 ^c	4.3–6.3
Height to the thickest branch (m)	7.8 ^a	1.9–11.7	8.8 ^{ab}	4.2–13.4	10.7 ^b	6.0–14.3
Relative location of the thickest branch within the crown (–) ^x	0.71 ^a	0.49–0.94	0.70 ^a	0.48–0.94	0.79 ^a	0.56–0.95
Number of branches tree ⁻¹ with insertion angle $\leq 45^\circ$ tree ⁻¹	8.2 ^a	0–31	7.3 ^a	2–19	7.8 ^a	2–23
Insertion angle of steepest branch tree ⁻¹	24.6 ^a	10–40	28.8 ^a	15–40	22.7 ^a	10–40
Height to steepest inserted branch tree ⁻¹	14.5 ^a	7.9–24.3	16.6 ^a	10.9–22.5	16.5 ^a	9.1–24.2
Relative location of the steepest inserted branch tree ⁻¹ within the crown (–) ^x	0.37 ^a	0.01–0.72	0.31 ^a	0.03–0.71	0.44 ^a	0.04–0.91

Treatment means in the same row marked with *different letters (superscript)* differ significantly ($P > 0.05$)

^x 0 = stem apex, 1 = crown base (height of the lowest living branch)

section. The relative sapwood area was calculated by dividing the sapwood area by the total cross sectional area (without bark) and expressed as a percentage value.

Similar to the efficiency of stem wood production, the relationship between branch wood production relative to crown size was also investigated by relating the total basal area of all living branches of a tree to crown projected area. Furthermore we related the sapwood area measured at each stem disc to the cumulative branch area above the respective stem disc.

Due to the hierarchical nature of the data, statistical significance of the differences between the treatments was analysed using mixed effects models. The random effects included in this analysis were random plot, tree, and whorl effects. Depending on the level of the measurements (at tree or whorl level), the model used to test the treatment effects was:

$$y_{lpt} = \mu + \delta_D + u_{lp} + u_{lpt} + \varepsilon$$

or

$$y_{lptw} = \mu + \delta_D + u_{lp} + u_{lpt} + u_{lptw} + \varepsilon$$

where y is a dependent variable, μ is the overall mean, δ_D the effect of stand density class, and u_{lp} , u_{lpt} , and u_{lptw} the

random effects for stand l , plot p , tree t , and whorl w and ε is the residual error at the lowest level. Comparisons between the experiments were performed by computing least-square means of the treatment effects and tested by least-squares means of the fixed effects with a Bonferroni adjustment. Restricted maximum likelihood estimation in the MIXED procedure of SAS (SAS Institute Inc. 2004) was used in the analysis.

Since each treatment was not replicated on every installation, this study has an unbalanced design and is clearly observational in nature. Thus, the scope of inference is limited and the detected differences may be due to confounding factors rather than purely treatment effects. For example, all of the highest density plots occur on loamy sands from sandstone sites. However, the use of a random installation effect was assumed to account for this unbalanced design. Preliminary analysis indicated that the random installation effects were purely random and uniformly distributed. Hence, they were not correlated with any site factors such as soil texture or drainage. Therefore, the design of this study was not expected to impede any of the interpretations of the results, except that caution on their generality is warranted.

Results

Tree size and stem increment

The mean diameter at 1.3 m of the sample trees differed by 9.8 cm between the densities of 100 and 1,200 ha^{-1} (Table 2). Mean stem radial increment of the dominant trees varied between 6.5 and 8.7 mm at 1.3 m during the years before the beginning of the experiment (Fig. 1a). In the densities of 100 and 200 ha^{-1} , annual radial increment increased continuously until it levelled off around the mid-1990s. The annual radial increment of the trees in the 1,200 ha^{-1} experiment decreased steadily between the start of the experiment until the end of observation. Even close to 2005 or nearly 15 years since the establishment of the experiment, the stem increment of the 100 and 200 ha^{-1} density was still 2 mm higher than the 1,200 ha^{-1} treatment. With respect to basal area increment, no obvious reduction occurred in the latter part of the study period (Fig. 1b), but there appeared some levelling off between 1995 and 2000. Inter-tree competition on plots at a density of 200 ha^{-1} did not reduce to a large extent stem diameter growth compared with those at a density of 100 ha^{-1} . In densities of 1,200 ha^{-1} , radial and basal area increments were clearly at a lower level during the whole experiment.

There was a significant difference between the heights of the trees from the lowest and highest densities (2.1 m, Table 2). Likewise, height increment from the lowest density was below the values from the higher densities, although it varied significantly between years (Fig. 1c). Also, stem form ($H/D_{1.3}$ -ratio) decreased significantly from the 1,200 ha^{-1} and to the 100/200 ha^{-1} experiments.

All crown properties differed significantly between the 100 and 1,200 ha^{-1} plots (Table 2). In some cases, even significant differences between the stand densities of the 100 and 200 ha^{-1} plots could be observed. Tree crowns were narrowest and shortest at the closest spacings. Accordingly, the crown ratio, the lowest living and the lowest dead branch, differed significantly between the 100 and the 1,200 ha^{-1} density. However, there was no difference between the two lowest densities. Thus, crown recession had started even at the 100 and 200 stems ha^{-1} densities as the lowest living branch was 1 m above the lowest dead branch for both densities.

Branch diameter

The diameter of the thickest branch of a sample tree decreased significantly with increasing stand density (Table 2). Irrespective of stand density, the height of the thickest branch was located between 0.70 and 0.79 within the crown (0 = stem apex, 1 = crown base). Also, for the absolute position of the thickest branch at the stem, the

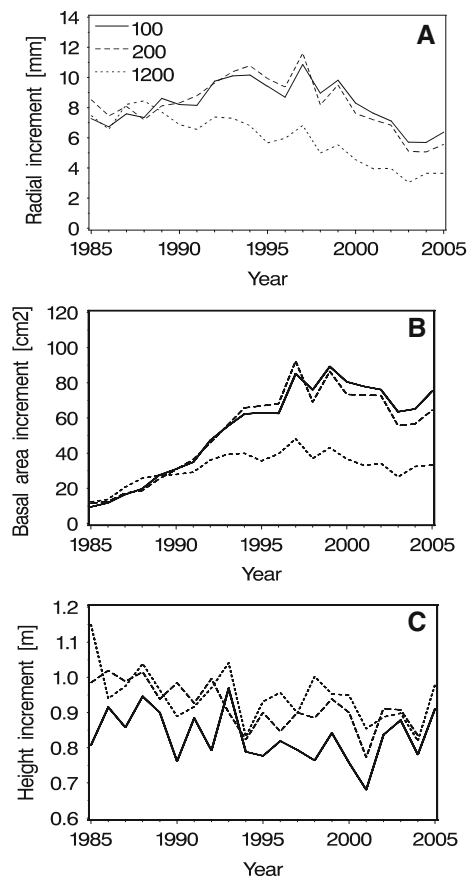


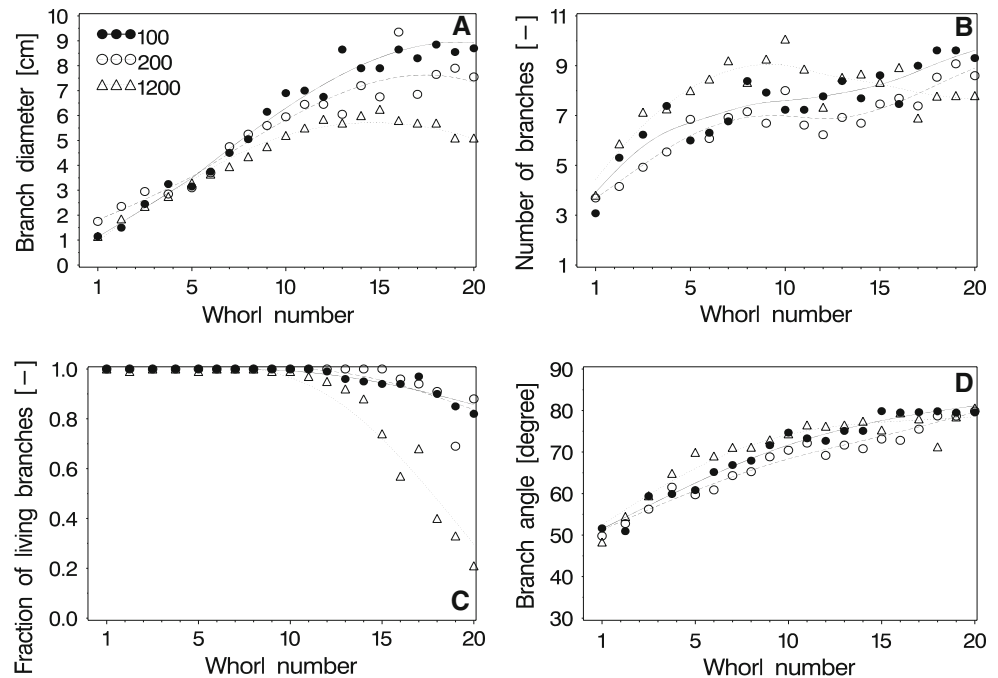
Fig. 1 Mean annual radial increments per year at breast height (a), basal area increments per year at breast height (b), and height increments per year (c) plotted against calendar year in stands with initial densities of 100, 200 and 1,200 trees ha^{-1}

between-tree variation was high and the differences between the treatments were not significant. In the uppermost crown (whorls 1–5 from the stem apex downwards), the maximum branch diameters did not differ among the treatments (Fig. 2a; Table 3). At lower parts of the stem, increasing stand density was associated with a decrease in branch diameter: deeper in the crown, all maximum diameter values differed significantly between the experiments. Only in the 1,200 ha^{-1} treatment did the maximum branch diameter clearly decrease again in the lowest part of the stem compared with the middle portion.

Number of living and dead branches

No clear trend in the total number of branches was found between the densities when moving from the stem apex downwards (Table 3). However, all the densities showed an increase in the total number of branches from the tree top to the whorl located downwards the crown (Fig. 2b). In the upper and middle crown (whorls 1–15) of trees from the 200 ha^{-1} density, a slightly lower total number of

Fig. 2 Diameter of the thickest branch (a), number of branches (b), fraction of living branches in a whorl (c) and branch angle (d) plotted against whorl number counted from the stem apex downwards in stands with initial densities of 100, 200 and 1,200 trees ha⁻¹. Interpolation (a): $y = a_1 \times x + a_2 \times x^2 + a_3 \times x^3$ where a_1 , a_2 and a_3 are parameters, (b–d): cubic smoothing spline – smoothing factor = (60 – 70 – 70)



branches was observed. However, the overall variability of the number of branches per whorl was high for all three densities (Table 3).

In the upper crown (whorls 1–10), almost all the branches were alive irrespective of stand density (Fig. 2c; Table 3). In the 1,200 ha⁻¹ density, the fraction of living branches started to be significantly lower from whorls 11–15 downwards to the crown base in comparison to the other densities. In the 100 and 200 ha⁻¹ densities, 90% of all branches were still alive at the whorls 16–20.

Branch angle

The angle of living branches increased from tree apex to the lower parts of the crown (Fig. 2d). The overall variability of branch angle was high for all three densities and the position within the crown (Table 3). Thus, branch angle differed between the densities only at whorls 16–20. At this height within the crown, branch angle was slightly lower at the 200 and 1,200 ha⁻¹ density compared to the 100 ha⁻¹ stand density.

The number of steeply inserted living branches (branch angle $\leq 45^\circ$; “spike knots”) was at a similar level among the three densities as there was no significant difference at any of the multiple paired comparisons. Similarly, no significant difference between densities was found for the insertion angle of the steepest branch per tree and its absolute height at the stem measured from the ground. The steepest inserted branch per tree was generally located around the upper and middle third within the crown

(Table 2). Again, the differences among the treatments were not statistically significant.

Stem wood growth efficiency

For all three densities the efficiency of stem volume production divided by sapwood area at breast height was examined in relation to current crown projection area (Fig. 3a). The ratio of stem volume and sapwood area at breast height of individual stems in relation to crown projection area appears to slightly decrease to some degree with decreasing stand density. However, trees from the 200 ha⁻¹ density showed slightly higher efficiency compared to the trees from the 100 ha⁻¹ density. Within observations from these two densities there was no clear trend of efficiency over crown projection area. The overall trend indicated that stem wood production could possibly be less efficient in more widely spaced stands. However, it should be noted that the data range of the crown projection areas did only overlap among the 100 and 200 ha⁻¹ stand density classes (Fig. 3a).

In contrast to stem volume production per sapwood area, the cumulative branch area (the total basal area of all living branches of a tree) per crown projection area appears higher in widely spaced stands (Fig. 3b). Likewise, the cumulative branch area per unit stem area was to some extent higher for widely spaced trees (Fig. 3c). However, similar to Fig. 3a (stem volume per sapwood area), the observations on branch area (Fig. 3c) provide no continuum from dense to widely spaced stands but show some

Table 3 Mean branch and whorl properties (minimum and maximum values in parenthesis) in different whorls along the stem counted from the stem apex downwards in stands with initial densities of 100, 200 and 1,200 trees ha⁻¹

Whorl	Branch diameter (cm) ¹			Number of branches (-)		
	100	200	1,200	100	200	1,200
1–5	1.7 ^a (0.6–3.3)	1.8 ^a (0.7–3.1)	1.7 ^a (0.6–3.3)	5.6 ^{ab} (0–17)	5.0 ^a (1–11)	6.4 ^b (0–17)
6–10	3.9 ^{ab} (2.2–6.9)	4.1 ^a (2.2–6.0)	3.7 ^b (2.1–5.2)	7.3 ^a (2–13)	7.0 ^a (2–16)	9.1 ^b (3–19)
11–15	6.1 ^a (3.7–8.7)	5.7 ^b (4.3–7.2)	4.7 ^c (2.2–6.3)	8.2 ^{ab} (2–15)	6.8 ^a (2–13)	8.3 ^b (3–18)
16–20	6.7 ^a (2.3–9.6)	5.9 ^b (4.9–9.4)	4.6 ^c (3.3–5.8)	8.6 ^a (2–18)	8.4 ^a (3–14)	7.8 ^a (4–14)

Whorl	Fraction of living branches (-)			Branch angle (°)		
	100	200	1,200	100	200	1,200
1–5	1.0 ^a (1.0–1.0)	1.0 ^a (1.0–1.0)	1.0 ^a (0.9–1.0)	58.8 ^a (25–90)	56.9 ^a (15–90)	58.4 ^a (10–125)
6–10	1.0 ^a (1.0–1.0)	1.0 ^a (1.0–1.0)	1.0 ^a (0.8–1.0)	70.6 ^a (15–110)	66.6 ^a (25–100)	70.9 ^a (10–120)
11–15	1.0 ^a (.7–1.0)	1.0 ^a (1.0–1.0)	0.9 ^b (0.1–1.0)	76.5 ^a (10–130)	72.4 ^a (20–100)	78.7 ^a (10–150)
16–20	0.9 ^a (0.6–1.0)	0.9 ^a (0.1–1.0)	0.5 ^b (0.1–1.0)	80.9 ^a (15–130)	78.4 ^b (20–120)	77.5 ^b (40–95)

Treatment means within a branch property in the same row marked with different letters (superscript) differ significantly ($P > 0.05$)

¹ Maximum branch diameter in each whorl

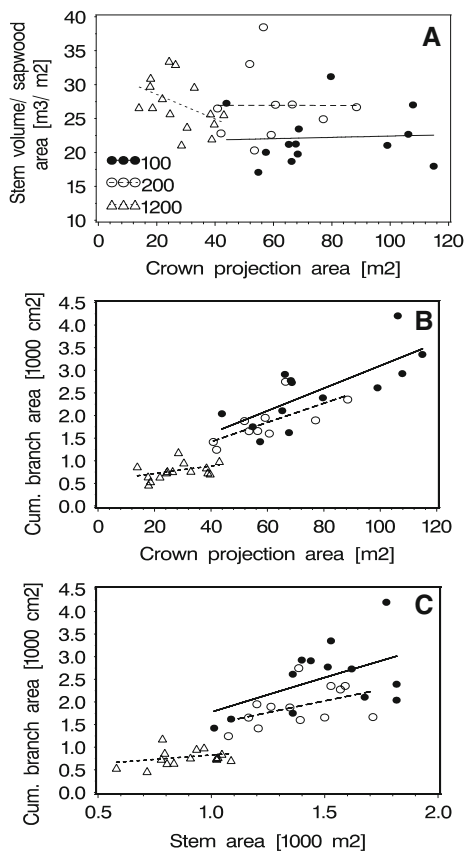


Fig. 3 Tree volume per tree sapwood basal area (a), and sum of basal areas of all living branches of a tree (b) plotted against current crown projection area. c Sum of basal areas of all living branches of a tree plotted against basal area of individual stems at breast height. Interpolation (a–c): $y = a_0 + a_1 \times x$ where a_0 , and a_1 are parameters

gaps. Thus, the results provide only circumstantial evidence that branch area per unit crown projection area is higher at lower stand densities. This means that a larger branch area was needed to yield a specific stem size at lower densities.

Sapwood area

Sapwood area decreased with higher position of the cross section within the stem (Fig. 4a). Generally, wide spaced trees showed larger absolute sapwood areas along the lower parts of the stem. At cross section ≤ 5 m, the sapwood area was smaller for the 100 ha⁻¹ versus the 200 ha⁻¹ density (Table 4). Between the 100 and 200 ha⁻¹ densities, significant differences in the absolute sapwood area were evident only at cross sections at breast height.

In general, the relatively young trees displayed rather high proportions of sapwood: half of the discs showed sapwood proportions (sapwood area relative to the whole stem area) exceeding 90% (Fig. 4b, Table 4). Along the stem, the sapwood proportion observed on the cross sectional discs increased from stem base to apex. The variability of the relative sapwood area was high for each of the densities. As there were no significant differences, no clear pattern between the densities could be derived from the tests.

Cumulative area of branches higher than the corresponding cross section of the sapwood area significantly increased with larger sapwood area (Fig. 4c). For discs with small absolute sapwood areas (i.e. in the upper crown), the relationship between sapwood area and

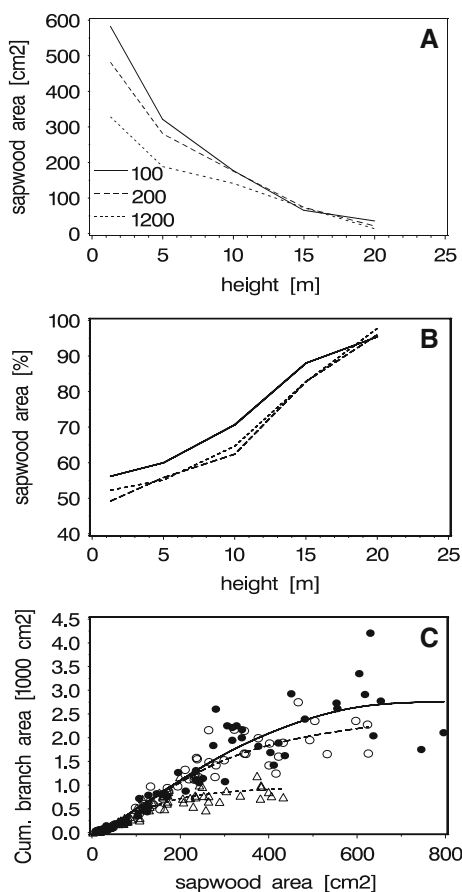


Fig. 4 Absolute sapwood area (a) and sapwood area relative to the total cross sectional area at 1.3, 5.0, 10.0–20.0 m height along the stem plotted against stem height, and sum of basal areas of all living branches of a tree above the stem cross section height plotted against the corresponding sapwood area per stem cross sectional cut (c), in stands with initial densities of 100, 200 and 1,200 trees ha⁻¹. Interpolation (c): cubic smoothing spline – smoothing factor = 70

cumulative branch area above the respective disc was rather consistent among the different density treatments. When moving downwards the stem at lower densities, the sapwood area was higher for the low densities compared to high densities.

Discussion

These density trials were established several years ago to highlight the importance of spacing on conifer growth and yield. In this analysis, the influence of density on important Douglas-fir stem and crown attributes was quantified and tested. In general, there were only a few tree and branch attributes that were significantly different between the 100 and 200 ha⁻¹ densities. The most important differences between these two densities were crown projection area, diameter of the thickest branch, and absolute sapwood area at breast height. The most obvious and significant differences in this study were between 100 and 1,200 ha⁻¹ densities, where nearly every examined tree and branch attribute were statistically significant. The variables that were not significantly influenced by density were tree age, the height to the lowest dead branch, several branch attributes, and relative sapwood area. Although the two lowest stand densities in this study are an extreme, these results still have important implications for the development of effective thinning regimes for Douglas-fir in south-western Germany.

Tree size and stem increment

Competition between trees is one of the strongest determinants of tree size and stem increment. The growth of trees in this study peaked approximately 8 years after the establishment of the experiment and has been declining (radial increment) or relatively steady (basal area increment) in the last 7 years. The mean basal area increment in the 100 and 200 ha⁻¹ densities has varied between 60 and 90 cm² in the last 10 years, which is indicative of these widely spaced trees being able to quickly utilize the growing space created by the thinnings. On the widest spaced plot, the crown diameter was nearly 10 m. This suggests that canopy is beginning to close and the dynamics of the stand will likely change as inter-tree competition increases.

Table 4 Sapwood properties (minimum and maximum values in parenthesis) at different heights along the stem measured from the ground in stands with initial densities of 100, 200 and 1,200 trees ha⁻¹

Height of stem disc (m)	Sapwood area (m ²)			Relative sapwood area (%)		
	100	200	1,200	100	200	1,200
1.3	582.6 ^a (114.4–795.8)	481.9 ^b (348.3–625.4)	328.4 ^c (229.0–432.9)	56.2 ^a (40.7–73.8)	49.2 ^a (38.6–62.2)	52.3 ^a (41.0–67.7)
5.0	321.1 ^a (234.7–422.1)	280.8 ^a (210.7–376.3)	188.5 ^b (129.5–264.4)	60.0 ^a (48.6–72.8)	55.8 ^a (42.6–67.8)	55.1 ^a (41.3–69.0)
10.0	177.3 ^a (103.5–301.0)	175.6 ^a (107.6–278.5)	141.1 ^a (101.1–207.2)	70.7 ^a (51.0–89.9)	62.4 ^a (44.1–75.8)	64.7 ^a (47.0–79.8)
15.0	65.2 ^a (15.2–127.5)	73.9 ^a (28.3–153.6)	72.5 ^a (30.3–108.2)	88.0 ^a (72.9–99.0)	82.8 ^a (71.0–90.9)	82.8 ^a (72.3–95.6)
20.0	35.6 ^a (23.2–48.0)	21.3 ^{ab} (10.5–37.3)	13.8 ^b (2.2–29.8)	95.4 ^a (93.4–97.4)	96.0 ^a (93.6–97.7)	97.7 ^a (94.8–99.9)

Treatment means within sapwood properties in the same row marked with different letters (superscript) differ significantly (P > 0.05)

The European norm for round wood grading of Douglas-fir allows for a maximum of 8 mm of average annual ring width for B-quality (“regular”) grade, while there is no limit on annual ring width for the C-quality grade (Anonymous 1998a). The mean radial increment in stands with initially 1,200 trees ha⁻¹ generally was below the 8 mm threshold, the very widely spaced stands with 100 and 200 trees ha⁻¹ initially exceed this threshold by a significant amount and peaked at almost 11 mm of mean radial increment. During the last 5 years of the observation, mean radial increment on the 100 and 200 ha⁻¹ densities has steadily declined and is now well below the 8 mm threshold. However, the majority of the log volume will be in the C-quality grade based on its mean ring widths.

From the point of view of ring width, trees from spacings close to the 1,200 ha⁻¹ density will not exceed the grading limits for B-quality. Similar findings have been reported by Weise et al. (2001). However, even at the 1,200 ha⁻¹ density, the mean radial increment exceeded the threshold of the best quality classes S13, S13K (\equiv C30) (6 mm) until 1997, but was close to the requirements of the quality classes S10 (\equiv C24) and S7 (\equiv C16) (both 8 mm) of German (S) and European (C) standards for classification of conifer sawn timber (Anonymous 1998b, c, 2003).

The rather large range of stand densities analyzed in this study had some significant effect on Douglas-fir height growth. This finding complements data obtained from a series of thinning experiments with Douglas-fir in south-western Germany as planting densities ranging from 500 to 4,000 trees ha⁻¹ had no significant impact on tree height even after almost 40 years of observation (Ehring and Kohnle 2006). We therefore hypothesize that only at the extremes significant differences (in our case: 100 vs. 1,200 ha⁻¹) can be found. This hypothesis is further corroborated by the result of Mäkinen and Hein (2006) obtained for widely spaced Norway spruce in south-western Germany and other studies in Douglas-fir (e.g. Curtis and Reukema 1970). In addition, the fact that in our sampling there is no location with all densities available, shows that we cannot fully elucidate such a pattern. Thus it is not surprising, that there is some controversial evidence from other experiments, that initial planting density may significantly alter Douglas-fir height growth patterns (Reukema 1979; Scott et al. 1998; Flewelling et al. 2001). For example, Reukema (1979) found that most of the effects of spacing on Douglas-fir height growth occurred after age 20 on a poor site in Washington, USA this might indicate, that a continued monitoring of the rather young plots in south-western Germany possibly will show at least some effects of stand density on Douglas-fir height growth in the future.

In contrast to tree height, spacing did have a significant influence on stem slenderness ($H/D_{1.3}$ -ratio) in our dataset.

In Douglas-fir stands, mean slenderness values above 80 are generally regarded to indicate a predisposition to wind and snow damage (Wilson and Oliver 2000). Although the slenderness increased with greater stand density, the vast majority of the sample trees were well below the 80 threshold. Actually, only two sample trees displayed values exceeding 80 and both trees grew on 1,200 ha⁻¹ density plots. This observation supports, at least to some extent, other findings with Douglas-fir that clearly demonstrate the provision of increased growing space by thinning results in reduced stem slenderness (Weise et al. 2001). This is assumedly associated with beneficial effects on stand stability.

Individual tree crown attributes were highly sensitive to stand density, even at a level between 100 and 200 trees ha⁻¹. For example, mean crown projection area and crown diameter were nearly 24 and 12% lower in the 200 ha⁻¹ density, respectively, when compared to the 100 ha⁻¹ despite having a similar crown ratio. Even at extremely low densities, the tree crowns had quickly filled the open spaces between trees and began to interlock. At the 200 ha⁻¹ density, this process has occurred and resulted in significantly smaller crown areas when compared to the 100 ha⁻¹ density. In addition, crown recession has initiated in all plots, regardless of density. These results suggest that although the trees at the lower densities are still widely spaced, the level of foliage biomass per tree has contributed to self-shading of their lower branches. Furthermore, the results clearly show, that although 200 Douglas fir ha⁻¹ might be justifiably regarded as “widely spaced” they certainly do not represent “open grown” trees. It remains to be clarified if a similar statement about the 100 trees ha⁻¹ plots can also be made.

Branch diameter

Branch diameter of Douglas-fir has been shown in earlier studies to be highly sensitive to silvicultural treatments (e.g. Kenk and Unfried 1980; Maguire et al. 1991; Schmidt 2001). Likewise in our study, branch diameter was significantly different between each of the stand densities examined in this study. However, these differences were only apparent in the lower half of the crown. Compared to the 1,200 ha⁻¹ density, mean branch diameters at whorls 16–20 were 45.6 and 28.3% larger in the 100 and 200 ha⁻¹ densities, respectively. The diameters of the branches were closely related to the diameter of the tree, which suggests that the general factors that promote tree growth are the same that influence branch growth.

The European standards for round wood grading of Douglas-fir allows only for up to 6 cm sound knots and less than 4 cm loose (dead) knots for B-quality, while C-quality may contain less than 8 cm sound knots and less than 6 cm

loose knots (Anonymous 1998a). Twenty-six trees of the 100/200 ha⁻¹ densities in this study exceeded the diameter limit of the B-quality log standards for living branches, but only one tree from the 1,200 density. However, as in this study, the relative position of the thickest branch within the crown was still close to the crown base (c.f. Table 2) where the thickest branches are still alive. Thus, even at the 1,200 density some further future increases in branch diameter can be expected. This clearly indicates that for Douglas-fir planted at the normally recommended densities in Europe, pruning as well as density management will be necessary to achieve the B-quality standard.

At the 1,200 ha⁻¹ density, the mean of the maximum branch diameter per tree (4.7 cm) was still within the threshold of the quality classes S7, S7K (\equiv C16) (assuming a square-shaped timber of 8 cm/ 18 m²) of German (S) and European (C) standards for classification of conifer sawn timber (Anonymous 1998b, c, 2003). This also indicates that for high quality sawn timber from a similar density, pruning will also be necessary. Furthermore, thinning regimes should target densities around 1,200 ha⁻¹ with artificial pruning to ensure good log quality. Thus, the conclusions of Kenk and Unfried (1980) as well as Weise et al. (2001) are supported by our results.

Number of living and dead branches

Although there were a few significant differences between densities in terms of number of branches, no general trends were apparent and there was a tremendous amount of variation within a given tree. In Douglas-fir, the number of branches has generally proven the most difficult branch attribute to predict accurately (Maguire et al. 1994; Weiskittel et al. 2007); a finding supported by the observations in our study. The number of branches is well correlated to the annual height increment of the stem (Maguire et al. 1994). Since our data do not indicate an influence of stand density on stem height increment, the lack of significant differences for the number of branches was expected. Likewise, Weiskittel et al. (2007) found the number of branches in Douglas-fir to be insensitive to Swiss needle cast disease, varying levels of vegetation control, pre as well as commercial thinning, or fertilization. In contrast, increased spacing resulted in a greater number of branches for some whorls in a 27-year-old Douglas-fir stand on Vancouver Island, British Columbia/CDN (Carter et al. 1986). It might be speculated, that a part of the large variation in number of branches observed in this study perhaps might be attributed to possible genetic differences between the installations. However, St Clair (1994) found relatively little genetic control for the expression of the variation of branch numbers in Douglas-fir.

The proportion of branches still alive at the time of measurement was fairly similar across the three densities examined in this study, except for the lowest four whorls. In these whorls, less than half of the branches were still alive in the 1,200 ha⁻¹ density, while the majority (>90%) were still alive in both the 100 and 200 ha⁻¹ densities. Even though the portion of living branches was still high between the whorls 16–20, this finding coincides with our observation of reduced crown width for the 200 ha⁻¹ density, where competition between neighboring trees has already started. This dynamic also has important implications for wood grading because it determines the ratio of loose to sound knots.

Branch angle

Branch angle has a major influence on lumber quality recovery as steeply inserted branches can cause several defects. In this study, no significant differences in branch angle were observed between the different densities, excepting that the 100 ha⁻¹ density displayed a significantly higher branch angle among the lowest four whorls. Given the high correlation between branch diameter and angle (Maguire et al. 1994), the finding that branches were generally flatter in the lower whorls of the 100 ha⁻¹ density simply reflects the presence of branches with significantly larger diameters observed in these same whorls. As branch diameter and branch length are very closely correlated (Kenk and Unfried 1980), large branch diameters are associated with long and thus heavy branches subjected to increased bending moments (gravity, lever).

Similar to the number of branches, high within-tree variability of branch angle was also observed in this study. In general, variation in Douglas-fir branch angle appears to be under little genetic control and this characteristic displays an almost negligible degree of heritability (St Clair 1994). In contrast, branch angles in whorls near the base of the tree can differ significantly among various Douglas-fir families (St Clair 1994). Douglas-fir branch angle has also been found to be insensitive to silvicultural treatments such as vegetation control, thinning or fertilization (Weiskittel et al. 2007). Furthermore, the study presented here indicates that this characteristic is also relatively insensitive to stand density.

Spike knots, large branches with an extremely low angle, are a serious defect in timber grading. For Norway spruce, Mäkinen and Hein (2006) found at the widest tree spacing (i.e. 350 ha⁻¹), that more than half of the Norway spruce trees in their study had at least one spike knot and the average number of spike knots was almost three times higher than at the higher stand densities. In contrast to these findings, our study on Douglas-fir resulted in similar number of spike knots across the three levels of stand

densities investigated. The reasons for these differences in the occurrence of spike knots between Norway spruce and Douglas-fir remain to be clarified. A potential explanation has been the definition for spike knots used here for Douglas-fir: the definition of a spike was solely based upon branch angle and branch diameter relative to other branches within a whorl was not considered in this analysis.

Stem wood growth efficiency

Measures on efficiency of stem wood production examine the relationship between growing space occupied by a tree and its size or increment (growing space efficiency, O'Hara 1988; Pretzsch and Schütze 2005). Our results suggest that trees from wide spacings tend to be slightly less efficient as these trees procured a lower stem volume/sapwood area ratio with crowns associated with relatively large projection areas. Similarly, the individual branches from widely spaced trees seemed to be less efficient compared to those from trees growing at higher stand densities, as a larger cumulative branch area was needed for a given stem basal area at breast height. When considering volume growth per sapwood basal area in Douglas-fir, O'Hara (1988) found tall trees with large crowns in unthinned stands to be the most efficient. In thinned stands, he found tall trees with medium sized crowns to be the most efficient and Douglas-fir thinned to very wide spacings proved relatively inefficient users of available growing space. Furthermore, analysis of volume increment per unit leaf area of Douglas-fir from mixed conifer stands (Gersonde and O'Hara 2005) showed a slow increase in growth efficiency in shaded understorey conditions, a peak for intermediate tree sizes in mid-canopy positions, and reduced growth efficiency in larger sized trees. Efficiency may also be altered by other effects like tree age, stand structure, site conditions or stress factors (O'Hara 1989; Gersonde and O'Hara 2005).

Sapwood area

Sapwood area is of special interest in both physiological and empirical growth and yield models as it links physiology to tree stem growth. For wood processing, the extent of sapwood and heartwood in a log is also important as they display different manufacturing properties (Bamber and Fukazawa 1985) and differ in their susceptibility to damage and decay (Wagenführ 2007). Sapwood area at crown base is strongly related to the photosynthetically active biomass of Douglas-fir tree crowns, often described by the total tree leaf area (e.g. Grier and Waring 1974; Waring et al. 1982; Espinosa Bancalari et al. 1987). Combinations of stem and crown attributes have performed well in predicting the sapwood area at crown base in Douglas-fir (Maguire and Hann 1989).

In our study, the extent of sapwood area was described longitudinally along the stem. Widely spaced Douglas-fir showed significantly larger absolute sapwood areas, particularly along the lower parts of the stem. Interestingly, if data on sapwood area were pooled from all three stand densities for analysis, sapwood area still increased from 5.0 m down to the 1.3 m stem section. This suggests that the few living branches at the crown base still contribute a small share to the tree net assimilation. Actually, sapwood area appears to increase even below the live crown (Waring et al. 1982). As we did not observe an effect of stand density on the cross-sectional sapwood proportion along the stem, the extent of sapwood appears to mirror stem taper quite well. From the modeling point of view, this offers a convenient approach for integrating a spatial heartwood model into a growth and yield simulator as part of a wood quality module.

Living branches carry the photosynthetically active biomass. Thus, the cumulative branch basal area was as expected related to the sapwood area along the stem. Dimensions of living branches thus might provide useful potential proxies for foliage mass or tree leaf area. Differences between densities at larger absolute sapwood area may indicate that at wider spacings the same sapwood area is able secure a sufficient water supply to a larger distal cumulative branch area. A potential explanation is the higher rate of sapwood conductivity in thinned stands because of larger earlywood/latewood ratios (Brix and Mitchell 1983). As the relationship between both measures is sufficiently strong, a model linking characteristics of living branches as provided by some tree growth and yield simulators to sapwood area could offer an alternative approach to modeling the extent of sapwood–heartwood transition in Douglas-fir.

Conclusions

The influence of three different spacings, 100, 200, and 1,200 ha⁻¹, on important tree- and branch-level attributes was examined for several replicated installations across south-western Germany. All individual tree attributes such as radial increment and crown projection area were significantly altered by density. Changes in the radial increment and branch size imposed by stand density caused significant downgrades in the potential product recovery in the widely spaced stands (<200 ha⁻¹). In addition, branch sizes on several trees in the 1,200 ha⁻¹ density did not fulfill the European quality requirement for the highest round wood category. This suggests that either planting at a higher density (>1,200 ha⁻¹) or pruning lower branches will be necessary to ensure a very high product recovery from current Douglas-fir stands in

south-western Germany. Also, residual thinning densities at young ages should be maintained over 200 ha⁻¹ to ensure that ring width and branch sizes will not negatively impact log quality.

Acknowledgments We thank Christian David Sagemüller, Dietmar Winterhalter and Klaus Freyler for the field work. We are also grateful to Olaf Drost for measuring annual radial increments. Thanks also to the Forest Research Institute of Baden-Württemberg together with the Ministry of Rural Space, Nutrition, Agriculture and Forestry for funding Aaron Weiskittel's travel to Germany.

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