Eur J Forest Res (2014) 133:1043–1056
DOI 10.1007/s10342-014-0821-7

ORIGINAL PAPER

Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) under acute drought stress in Southern Germany

Andreas Rais · Jan-Willem G. van de Kuilen · Hans Pretzsch

Received: 12 November 2013 / Revised: 15 May 2014 / Accepted: 20 May 2014 / Published online: 4 June 2014

Abstract Climate change in Central Europe may come along with acute drought stress, which can severely reduce growth and vitality of forest trees and whole stands. For a tree species such as Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) which is cultivated far beyond its natural range in Europe, knowledge of its behaviour under stress is crucial for the cultivation of Douglas-fir in view of a changing climate. Because of its easy accessibility, growth response to stress was mainly studied based on diameter growth at breast height. In long-term experiments on one dry and one moist site in Southern Germany, stem analyses of 133 mature and even-aged Douglas-firs were performed. The short-term growth reaction pattern under acute drought stress of 2003 had not only consequences on diameter but more pronounced effects can be observed when studying tree height: Respecting the different age trends by previous detrending, height increment only reacted more sensitive on the dry site. We also showed that extrapolating a particular decline in basal area increment to the whole stem can result in misunderstandings. However, results were less biased, when original data were smoothed or short-term assessment of volume growth was based on basal area measurements. By means of a linear mixed model approach, the influence of site, tree, and stand characteristics on Lloret's indices of resistance and resilience (Lloret et al. in Oikos 120:1909–1920. doi:10.1111/j.1600-0706.2011.19372.x, 2011) were analysed. For Douglas-fir, site played a crucial role and became more important considering the age trend. On the contrary, the positive influence of site quality on drought tolerance decreased with data processing. However, more growing space by thinning can advance tree resistance and resilience regarding height, diameter, and volume growth. Large individual crown volume improved the growth pattern under drought, and large stand density impaired it. Douglas-fir is obviously equipped with a morphological variability, which fosters lateral rather than vertical growth allocation under severe stress. Silviculture can mitigate stress through the choice of the site and through lower stand densities by thinning. Our refined stress response analysis confirmed a favourable growth and resilience of Douglas-fir even under extreme drought events.

Keywords Stress resilience · Stress resistance · Drought stress event · Morphological variability · Adaptation to climate change · Stress mitigation · Silvicultural prescriptions

Introduction

The retrospective analysis of tree growth based on annual rings before, during, and after stress periods is a suitable and abundant approach to assess drought tolerance of trees. Drought stress influenced tree growth at first, even more than physiological processes such as photosynthesis and

---

Communicated by Miren del Rio.

A. Rais (✉) · H. Pretzsch
Chair for Forest Growth and Yield Science, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
e-mail: rais@hfm.tum.de

A. Rais · J.-W. G. van de Kuilen
Holzforschung München, Technische Universität München, Winzererstrasse 45, 80797 Munich, Germany

J.-W. G. van de Kuilen
Faculty of Civil Engineering and Geosciences, TU Delft, Delft, The Netherlands

respiration (McDowell and Sevanto 2010). There is a long tradition in forest science to use diameter or basal area increment at breast height measured on increment cores or stem discs for assessing a tree's vitality and growth reaction to stress retrospectively. Basal area increment was used as sensitive indicator (Dobbertin 2005) in almost all studies on softwood (Pichler and Oberhuber 2007; Martínez-Vilalta et al. 2012; Zang et al. 2012) as well as on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Chen et al. 2010; Sergent et al. 2012). Basal area growth at breast height was a sensitive indicator of stress as previous investigations observed a low priority of carbon allocation to stem wood compared to fine roots or branches (Waring and Schlesinger 1985) and narrow and incomplete (Pollanschütz 1975; Elling 1993) or even missing tree rings (Rubner 1910; Elling 1993) in the lower part of the stem under stress. Within a tree, the sensitivity of radial growth to the climate decreased with stem height (Bouriaud et al. 2005). Kramer (1986) and Sterba (1996) showed growth declines mostly in the lower third of the stem during stress periods for softwoods such as Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and silver fir (*Abies alba* Mill.). Similar growth patterns were obtained for Norway spruce (*Picea abies* (L.) Karst.) under drought stress (Sohn et al. 2012) and under ozone stress (Pretzsch et al. 2010).

The behaviour of height growth under drought stress has rarely been investigated on individual mature trees of Scots pine (Mäkinen 1998) and Smith fir (*Abies georgei* var. *smithii*) (Wang et al. 2012). This is probably due to the fact that direct and accurate measurement of height increment of mature trees requires felling of trees (Hasenauer and Monserud 1997). Alternatively, young trees or seedlings of Douglas-fir were analysed for which height increment was easily measurable (Newton and Preest 1988; Olszyk et al. 1998). Height growth of most coniferous species is a complex two-year process involving the formation of terminal buds during late summer of the first year and shoot elongation during spring in the second year (Bréda et al. 2006), whereas radial growth was primarily driven by only current growing season precipitation (Feliksik and Wilczyński 2004; Zhang and Hebda 2004; Griesbauer and Green 2010) and more precisely by the occurrence of water limitation (Eilmann et al. 2013; Taeger et al. 2013). Mäkinen (1998) concluded that the predestination of shoot elongation and the weak connection with the current conditions reduced the suitability of height increment for describing the conditions during a specific growing season.

In line with expected changes in the climatic conditions (Schär et al. 2004), Douglas-fir is discussed to be part of forest management strategies in Germany (Spiecker 2010). Under favourable climatic conditions, Douglas-fir growth exceeded that of other softwood species and also under dry conditions indicated a clear advantage over native species such as Scots pine and European larch (*Larix decidua* Mill.) (Eilmann and Rigling 2012). The reasons are various: Douglas-fir as a softwood has small and sunken stomata, shedding and abundant leaf waxes, and—physiologically—an effective stomatal control mechanism (Lassoie and Salo 1981). Douglas-fir was also most resistant to cavitation as a consequence of drought compared to other Pinaceae (Pinol and Sala 2000).

Forest management must be adapted in order to respond effectively to climate change challenges and mitigation opportunities. In general, site characteristics have a large influence on the occurrence of water stress (Bauwe et al. 2011). Carnwath et al. (2012) considered site condition as an important silvicultural option and showed that Douglas-firs' basal area was more sensitive to water availability on xeric sites. There is still much debate as to how stand density or individual competitive situations—regulated by thinning or initial spacing—modify the growth reaction patterns of trees in dry years. For instance, thinning enhanced Douglas-fir growth of individual trees as a result of a longer growing period due to the absence of summer drought and higher rates of growth (Aussenac and Granier 1988). For other softwoods, thinning improved the tree radial growth under drought stresses (Laurent et al. 2003; Kohler et al. 2010). By wider spacing, silvicultural practice aims at increasing growth and stability of individual trees. This issue is even more relevant because recent forest management of softwood has moved towards wider initial spacings (Hein et al. 2007). Growing space and rooted soil volume, which have been developed for many years since seedling, seem to foster drought resilience (Sohn et al. 2012).

On the one hand, foresters and forest-yield researchers are interested in volume increment of individual trees and stands, because the economic value depends mainly on volume. On the other hand, radial (or basal area) growth is the preferred and considerable indicator of a change in tree vitality and forest productivity. However, is it acceptable to extrapolate a particular increment loss or acceleration at breast height to the whole stem or even to the whole tree? In order to clarify this, we did not only focus on the diameter growth of individual trees, but we also directly measured the height growth. Hence, we could assess the volume growth under drought stress more precisely. We further analysed which site, tree, and stand characteristics modify the impact of drought on tree increment. By using a framework presented by Lloret et al. (2011), we addressed the following questions:

1. Do height, basal area, and volume growth of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) react differently to drought stress?

Table 1 Tree and stand parameters

	Ansbach AN	Heigenbrücken HE
Sampled trees		
n	95	38
dbh without bark[a] (cm)	22.3 (*2.9*)	23.4 (*4.9*)
h[a] (m)	21.9 (*1.1*)	22.7 (*1.5*)
Stand characteristics for survey 1999		
n (ha^{-1})	690 (*28*)	692 (*14*)
d_g (cm)	23.1 (*1.5*)	22.3 (*1.2*)
SDI (ha^{-1})	787 (*85*)	835 (*87*)
h_0 (m)	21.4 (*0.4*)	22.2 (*0.5*)
BA (m^2 ha^{-1})	29.2 (*4.2*)	27.1 (*2.6*)
Total yield (m^3 ha^{-1})	420 (*49*)	440 (*22*)
Stand characteristics for survey 2004		
n (ha^{-1})	641 (*49*)	500 (*9*)
d_g (cm)	25.8 (*1.4*)	26.4 (*1.4*)
SDI (ha^{-1})	611 (*72*)	460 (*41*)
h_0 (m)	24.4 (*0.5*)	26.7 (*0.5*)
BA (m^2 ha^{-1})	33.7 (*4.4*)	27.5 (*2.8*)
Total yield (m^3 ha^{-1})	519 (*55*)	589 (*26*)

Mean value and *standard deviation* are in brackets

[a] For survey 2002; *n* = number of trees, *dbh* = diameter at breast height, *h* = height, d_g = basal area mean diameter, SDI = stand density index, h_0 = dominant height, BA = basal area of remaining stand, total yield = total volume production

Table 2 Site characteristics

	Ansbach AN	Heigenbrücken HE
Site characteristics		
Altitude above sea level (m)	460	415
Coordinates	N49°13′24.0″ E10°33′38.2″	N49°59′20.2″ E9°22′50.6″
Climate (growing season)[a]		
1998–2008 (excl. 2003)		
Temperature (°C)	15.6 (*0.4*)	15.3 (*0.5*)
Precipitation (mm)	346 (*106*)	379 (*41*)
2003		
Temperature (°C)	17.8	17.1
Precipitation (mm)	181	240
Soil		
Soil type	Sand (SI)	Loamy sand (lS)
Soil depth (cm)	30	>200

Mean value and *standard deviation* are in brackets

[a] Growing season is defined as May 1 to September 30

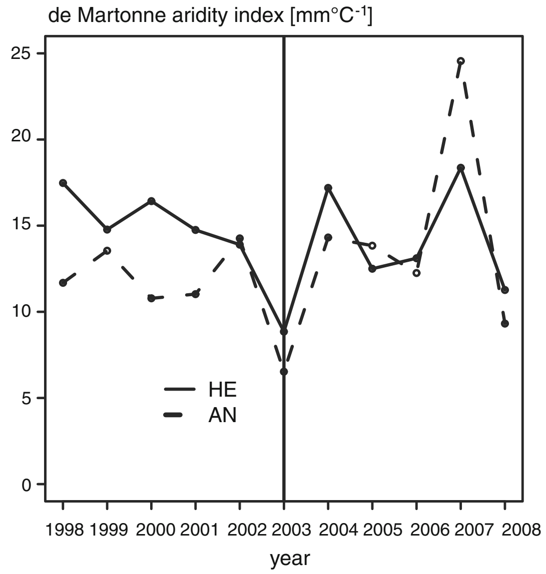


Fig. 1 The de Martonne aridity index—calculated from May to September—characterizes the climate in the growing season over time (de Martonne 1926)

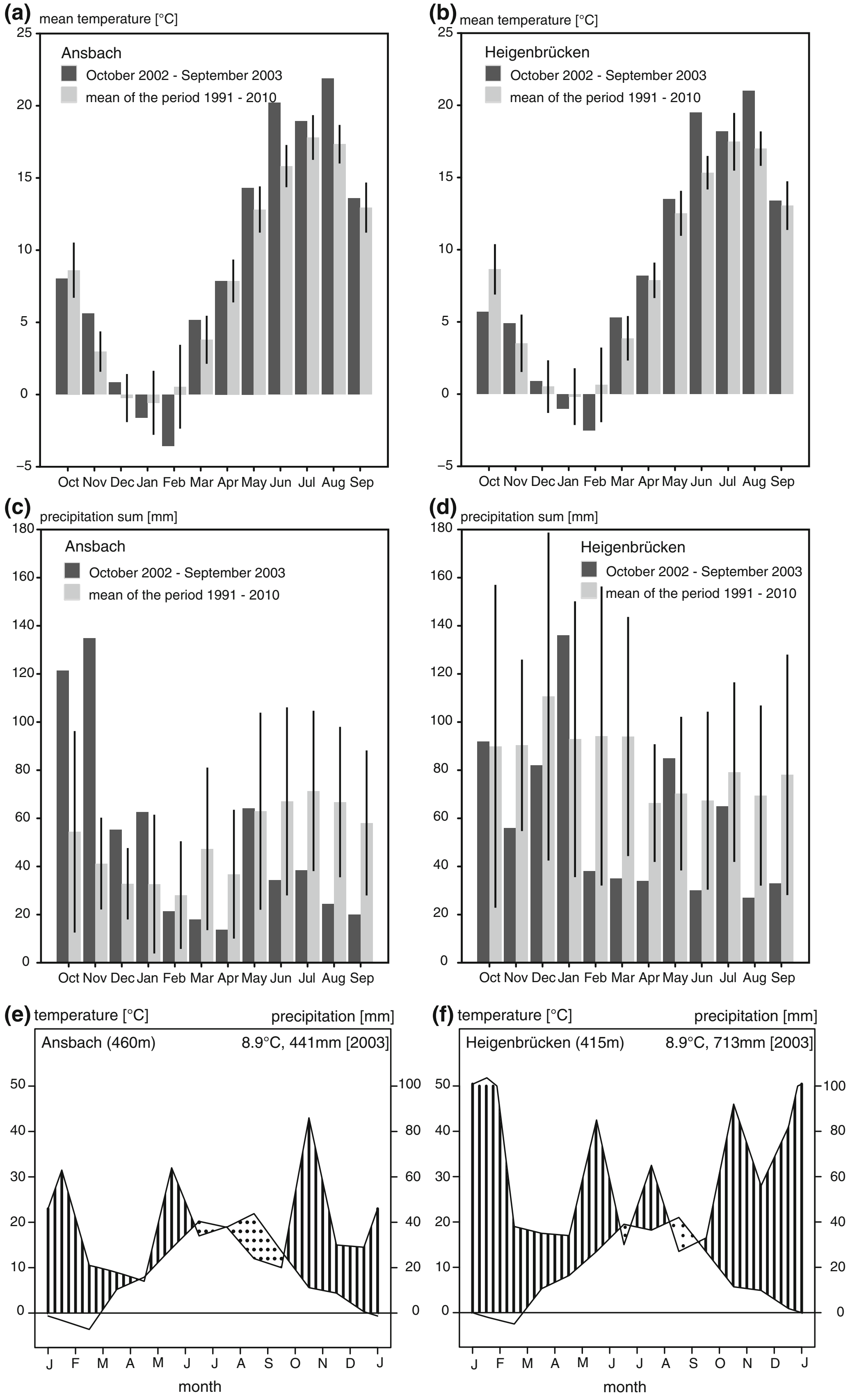
2. Which characteristics at the individual and at the stand level affect the growth response under drought stress?

Material and methods

Even-aged Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) thinning trees—selected by a forester—were removed in a thinning intervention in fall/winter 2010/2011. We sampled trees with a diameter at breast height of at least 25 cm with bark, in total 133. In 2003, the trees were about 30 years old. Table 1 gives an overview of the tree and stand describing parameters used.

The trees originated from two experimental trials in Bavaria. One site was located at Heigenbrücken (HE) next to the city of Aschaffenburg (North of Bavaria) in the low mountain range Spessart. The other site was located about 15 km south of the city of Ansbach (AN) or 50 km west of the city of Nuremberg. Table 2 summarizes important site characteristics. Both experimental trials were initiated at the beginning of the 1970s in order to comprehend the dependencies of growth on different spacing treatments. In fact, the experimental trials (HE and AN) are divided into smaller single plots at both sites. They are square-shaped with an edge length of 30 m and a buffer zone of 5 m around the plot. The sampled trees represented a wide range of managed Douglas-fir forests, because initial plant density differs within the single plots: 1,000, 2,000, and 4,000 trees per hectare. We did not take into account this kind of information, because preliminary analysis did not show any influence of initial plant density on growth under drought.

Figure 1 shows the modified de Martonne aridity index introduced by de Martonne (1926) and applied, for instance, by Uhl et al. (2013). We calculated this index between May and September over the observation period


(a) mean temperature [°C]
Ansbach
October 2002 - September 2003
mean of the period 1991 - 2010
25
20
15
10
5
0
−5
Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep
(b) mean temperature [°C]
Heigenbrücken
October 2002 - September 2003
mean of the period 1991 - 2010
(c) precipitation sum [mm]
Ansbach
180
160
140
120
100
80
60
40
20
0
(d) precipitation sum [mm]
Heigenbrücken
(e) temperature [°C]
precipitation [mm]
Ansbach (460m)
8.9°C, 441mm [2003]
J F M A M J J A S O N D J
month
(f) temperature [°C]
precipitation [mm]
Heigenbrücken (415m)
8.9°C, 713mm [2003]
J F M A M J J A S O N D J
month

◀**Fig. 2** Average monthly temperature for Ansbach (**a**) and Heigenbrücken (**b**), monthly precipitation sum separated into sites (**c**, **d**); within the year 2003, the *dotted area* is larger for Ansbach (**e**) than for Heigenbrücken (**f**)

1998–2008. This index is a ratio of the annual precipitation (in mm) and the sum of annual mean temperature (in °C) and a summand of ten. On both sites, drought occurred in 2003. Drought was more severe at AN.

Figure 2a, b presents the average monthly temperature for the period from autumn 2002 to autumn 2003 and for a reference period. Similarly, charts were prepared for the monthly precipitation sum separated into the two sites (Fig. 2c, d). A promising approach was introduced by Walter and Lieth (1967) which summarizes temperature and precipitation information and indicates water availability (Fig. 2e, f). Monthly water availability is graphically displayed as precipitation sum (in mm) divided by two, minus average monthly temperature (in °C). Negative values indicate water deficit illustrated by dots, and positive values indicate water surplus illustrated by vertical lines. The dotted area of the Walter and Lieth climate diagram (when the temperature line runs above the precipitation line) clarifies the longer dry periods for AN from June to September of 2003.

The competitive situation of an individual tree was described by the $\mathrm{SDI_{local}}$ (Pretzsch and Biber 2010). They defined the competition situation by means of a modified local version of the original stand density index SDI (Reineke 1933). The modified $\mathrm{SDI_{local}}$ was calculated for a subcollective of taller trees only in the proximity of the tree of interest, as this area includes its most important competitors. In particular, all neighbouring trees of a tree were considered with a distance of less than twice its mean crown radius. Each tree had on average four competitors. Thinning was performed according to a standardized experimental programme described by Klädtke et al. (2012): when dominant height reached 12 m, a number of 150 future trees was selected. Thinning type was defined as a final crop-tree system. Thinning frequency was determined by the dominant height. A guide curve gave the number of thinning trees per hectare depending on the dominant height. In the past, thinning was done in autumn/winter of 1989, 1994, 1999, and 2004. For this study, the intensity of thinning was quantified by the ratio between $\mathrm{SDI_{local}}$ before thinning and $\mathrm{SDI_{local}}$ after thinning, respectively: the higher the ratio, the higher the competition release. Furthermore, we calculated a ratio between height of the particular tree and its five nearest neighbours to explain the social situation (social class) of an individual tree. The crown volume was calculated based on measured crown length (height—crown base height) and crown projection area assuming that the crown shape is simply described by a cone.

Annual increment of height, basal area, and volume

After felling, the current annual increment of height (CAI_h) was measured along the main trunk from the top downwards as the distance between branch whorls to an accuracy of ±2.5 cm. The 133 discs at breast height were polished on a sanding machine using sandpaper with a coarseness of 60–120 grids. Tree-ring width was measured to the nearest 1/100 mm in the four cardinal directions (deviations due to the presence of branches or fissures possible) with a Digital Positiometer (Kutschenreiter and Johann; Digital positiometer, Biritz and Hatzl GmbH, Austria) using the software Lignometer. Crossdating accuracy was checked visually within (four time series per disc) and between ring-width time series. Due to the short period considered, we refrained from using COFECHA (Holmes 1983) as recommended by many long-time investigations. Besides, annual rings of the sampled Douglas-fir stem discs were clearly identifiable. Because of their low percentage of latewood, the annual rings of 2003 were especially obvious. The basal area was calculated by means of quadratic mean radius of the four cardinal directions. The difference between the basal areas of two consecutive years gave the current annual increment of basal area ($\mathrm{CAI_{ba}}$). We applied a generalized constant form factor of 0.5 to reduce the volume of a cylinder to tree volume ($v = h \times d^2/4 \times \pi \times 0.5$). As the form factor changes very sluggishly with tree size development and our analysis was restricted to a rather short part of tree ontogeny, we assumed it as constant. The difference of two subsequent tree volumes results in the current annual increment of volume (CAI_v).

Height, basal area, and volume increment culminate at different ages and vary in their curve shape. Therefore, we chose the moving average as smoothing, because it was best suited to consider short-term deviations (Riemer 1994; Schlittgen and Streitberg 1997; Pretzsch 2010). Individual series were detrended by Eq. 1:

$$I_q = \frac{\mathrm{CAI}_q}{Y_q} \tag{1}$$

The parameter I_q is the relative growth index of q (height, basal area, or volume). CAI_q is the original (measured) increment, and Y_q is the increment calculated by moving average value of 5 years (the year itself, two previous years, and two subsequent years). The resulting index curves I_h, I_{ba}, and I_v were free of age trends. Figure 3 illustrates the method of detrending for the basal area increment of an individual tree.

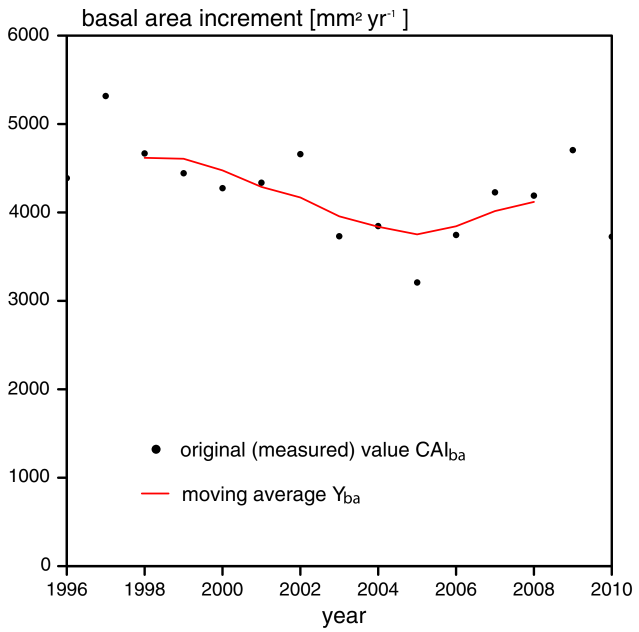


Fig. 3 Original data were smoothed by five-year moving average

Lloret's indices R_t and R_s for quantifying stress response

For comparing the performance of trees with intra-specific environment under episodic drought stress, we applied the numerical indices for resistance R_t and resilience R_s introduced and explained in detail by Lloret et al. (2011). R_t and R_s were calculated individually on the basis of CAI_h, $\mathrm{CAI}_{\mathrm{ba}}$, and CAI_v as well as on the basis of the detrended data I_h, I_{ba}, and I_v for all individual trees. The basic components of the indices were the following:

- PreDr is the mean mid-term increment in a period of 5 years before the drought period.
- Dr is the increment in the year of drought 2003 (shoot formation itself is a two-year process—bud formation during late summer of the first year and shoot expansion during spring/early summer in the second year. Describing the height pattern, Dr is the mean increment in the years 2003 and 2004).
- PostDr is the mean increment in a period of 5 years after the drought period (regarding height only a period of 4 years after the drought period).
- R_t = Dr/PreDr is the resistance and quantifies the decrease from the pre-drought period (5 years: 1998–2002) to the drought period. The case of $R_t = 1$ means complete resistance; the more the value falls below 1, the lower the resistance.
- R_s = PostDr /PreDr is called resilience and represents the ratio between post-drought (5 years: 2004–2008 for basal area and volume, 4 years: 2005–2008 for height) and pre-drought increment. $R_s \geq 1$ indicates full recovery or even an increase after the episodic stress, while values of $R_s < 1$ indicate growth decline and low resilience.

Linear mixed models were performed to verify whether R_t or R_s were related to any of the following explanatory variables: site, stand density (SDI), intensity of thinning (1999 and 2004), crown volume, competition ($\mathrm{SDI}_{\mathrm{local}}$), and social class. The models to be fitted were then formulated as

$$\begin{aligned} R_t = {} & a_0 + a_1\mathrm{site} + a_2\mathrm{SDI} + a_3\mathrm{thinning}_{1999} \\ & + a_4\mathrm{crown\ volume} + a_5\mathrm{SDI}_{\mathrm{local}} + a_6\mathrm{social\ class} \\ & + b_i + \varepsilon \\ R_s = {} & a_0 + a_1\mathrm{site} + a_2\mathrm{SDI} + a_3\mathrm{thinning}_{1999} \\ & + a_4\mathrm{thinning}_{2004} + a_5\mathrm{crown\ volume} + a_6\mathrm{SDI}_{\mathrm{local}} \\ & + a_7\mathrm{social\ class} + b_i + \varepsilon \end{aligned}$$

where i indexed the plot and a_0, a_1, a_2, a_3, a_4, a_5, a_6, and a_7 were the fixed effect coefficients to be estimated. The explanatory variable site (Ansbach, Heigenbrücken) was of categorical type and dummy coded, and the other variables were covariates (quantitative predictors). Additionally, we took into account interactions between site and the remaining explanatory variables.

Beyond these fixed effects, random effects were considered to match the error structure of the data. The parameter b_i was a nested random effect at plot level (Pinheiro and Bates 2000; Zuur et al. 2009). The random effects were assumed to be normally distributed with zero mean and constant variance. This nesting-level specific variance was estimated during the model fitting process. The symbol ε represented the independent and identically distributed random error.

The statistical method included three steps: first, the Akaike information criterion (AIC) was used as fitting criterion for selecting the best (multiple) linear model (Burnham and Anderson 2002). This model simplification procedure was carried out to obtain the adequate model. The model with the lowest AIC was selected and used for further analysis. It was also tested whether this model performed better than a model including only random effects. Second, the fixed and random effects of the selected model were estimated, and third, the significance level of each effect was calculated.

All data were analysed using R (R Development Core Team 2012) and the R package *lme4* (Bates and Maechler 2009) and *languageR* (Baayen 2008). The default behaviour of *lmer* to optimize the maximum likelihood criterion ML was used (Pinheiro and Bates 2000). Normality and homogeneity were checked by visual inspections of diagnostic plots of residuals against fitted values (Zuur et al. 2009, 2010).

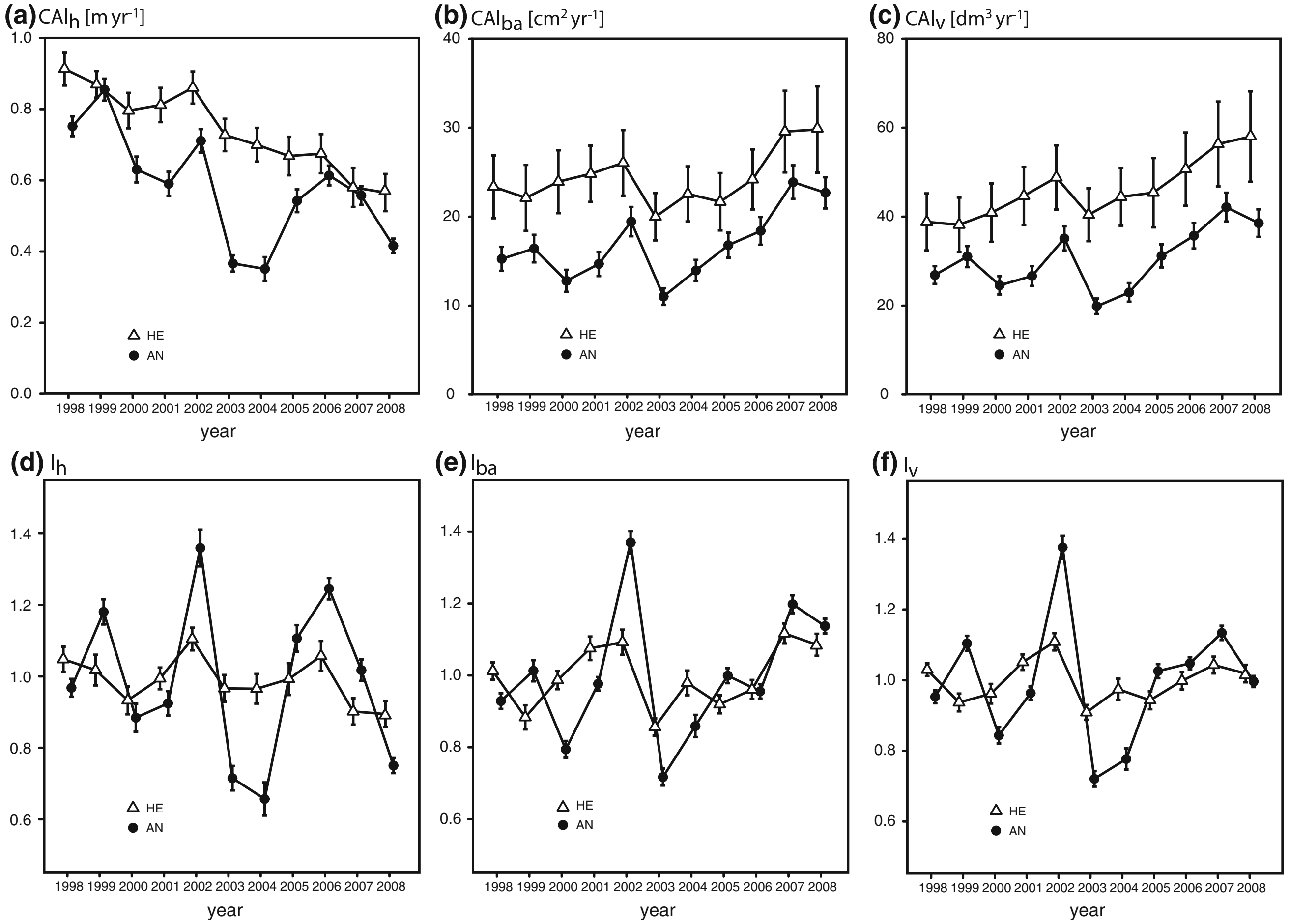


Fig. 4 Current original annual increment of height CAI_h (m yr^{-1}) (**a**), basal area $\mathrm{CAI}_{\mathrm{ba}}$ (cm^2 yr^{-1}) (**b**), and volume CAI_v (dm^3 yr^{-1}) (**c**) as well as current detrended annual increment of height I_h (**d**), basal area I_{ba} (**e**), and volume I_v (**f**) mean with twice *standard error* bars for 133 Douglas-fir trees from two sites AN (*circle*) and HE (*triangle*)

Results

The current annual increment of height CAI_h, basal area $\mathrm{CAI}_{\mathrm{ba}}$, and volume CAI_v in the period 1998–2008 is shown for both sites HE and AN (Fig. 4a–c). The level of all three kinds of CAI was always higher for HE. The CAI_h—averaged per tree and over the reference period of 11 years (1998–2008)—was 0.58 m yr^{-1} for AN and 0.74 m yr^{-1} for HE. For the drought year 2003, mean CAI_h slumped to 0.37 m yr^{-1} (AN) and 0.73 m yr^{-1} (HE). The course of $\mathrm{CAI}_{\mathrm{ba}}$ remained rather constant during the observation period; on average, it was 16.9 cm^2 yr^{-1} for AN and 24.4 cm^2 yr^{-1} for HE. In 2003, $\mathrm{CAI}_{\mathrm{ba}}$ was 11.0 cm^2 yr^{-1} for AN and 20.0 cm^2 yr^{-1} for HE on average over all 133 trees. A similarly synchronous behaviour was observed between the two sites for CAI_v. The mean CAI_v for AN was 19.9 dm^3 yr^{-1} in 2003 and 30.4 dm^3 yr^{-1} for the 11-year reference period, analogous for HE 40.5 and 46.1 dm^3 yr^{-1}.

The current detrended annual increment of height I_h, basal area I_{ba}, and volume I_v varied more widely (Fig. 4d–f). Standard deviations of the 11 (mean) annual indices I_h, I_{ba}, and I_v were higher for AN (0.23, 0.19, and 0.18) than for HE (0.07, 0.09, and 0.06). Looking at the site AN, the high increment of 2002 and the deep descent of the following year 2003 are clearly visible.

Table 3 shows two aspects of tree tolerance to drought-induced low-growth periods: the resistance R_t as the growth performance during the drought and the resilience R_s as ability to return to the pre-drought growth level. At site AN, growth declined more severely. The height growth was strongly reduced in 2003 and reached only half of the previous period ($R_{t,h}$, original). In 2003, the basal area increment was 73 % ($R_{t,\mathrm{ba}}$, original) compared to the previous period, and the volume increment was 69 % ($R_{t,v}$, original). Consequently, volume growth decline ($R_{t,v}$, original) was 4 % higher than the basal area growth decline

Table 3 Resistance R_t and resilience R_s of height, basal area, and volume growth divided into site

	Original		Detrended	
	HE	AN	HE	AN
$R_{t,h}$ (−)	0.84 (*0.02*)	0.51 (*0.02*)	0.95 (*0.01*)	0.65 (*0.02*)
$R_{t,\mathrm{ba}}$ (−)	0.86 (0.04)	0.73 (*0.03*)	0.85 (*0.01*)	0.71 (*0.01*)
$R_{t,v}$ (−)	0.98 (*0.03*)	0.69 (*0.02*)	0.89 (*0.01*)	0.69 (*0.01*)
$R_{s,h}$ (−)	0.73 (*0.02*)	0.76 (*0.02*)	0.94 (*0.01*)	0.97 (*0.00*)
$R_{s,\mathrm{ba}}$ (−)	1.17 (*0.10*)	1.32 (*0.05*)	1.00 (*0.01*)	1.01 (*0.01*)
$R_{s,v}$ (−)	1.23 (*0.06*)	1.21 (*0.03*)	0.98 (*0.01*)	0.95 (*0.01*)

Mean value and *standard deviation* are in brackets

($R_{t,\mathrm{ba}}$, original). Without the age trend, the difference decreased between height, basal area, and volume, but height increment remained most affected by drought ($R_{t,h} < R_{t,\mathrm{ba}}$, detrended). At site HE, growth in 2003 seemed to be similar to the growth in previous periods (R_t, original). The highest growth decline with an average of 16 % was observed for height; for volume, the decline was only 2 %. Volume growth decline of 2003 ($R_{t,v}$, original) was about 10 % less than the basal area growth decline ($R_{t,\mathrm{ba}}$, original). Considering the age trend, the order between height and basal area changed: $R_{t,\mathrm{ba}}$ was most reduced (0.85); $R_{t,h}$ lost only 5 % of increment compared to the height increment of the previous period (detrended data).

With respect to the stress resilience (R_s), the differences between the sites were smaller (Table 3). The mid-term height growth of HE decreased by 27 % (original). Some of this reduction can be attributed to the decreasing age-related curve of the individual current annual height increment CAI_h (Fig. 4a), which was confirmed by $R_{s,h}$ (0.76) calculated by the detrended height data $\mathrm{I_h}$. Considering basal area and volume increment, a complete and mid-term recovery was observed ($R_{s,\mathrm{ba}}$ and $R_{s,v} > 1$, original). Contrary to current annual height growth, the culmination of the individual current annual increment of basal area ($\mathrm{CAI_{ba}}$) and of volume (CAI_h) has not been reached. Bearing in mind the age trend, $R_{s,\mathrm{ba}}$ and $R_{s,v}$ were close to one (detrended).

The selected models with the lowest AIC values are shown in Table 4 for the original data and in Table 5 for the detrended data, respectively. Predictors with a p value lower than 0.05 are in bold.

Original data

Primarily, thinning modified growth depression in the year of the drought event and also reduced drought stress at least for some years—whether for height, basal area, or volume growth (Table 4). Furthermore, site and SDI significantly influenced $R_{t,h}$, and crown volume significantly influenced $R_{s,h}$ and $R_{s,v}$. We observed a change in significant predictors: Large crown volume influenced the stem growth under

Table 4 Original data: resistance, R_t, and resilience, R_s, as modified by site, tree, and stand characteristics

	$R_{t,h}$	$R_{t,\mathrm{ba}}$	$R_{t,v}$	$R_{s,h}$	$R_{s,\mathrm{ba}}$	$R_{s,v}$
Intercept a_0	+1.05	+0.74	+0.66	+0.36	−0.76	+0.02
Site[a]	$\mathbf{-0.32}$***		−0.19		+1.03	+1.05
SDI (trees^{-1} ha)	$\mathbf{-0.08 \times 10^{-2}}$**	-0.07×10^{-2}	-0.06×10^{-2}			
Thinning, 1999 (trees ha^{-1}/trees ha^{-1})		$\mathbf{+0.36}$***	$\mathbf{+0.24}$***	$\mathbf{+0.14}$**	$\mathbf{+0.40}$**	$\mathbf{+0.37}$***
Thinning, 2004 (trees ha^{-1}/trees ha^{-1})					$\mathbf{+1.02}$***	$\mathbf{+0.31}$**
Crown volume (m^{-3})				$\mathbf{+0.07 \times 10^{-2}}$***		$\mathbf{+0.14 \times 10^{-2}}$*
$\mathrm{SDI_{local}}$ (trees^{-1} ha)				$+0.01 \times 10^{-2}$		
Social class (mm^{-1})	+0.28		+0.29			
Interactions[a]						
Site × thinning, 1999 (trees ha^{-1}/trees ha^{-1})			−0.01		+0.45	+0.13
Site × thinning, 2004 (trees ha^{-1}/trees ha^{-1})					−1.09	−0.97
Site × crown volume (m^{-3})						$+0.13 \times 10^{-6}$
b_i (σ^2)	0.002	0.009	0.004	0.006	0.018	0.006
ε (σ^2)	0.02	0.04	0.02	0.02	0.18	0.07
AIC	−154.7	−31.2	−113.9	−141.5	176.9	52.8

Results of the mixed model analysis

[a] Site HE is the reference; significance level *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 5 Detrended data: resistance, R_t, and resilience, R_s, as modified by site, tree, and stand characteristics

	$R_{t,h}$	$R_{t,\mathrm{ba}}$	$R_{t,v}$	$R_{s,h}$	$R_{s,\mathrm{ba}}$	$R_{s,v}$
Intercept a_0	+0.90	+0.80	+0.89	+1.01	+1.25	+1.05
Site[a]	$\mathbf{-0.44}$***	$\mathbf{-0.26}$***	$\mathbf{-0.21}$***	+0.04	−0.03	$\mathbf{-0.07}$*
SDI (trees^{-1} ha)				$\mathbf{-0.03 \times 10^{-2}}$***	$\mathbf{-0.03 \times 10^{-2}}$*	−0.0002
Thinning, 1999 (trees ha^{-1}/trees ha^{-1})	+0.03	+0.03	$\mathbf{+0.24}$***	+0.02	+0.03	$\mathbf{+0.03}$*
Thinning, 2004 (trees ha^{-1}/trees ha^{-1})					$\mathbf{+0.05}$*	
Crown volume (m^{-3})					$+0.03 \times 10^{-2}$	
SDI$_{\mathrm{local}}$ (trees^{-1} ha)						
Social class (mm^{-1})			+0.29	0.11	$\mathbf{-0.21}$*	
Interactions[a]						
Site × thinning, 1999 (trees ha^{-1}/trees ha^{-1})	0.11		−0.01	+0.002	+0.06	$\mathbf{+0.04}$*
Site × thinning, 2004 (trees ha^{-1}/trees ha^{-1})					+0.03	
Site × crown volume (m^{-3})					−0.0001	
b_i (σ^2)	0.001	0.004	0.002	0.001	0.0005	0.0003
ε (σ^2)	0.02	0.01	0.01	0.002	0.003	0.001
AIC	−138.5	−200.7	−226.2	−440.1	−369.5	−457.0

Results of the mixed model analysis

[a] Site HE is the reference; significance level *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

drought positively, but did not affect basal area growth. We also scrutinized each model for interactions, because, for instance, due to a storm in winter of 1999, the thinning degree of 2004 was much lower at the site AN (Table 2, stand characteristics for survey 2004). However, by means of a powerful statistical analysis, the large degree of variation within the explanatory variables was considered. No significant interactions were found.

Detrended data

Table 5 shows the results for R_t and R_s using detrended data. The site gained in importance, as it was significant for $R_{t,h}$, $R_{t,\mathrm{ba}}$, $R_{t,v}$, and $R_{s,v}$. The results showed that the growth of Douglas-fir at the site AN with more severe drought suffered more. Compared to the original data (Table 4), thinning became less important, but had still a positive impact on volume increment ($R_{t,v}$ and $R_{s,v}$). On the site of AN (more severe drought), thinning of the year 1999 was twice as important as on the site HE (0.03 + 0.04). The basal area increment of Douglas-fir trees which were thinned in 2004 grew more ($R_{s,\mathrm{ba}}$)—also without the increasing age trend. Simultaneously, recovery of basal area increment ($R_{s,\mathrm{ba}}$) was higher for trees with lower social status. The stand density SDI had a negative effect on $R_{s,h}$ and $R_{s,\mathrm{ba}}$: the higher the SDI, the lower the recovery.

Discussion

The analysis emphasized the relevance and key role of data processing. Annual height, basal area, and volume increment have different growth patterns at the same age. In a first step, we used untransformed data for analysing R_t and R_s as done by Pretzsch et al. (2013) and Taeger et al. (2013), although height, basal area, and volume increment culminate at different ages and vary in their curve shape. So we stayed as close as possible to the originally measured data and avoided nontransparency of the results by trend elimination and indexing. The possible bias by using the original data was assumed to be small due to the short period considered (Pretzsch et al. 2013). In general, R_s was assumed to be more influenced than R_t, because, in fact, a time interval of 11 years was considered for R_s, but only of 6 years for R_t. Consequently, the natural curve shape of the current annual increment might become more important for R_s: We hypothesized that Douglas-fir height growth course has already culminated and the development of CAI$_h$ decreases throughout the period considered (Fig. 4a). On the contrary, CAI$_{\mathrm{ba}}$ and CAI$_v$ increased slightly within the period between 1998 and 2008. In a second step, we kept in mind the still increasing (natural) course of CAI$_{\mathrm{ba}}$ and CAI$_v$ and the already decreasing course of CAI$_h$: we detrended the original data before calculating the Lloret's indices. The discussion deals with this aspect of data processing.

Stress response of height versus basal area and volume increment

In general, allocation and resulting tree allometry can be modified by stress (Lassoie and Salo 1981). Our analysis revealed different behaviours of height and basal area increment during drought stress. Particularly, during a period of high drought stress like at the site AN, height growth seems to be a more sensitive indicator of vitality than basal area growth—both using original and detrended data. Other studies emphasized the lower sensitivity of the upper part of the trunk to drought based on basal area measurements at different height levels (Sterba 1981; Bouriaud et al. 2005). Our investigation verified those results only for the detrended data for the site HE which was characterized by lower water stress. A possible explanation for the stronger decline of height versus basal area increment might be the occurrence of water stress within the vegetation period. Another explanation might be the restricted water transport to the upper tree parts that reduces growth. In addition, the tree might change its allocation pattern from crown expansion and carbon assimilation—which is mainly achieved by height development—to root extension in order to capture additional water and thus reduce the growth limiting factor (Sharp 2002; Pretzsch et al. 2010). This would be in line with the optimal partitioning theory that a plant always invests in those organs which improve access to the currently limiting resource (McCarthy and Enquist 2007). For instance, light limitation enhanced shoot growth in relation to root growth (Oliver and Larson 1996).

The level of observed basal area growth reduction was consistent with that of Sergent et al. (2012) who found for French Douglas-fir—depending on the site—a reduction of 20–30 % in 2003 compared to the previous years' growth. However, conclusions extrapolating a particular decline in increment at breast height to the whole stem can result in misunderstandings depending on the site: based on the original data, an overestimation of 4 % of the stem growth decline at the dryer site (AN, R_t) and an underestimation of 12 % of the stem growth decline at the moister site (HE, R_t). Results were also biased, when short-term assessment of growth reactions was only based on original height measurements ($R_{t,h}$ vs. $R_{t,v}$): height decline underestimated stem growth decline at both sites by 12 % (HE) and 18 % (AN). When we look at the resilience to drought stress (R_s, original data), the average four-year height growth of the subsequent period was 73 and 76 % of the previous period ($R_{s,h}$). We found that $R_{s,h}$ underestimated $R_{s,v}$ in a dry stand by 45 %, in a moist stand by 50 %. The basal area defined the volume much more precisely, but—depending on the site—too low (6 %) or too high (11 %). When we transferred the decline in increment at breast height to the whole stem based on detrended data, the situation changed considerably. We observed in all cases for both height and base area increment, deviations from the volume increment equal to or less than 6 %.

Modification of stress response by site, thinning, tree, and stand characteristics

Site, stand density, thinning, individual crown volume, and social class can affect growth response under drought stress (Pretzsch and Dieler 2011). Site played a crucial role in our investigation. A clear relationship existed between growth and soil water deficit for Douglas-fir (Sergent et al. 2012). Precipitation sum appeared to be the most differentiated climatic factor between sites AN and HE and probably was the main reason for the significance of site (Tables 4, 5). Feliksik and Wilczyński (2007) investigated increment cores of different Douglas-fir stands in western and northern Poland and found an interregional variation in tree-ring chronologies mainly determined by air temperature for January–March and by precipitation sum for June–August. Douglas-fir growth seems to be mainly sensitive to the pluvial conditions of summer (June–August). Kantavichai et al. (2010) associated soil moisture content with wood quality. Analysing 76-year-old Douglas-firs from Western Washington, they found that July soil moisture deficit was an important predictor for wood density of annual growth rings. This is very interesting, because many aspects are linked to wood density: on the one hand, wood density was a commonly used predictor and indicator of wood quality (Rais et al. 2014). Although we did not measure early and latewood width separately, the small latewood width in 2003 was very obvious and most helpful for visual cross dating and synchronization. Growth response of Douglas-fir in 2003 was distinct in latewood since rainfall was low in the latewood forming months June–September (Eilmann et al. 2013). On the other hand, wood density was also responsible for the survival of trees during severe droughts. Martinez-Meier et al. (2008) analysed the behaviour of wood density to the 2003 drought by means of about 40-year-old Douglas-firs from provenance trial in France and observed for the surviving trees higher wood density at tree ring and tree level. In our analysis, the low penetrable soil depth for roots (about 30 cm, Table 2) might intensify the drought stress at site AN. A lack of water might occur earlier at AN and might persist even longer (Fig. 1b, c). Up to now, Douglas-fir grew better at HE than at AN, because, generally, water supply was higher due to both the soil conditions as well as the precipitation in the vegetation periods. Consequently, dominant height, total volume production, and level of annual increment were higher (Table 1). During drought, height growth response was influenced most negatively and significantly affected by site (Table 4). For the annual height increment of 1 year, both the weather of the previous year (bud formation) and the current year (shoot expansion) were crucial (Bréda et al. 2006). Douglas-fir is able to form Lamma shoots; this adaption was responsible for up to 20 % of height growth in younger trees (Bongarten 1978). Although we did not separately measure the length of the Lamma shoots, it is very likely that at the site AN, they could not be developed due to the drought stress at summer (Roth and Newton 1996). For AN, a decline in height growth was observed also in the years 2000 and 2001 (Fig. 4a), which might be possible due to the poor water supply. A storm called Lothar caused widespread windthrow in German forests and also at the site AN on 26 December 1999 (Albrecht 2009; Schmidt et al. 2010). As a result of the storm, four single plots could not be used further and had to be dismissed, because most of the trees were windthrown. The trees of the remaining plots at AN were presumably affected by root damages. In the years 2000 and 2001 (Fig. 4a), the damaged trees probably enhanced root growth in relation to shoot growth (Pretzsch et al. 2010).

Our investigation showed that thinning is one of the silvicultural options for adaption and mitigation to climate change. Douglas-fir recovered very well in terms of basal area ($R_{s,\mathrm{ba}}$) and volume ($R_{s,v}$) on both sites, and it responded to thinning with more growth due to higher access to light, nutrients, and especially water. This might be due to a combined ecophysiological effect on the water balance which many studies have already analysed before (Donner and Running 1986; Bréda et al. 1995; Laurent et al. 2003): first, soil water availability generally increased in thinned stands. On individual tree level, thinning increased transpiration, but on stand level, transpiration decreased because of the more important effect of reduced stem number. Besides, more rainfall reached the forest soil as a result of reduced canopy water interception (Bréda et al. 1995). For Douglas-fir, the increase of the soil water reserve led to a lower duration and level of water stress in the thinned plot of 19-year-old plantation, especially during the first 3 years after thinning (Aussenac and Granier 1988). For Norway spruce, resilience was more rapid in trees from heavily thinned stands, even if the drought event occurred more than 10 years after the last thinning intervention (Kohler et al. 2010). Second, water-use efficiency may be increased by thinning (Sergent et al. 2012). In contrast, however, Martín-Benito et al. (2010) did not observe any improvement of water-use efficiency for *Pinus nigra* as a consequence of thinning. In general, Sterba (1981) found that particularly, the basal area increment of the lower part of a tree reacted positively to thinning and not the whole bole. This occurred even years after thinning and may partly explain the high significance of thinning in terms of basal area and volume (standard volume calculation including basal area) (Sterba 1981; Sohn et al. 2012).

The increased portion of water for each tree caused by stand density reduction seems to also be responsible for the relevance of the SDI (Tables 4, 5). The stand density was significant in explaining height growth (original data) and basal area as well as volume growth (detrended data). The stand density index (SDI) influenced growth negatively, i.e. current annual increment of trees from plots with lower tree density was less affected by 2003 drought: It is likely that the increased availability of soil space is associated with a larger root system of the individual tree; water stress occurred later, and growth was less influenced. We barely observed an influence of tree characteristics on growth behaviour around the 2003 drought. A reason for this might be the limited sampling of trees which were regarded as predominant, dominant, and co-dominant [social tree class 1–3 (Kraft 1884)]. Assumably, the effect of competition on the incremental response of Douglas-fir was strongly reduced, but not completely eliminated: large crown volumes improved the growth pattern (original data), and co-dominant trees were less affected by drought than dominant ones (detrended data). New investigations with a more balanced selection of trees have to provide reliable results regarding the influence of tree characteristics on growth performance during drought.

Conclusions

Height growth response to severe drought stress was an even more sensitive indicator than basal area growth. With regard to forest inventories and damage expertise, the short-term assessment of tree's ability to recover from stress or vitality should ideally respect volume growth. Using original data, we showed that the direct use of just one of these indicators—height or basal area—to estimate relevant volume growth is questioned as it creates errors when the other indicator is neglected at the same time. Growth pattern of basal area described volume growth better than height growth pattern: for the two sites, an underestimation of 6 % and an overestimation of 11 % were obtained. Considering the age trend, both height and basal area growth pattern can be used to indicate volume growth pattern; a false estimation of less than 6 % was observed.

In our investigation, Douglas-fir was characterized by a high drought tolerance, even outside its natural range. Differences in site and site management can significantly influence climate–growth relationships of Douglas-fir. The right choice of site with adequate water supply might be the primary silvicultural option for the adaption of stands to climate change. Secondly, thinning was advantageous for the growth performance, because thinning could decrease the susceptibility of Douglas-fir to drought stress by increasing water availability for the remaining trees. More growing space might lead to shorter stress period for individual trees. In that way, large individual crown volume improved the growth pattern under drought, and large stand density impaired it.

Douglas-fir might be to some extent representative of the behaviour of conifers, and so the results are of general relevance for forest ecology and management. Conifers rather pursue an isohydric stomatal control strategy (for instance, early closure of stomata under moderate droughts) which should prevent hydraulic dysfunction or cavitation (Hartmann 2011). Douglas-fir seems to have ecophysiological adaptations of an isohydric species for avoiding drought stress like in 2003 (Grieu et al. 1988; Pinol and Sala 2000).

Acknowledgments We thank the Bavarian State Ministry for Nutrition, Agriculture, and Forestry for funding the project X36 entitled “Relationship between spacing and wood quality of Douglas-fir in Bavaria”. We also thank Ulricke Nickles, Fabian Dawo, Johanna Lintl, Gerhard Schütze, Thomas Zimmerer, Ralf Polzer, and the students of the Fachoberschule Triesdorf, Forstwirtschaft for their strong support during collecting the data. Thanks are also due to Ulrich Kern for the graphical artwork and the anonymous reviewers for their helpful comments.

References

Albrecht A (2009) Sturmschadenanalysen langfristiger waldwachstumskundlicher Versuchsflächendaten in Baden-Württemberg, 174 p

Aussenac G, Granier A (1988) Effects of thinning on water stress and growth in Douglas-fir. Can J For Res 18:100–105. doi:10.1139/x88-015

Baayen RH (2008) Analyzing linguistic data: a practical introduction to statistics, 390 p

Bates DM, Maechler M (2009) lme4: Linear mixed-effects models using S4 classes. R Packag. version 0.999375-32

Bauwe A, Criegee C, Glatzel S, Lennartz B (2011) Model-based analysis of the spatial variability and long-term trends of soil drought at Scots pine stands in northeastern Germany. Eur J For Res 131:1013–1024. doi:10.1007/s10342-011-0573-6

Bongarten BC (1978) Genetic and environmental variation in shoot growth and other traits of blue spruce (*Picea pungens*), 104 p

Bouriaud O, Leban J-M, Bert D, Deleuze C (2005) Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiol 25:651–660. doi:10.1093/treephys/25.6.651

Bréda N, Granier A, Aussenac G (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol 15:295–306. doi:10.1093/treephys/15.5.295

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–644. doi:10.1051/forest:2006042

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn, 488 p

Carnwath GC, Peterson DW, Nelson CR (2012) Effect of crown class and habitat type on climate–growth relationships of ponderosa pine and Douglas-fir. For Ecol Manag 285:44–52. doi:10.1016/j.foreco.2012.07.037

Chen P-Y, Welsh C, Hamann A (2010) Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Glob Change Biol 16:3374–3385. doi:10.1111/j.1365-2486.2010.02166.x

De Martonne E (1926) Une nouvelle fonction climatologique: L’indice d’aridité. La Meteorol, pp 449–458

Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. Eur J For Res 124:319–333. doi:10.1007/s10342-005-0085-3

Donner BL, Running SW (1986) Water stress response after thinning *Pinus contorta* stands in Montana. For Sci 32:614–625

Eilmann B, Rigling A (2012) Tree-growth analyses to estimate tree species’ drought tolerance. Tree Physiol 32:178–187. doi:10.1093/treephys/tps004

Eilmann B, de Vries SMG, den Ouden J et al (2013) Origin matters! Difference in drought tolerance and productivity of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) provenances. For Ecol Manag 302:133–143. doi:10.1016/j.foreco.2013.03.031

Elling W (1993) Immissionen im Ursachenkomplex von Tannenschädigung und Tannensterben. Allg Forstzeitschrift 48: 87–95

Feliksik E, Wilczyński S (2004) Dendroclimatological regions of Douglas fir (*Pseudotsuga menziesii* Franco) in western Poland. Eur J For Res 123:39–43. doi:10.1007/s10342-004-0017-7

Feliksik E, Wilczyński S (2007) Dendroclimatic regions of Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco in western and northern Poland. Dendrobiology 52:9–15

Griesbauer HP, Green DS (2010) Regional and ecological patterns in interior Douglas-fir climate: growth relationships in British Columbia, Canada. Can J For Res 40:308–321. doi:10.1139/X09-197

Grieu P, Guehl JM, Aussenac G (1988) The effects of soil and atmospheric drought on photosynthesis and stomatal control of gas exchange in three coniferous species. Physiol Plant 73:97–104. doi:10.1111/j.1399-3054.1988.tb09199.x

Hartmann H (2011) Will a 385 million year-struggle for light become a struggle for water and for carbon? How trees may cope with more frequent climate change-type drought events. Glob Change Biol 17:642–655. doi:10.1111/j.1365-2486.2010.02248.x

Hasenauer H, Monserud RA (1997) Biased predictions for tree height increment models developed from smoothed “data”. Ecol Model 98:13–22. doi:10.1016/S0304-3800(96)01933-3

Hein S, Mäkinen H, Yue C, Kohnle U (2007) Modelling branch characteristics of Norway spruce from wide spacings in Germany. For Ecol Manag 242:155–164. doi:10.1016/j.foreco.2007.01.014

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull 43:69–78

Kantavichai R, Briggs D, Turnblom E (2010) Modeling effects of soil, climate, and silviculture on growth ring specific gravity of Douglas-fir on a drought-prone site in Western Washington. For Ecol Manag 259:1085–1092. doi:10.1016/j.foreco.2009.12.017

Klädtke J, Kohnle U, Kublin E et al (2012) Wachstum und Wertleistung der Douglasie in Abhängigkeit von der Standraumgestaltung. Schweizerische Zeitschrift für Forstwes 163:96–104. doi:10.3188/szf.2012.0096

Kohler M, Sohn J, Nägele G, Bauhus J (2010) Can drought tolerance of Norway spruce (*Picea abies* (L.) Karst.) be increased through thinning? Eur J For Res 129:1109–1118. doi:10.1007/s10342-010-0397-9

Kraft G (1884) Beiträge zur Lehre von den Durchforstungen, Schlagstellungen und Lichtungshieben. Schlagstellungen und Lichthieben, Hann 147

Kramer H (1986) Beziehungen zwischen Kronenschadbild und Volumenzuwachs bei erkrankten Fichten. Allg Forst- und Jagdzeitung 157:22–27

Lassoie JP, Salo DJ (1981) Physiological response of large Douglas-fir to natural and induced soil water deficits. Can J For Res 11:139–144. doi:10.1139/x81-019

Laurent M, Antoine N, Joël G (2003) Effects of different thinning intensities on drought response in Norway spruce (*Picea abies*

(L.) Karst.). For Ecol Manag 183:47–60. doi:10.1016/S0378-1127(03)00098-7

Lloret F, Keeling EG, Sala A (2011) Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120:1909–1920. doi:10.1111/j.1600-0706.2011.19372.x

Mäkinen H (1998) The suitability of height and radial increment variation in *Pinus sylvestris* (L.) for expressing environmental signals. For Ecol Manag 112:191–197. doi:10.1016/S0378-1127(98)00337-5

Martín-Benito D, Del Río M, Heinrich I et al (2010) Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. For Ecol Manag 259:967–975. doi:10.1016/j.foreco.2009.12.001

Martinez-Meier A, Sanchez L, Pastorino M et al (2008) What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. For Ecol Manag 256:837–843. doi:10.1016/j.foreco.2008.05.041

Martínez-Vilalta J, López BC, Loepfe L, Lloret F (2012) Stand- and tree-level determinants of the drought response of Scots pine radial growth. Oecologia 168:877–888. doi:10.1007/s00442-011-2132-8

McCarthy MC, Enquist BJ (2007) Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. Funct Ecol 21:713–720. doi:10.1111/j.1365-2435.2007.01276.x

McDowell NG, Sevanto S (2010) The mechanisms of carbon starvation: how, when, or does it even occur at all? New Phytol 186:264–266. doi:10.1111/j.1469-8137.2010.03232.x

Newton M, Preest DS (1988) Growth and water relations of Douglas fir (*Pseudotsuga menziesii*) seedlings under different weed control regimes. Weed Sci 36:653–662

Oliver CD, Larson B (1996) Forest stand dynamics, 467 p

Olszyk DM, Wise C, VanEss E, Tingey D (1998) Elevated temperature but not elevated CO2 affects long-term patterns of stem diameter and height of Douglas-fir seedlings. Can J For Res 28:1046–1054. doi:10.1139/x98-114

Pichler P, Oberhuber W (2007) Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. For Ecol Manag 242:688–699. doi:10.1016/j.foreco.2007.02.007

Pinheiro J, Bates D (2000) Mixed-effects models in S and S-PLUS, 528 p

Pinol J, Sala A (2000) Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. Funct Ecol 14:538–545. doi:10.1046/j.1365-2435.2000.t01-1-00451.x

Pollanschütz J (1975) Zuwachsuntersuchungen als Hilfsmittel der Diagnose und Beweissicherung bei Forstschäden durch Luftverunreinigung. Allg Forstzeitung 86:187–192

Pretzsch H (2010) Forest dynamics, growth and yield. 664. doi:10.1007/978-3-540-88307-4

Pretzsch H, Biber P (2010) Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Can J For Res 40:370–384. doi:10.1139/X09-195

Pretzsch H, Dieler J, Matyssek R, Wipfler P (2010) Tree and stand growth of mature Norway spruce and European beech under long-term ozone fumigation. Environ Pollut 158:1061–1070. doi:10.1016/j.envpol.2009.07.035

Pretzsch H, Dieler J (2011) The dependency of the size-growth relationship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. Trees 25(3):355–369. doi:10.1007/s00468-010-0510-1

Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant Biol (Stuttg) 15:483–495. doi:10.1111/j.1438-8677.2012.00670.x

Rais A, Poschenrieder W, Pretzsch H, Kuilen J-WG (2014) Influence of initial plant density on sawn timber properties for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Ann For Sci. doi:10.1007/s13595-014-0362-8

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638

Riemer T (1994) Über die Varianz von Jahrringbreiten. Berichte des Forschungszentrums Waldökosysteme der Univ Göttingen A121:375

Roth BE, Newton M (1996) Role of lammas growth in recovery of Douglas-fir seedlings from deer browsing, as influenced by weed control, fertilization, and seed source. Can J For Res 26:936–944. doi:10.1139/x26-103

Rubner K (1910) Das Hungern des Cambiums und das Aussetzen der Jahrringe. Naturwissenschaftliche Zeitschrift Forst- und Landwirtschaft 8:212–262

Schär C, Vidale PL, Lüthi D et al (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427:332–336. doi:10.1038/nature02300

Schlittgen R, Streitberg BHJ (1997) Zeitreihenanalyse, 7th edn, p 574

Schmidt M, Hanewinkel M, Kändler G et al (2010) An inventory-based approach for modeling single-tree storm damage: experiences with the winter storm of 1999 in southwestern Germany. Can J For Res 40:1636–1652. doi:10.1139/X10-099

Sergent A-S, Rozenberg P, Bréda N (2012) Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Ann For Sci. doi:10.1007/s13595-012-0220-5

Sharp RE (2002) Interaction with ethylene: changing views on the role of abscisic acid in root and shoot growth responses to water stress. Plant Cell Environ 25:211–222. doi:10.1046/j.1365-3040.2002.00798.x

Sohn JA, Kohler M, Gessler A, Bauhus J (2012) Interactions of thinning and stem height on the drought response of radial stem growth and isotopic composition of Norway spruce (*Picea abies*). Tree Physiol 32:1199–1213. doi:10.1093/treephys/tps077

Spiecker H (2010) Opportunities and risks for Douglas fir in a changing climate - Abstracts. Berichte Freiburger Forstliche Forschung 85:65 p

Sterba H (1981) Radial increment along the bole of trees: problems of measurement and interpretation. Dickenwachstum der Bäume—radial growth trees—la croissance des arbres en diamètre. IUFRO proceedings: physiological aspects of forest ecology Mitteilungen der Forstlichen Bundesversuchsanstalt Wien, Wien, pp 67–74

Sterba H (1996) Forest decline and growth trends in central Europe. In: Spiecker H, Mielikäinen K, Köhl M, Skovsgaard JP (eds) European forest institute, research report 5. Springer, Heidelberg, pp 149–165

Taeger S, Zang C, Liesebach M et al (2013) Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. For Ecol Manag 307:30–42. doi:10.1016/j.foreco.2013.06.053

Uhl E, Ammer C, Spellmann H, et al (2013) Zuwachstrend und Stressresilienz von Tanne und Fichte im Vergleich. Allg. Forst- und Jagdzeitung 184(11–12):278–292

Walter H, Lieth H (1967) Climate diagram world atlas. VEB Gustav Fischer Verlag Jena, Jena

Wang Y, Čufar K, Eckstein D, Liang E (2012) Variation of maximum tree height and annual shoot growth of Smith fir at various elevations in the Sygera Mountains, southeastern Tibetan Plateau. PLoS One 7:e31725. doi:10.1371/journal.pone.0031725

Waring RH, Schlesinger WH (1985) Forest ecosystems: concepts and management. Academic Press, Waltham, p 340

Zang C, Pretzsch H, Rothe A (2012) Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. Trees 26:557–569. doi:10.1007/s00468-011-0617-z

Zhang Q-B, Hebda RJ (2004) Variation in radial growth patterns of *Pseudotsuga menziesii* on the central coast of British Columbia, Canada. Can J For Res 34:1946–1954. doi:10.1139/x04-078

Zuur AF, Ieno EN, Walker N, et al (2009) Mixed effects models and extensions in ecology with R. doi:10.1007/978-0-387-87458-6

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14. doi:10.1111/j.2041-210X.2009.00001.x