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Increment allocation along the stem axis of dominant and suppressed trees in reaction to drought – results from 123 stem analyses of Norway spruce, Scots pine and European beech

Stammzuwachs-Muster dominanter bis unterständiger Bäumen in Reaktion auf Dürre – Ergebnisse von 123 Stammanalysen in Fichte, Kiefer und Buche

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Key words: Drought stress, stress reaction pattern, stem analysis, stem increment allocation, tree social class

Schlagworte: Trockenstress, Stammanalysen, Stammzuwachs, Soziale Stellung im Bestand

Summary

Stem analyses were carried out on three common tree species in Central Europe to evaluate whether the strong drought of 2003 affected stem increment patterns in dominant and suppressed trees differently. Following Sterba (1981) we expected that dominant trees would react with an increased stem increment in the upper stem section (= acrotone) while suppressed trees would not change their stem increment pattern. Our data set included 41 Norway spruce (*Picea abies* [L.] Karst), 46 Scots pine (*Pinus sylvestris* L.) and 36 European beech (*Fagus sylvatica* L.) trees of social classes 1-4 (acc. to Kraft 1884) from stands distributed over Eastern Bavaria. To compare stem

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increment patterns for trees of different heights the basal area increment BAI was calculated in relative heights (10 % intervals). Drought (2003) and post-drought BAI (2004-2007) were compared with the pre-drought BAI (1999-2002). The BAI at 50 % height (BAI50) and 10 % height (BAI10) and the ratio BAI50/BAI10 were used to test increment differences between the classes.

The drought in 2003 led to a loss in BAI10 of 35 % in spruce and 20 % in pine and beech. The BAI50 loss was generally weaker with 25 % in spruce, 5 % in pine and 15 % in beech. However, in terms of differences between the classes, only spruce exhibited a growth behaviour as expected: allocation pattern along the stem axis in the dominant classes 1-3 turned stronger acrotone but remained unchanged in suppressed class 4. In pine and beech, the loss in BAI10 and BAI50 during drought was higher for dominant trees than for suppressed trees, but changes in the BAI50/BAI10 ratio were independent of the social status. For all species, post-drought recovery in 2004-2007 was stronger for dominant than for suppressed trees.

In spruce – which reacted strongest to drought – the more acrotone stem increment allocation in class 1-3 in 2003 is interpreted as drought stress – a reaction that has been shown also for other stress sources. Class 4 trees in spruce reacted equally strong as class 1-3 but the stem increment did not become more acrotone which indicates a high pre-drought stress level due to suppression. Pine and beech reacted less strong to drought. In contrast to spruce, increment loss increased from dominant to suppressed trees. In pine, the stem increment pattern in class 1 did not change while in class 2-4 a trend towards more acrotone increment is in correspondence with the higher drought stress in these classes. Beech, finally, did not significantly change its increment pattern in all of the classes.

Zusammenfassung

Stammanalysen dreier forstlich wichtiger Baumarten in Mitteleuropa wurden ausgewertet in Bezug auf die Feststellung Sterbas (1981), dass in einem Fichtenbestand dominante Bäume bei Dürre ihren Stammzuwachs in den oberen Stammbereich (= akroton) verlagern, wohingegen unterständige nicht reagieren. Unser Datensatz umfasste neben 41 Fichten (*Picea abies* [L.] Karst) auch 46 Kiefern (*Pinus sylvestris* L.) und 36 Buchen (*Fagus silvatica* L.) der sozialen Klassen 1-4 nach Kraft (1884), aus verschiedenen Beständen Ostbayerns. Um die Stamm-Zuwachsmuster von Bäumen unterschiedlicher Dimensionen zu vergleichen, wurde der Grundflächenzuwachs BAI in relativen Höhen (10 % Intervalle) berechnet. Für die Dürre beziehen wir uns auf das Jahr 2003, ein europaweites Extremereignis. Der BAI im Dürrejahr 2003 und den Folgejahren 2004-2007 wurde mit dem BAI vor der Dürre 1999-2002 verglichen. Der BAI in 10 % Höhe (BAI10) und in 50 % Höhe (BAI50) sowie das Verhältnis BAI50/BAI10 wurden auf Abhängigkeit der Zuwachsreaktionen von der sozialen Klasse getestet.

Im Dürrejahr brach der BAI10 bei Fichte 35 % ein, bei Kiefer und Buche 20 %. Der

Verlust des BAI50 war generell geringer: 25 % bei Fichte, 5 % bei Kiefer und 15 % bei Buche. Bzgl. der Klassen verhielt sich nur Fichte erwartungsgemäß: in den dominanten Klassen 1-3 wurde der Zuwachs im unteren Stammbereich stärker eingeschränkt als im oberen, in der unterständigen Klasse 4 nicht. Zwar war bei Kiefer und Buche der Verlust des BAI10 und BAI50 während der Dürre 2003 bei dominanten Bäumen stärker als bei unterständigen, allerdings waren die Änderungen im Verhältnis BAI50/BAI10 nicht klassenabhängig. Der Erholung in den Jahren 2004-2007 war für die dominanten Bäume stärker als für die unterständigen – bei allen Arten.

Im Fall der Fichte, die am stärksten auf die Dürre reagiert, interpretieren wir die höhere akrotone Stammzuwachsverteilung in den Klassen 1-3 als Dürre-Stress, ein Reaktionsmuster, wie es auch für andere Stress-Faktoren beschrieben wird. Dass dies bei Bäumen der Klasse 4 ihre Stammzuwachs-Allokation nicht ändern, ist nicht ein Zeichen geringeren Dürre-Stresses, sondern zeigt eher den hohen Konkurrenz-Stress vor der Dürre. Kiefer und Buche reagierten schwächer auf die Dürre. Im Gegensatz zu Fichte, nimmt der Zuwachsverlust von dominanten zu unterständigen Bäumen zu. Bei Kiefer ändert sich die Zuwachs-Allokation in Klasse 1 nicht, während Klasse 2-4 der Trend zu verstärkt akrotonem Stammzuwachs wahrscheinlich auf den höheren Dürrestress in diesen Klassen zurückzuführen ist. Für Buche, schließlich, werden keine signifikanten Änderungen im Stammzuwachsmuster in keiner der Klassen verzeichnet.

Introduction

The summer heat and drought of 2003 was the severest of its kind in Europe's recent climate history. It was characterised by extremely high temperatures from May to August up to 5-6 °C above average and precipitation of 50 % or more below average in early spring from February to April and later summer from July-September (Rebetez et al. 2006; average referring to the climate standard period 1961-1990). As Schär et al. (2004) pointed out such extreme conditions are the result of an "increased variability of temperatures (in addition to increases in mean temperature)"; and 2003 may only have been a precursor for more intense and frequent droughts in the second half of the 21st century (Meehl and Tibaldi 2004, Schär et al. 2004, Jacob et al. 2008, p. 135). While extreme heat and ozone peaks affect plants directly by exceeding the lethal threshold of leaf tissues, the most severe stress factor in 2003 was the water deficiency (Breda et al. 2006, Rennenberg et al. 2006).

A classical method of forest yield science to quantify a tree's response to environmental stress is tree ring analysis, i.e. the retrospective measurement of radial increment from tree cores extracted at breast height, 1.3 m above ground (e.g. Zang et al. 2011, Friedrichs et al. 2009, Lebourgeois et al. 2005). Tree rings are a very sensitive stress indicator since stem growth has a lower priority than e.g. foliage or root growth (Dobbertin 2005, Waring 1987). Yet, the tree ring formation along the stem is not uniform. Tree rings that may be missing in lower stem sections often still appear in higher

stem sections – a fact documented as early as 1882 (Böhmerle 1882), but not fully appreciated until the investigations on novel forest damages in Germany in the 1980s (cf. Pollanschütz 1980, Nogler 1981, Athari and Kramer 1983). Sterba (1984) therefore demanded that forest growth and yield science should study the response to stress in terms of height-, diameter- and form factor-development of trees and stands which merged into an official recommendation by the German association of forest research institutes DVFFA in 1988. Already in 1981, Sterba published evidence on changes in the increment pattern along the stem axis – quantified by the basal area increment at different relative heights - in response to drought. Stem analyses of 15 40-year old Norway spruce trees showed an increased acrotone allocation (at the top) during dry years for dominant trees; while suppressed trees did not modify their allocation pattern along the stem (Fig. 1).

To scrutinize whether the strong drought of 2003 produced shifts in stem increment patterns on large scale, we evaluated stem analyses of three tree species: Norway spruce (*Picea abies* [L.] Karst), Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) on a transect in East Bavaria covering different sites, ages and social classes. The questions in focus were:

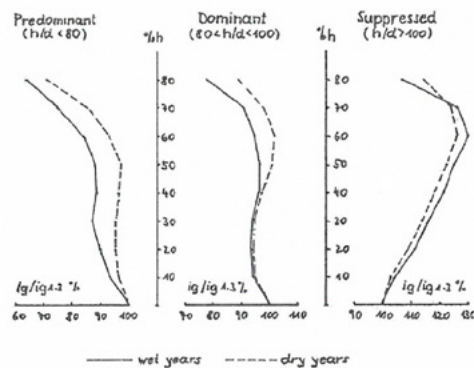


Fig. 1: Stem increment allocation of 40 years old predominant, dominant and suppressed spruce trees in dry and wet years (courtesy, Sterba 1981). The basal area increment (ig) was scaled in 10 % height intervals relative to the basal area increment at breast height, 1.3 m above ground.

Q1: Did the increment allocation along the stem change during the 2003-drought and in the follow-up period 2004-2007?

Q2: Was there a common dependency between changes in stem increment pattern and social class as suggested by Sterba (1981) for Norway spruce?

Sterba (1981) pointed out that an alteration of stem shape leads to biased form factor estimates and hence volume calculation. This certainly has to be considered where high precision is necessary. Besides these biometric aspects, also in

eco-physiological terms, stem analysis reveal allocation patterns and contribute to our understanding of trees' reaction to drought. The consideration of pine and beech, two ecologically very different species from spruce, will show how species-specific are drought-related changes in stem allocation patterns.

Materials and methods

Sample plots and sample preparation

The sample of 123 stem analyses originate from 34 different plots on a transect through East Bavaria between Flossenbürg, Regensburg and Riedenburg (Fig. 2). The sample plots intersect five geologic substrates: granite (1) and gneiss (2) as a part of the precambrian base rock to the north-east, upper Jurassic (3, "Malm") and upper Cretaceous (4, "Oberkreide") as part of the jurassic/ cretaceous scarplands to the north-west, and loess (5) above tertiary sediments to the south. On each of the five geologic substrates, three spruce (*Picea abies* [L.] Karst), pine (*Pinus sylvestris* L.) and beech (*Fagus sylvatica* L.) stands were selected in the age groups: ~30-40 yrs, 40-80 yrs and 80+ yrs. In each of the 45 stands 3-5 trees were harvested between 2008 and 2010 covering the social classes 1-4: 1= predominant, 2= dominant, 3= co-dominant and

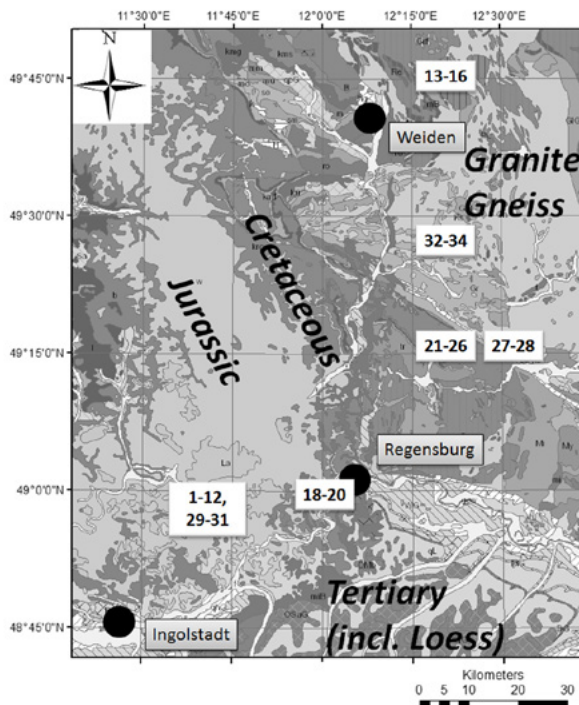


Fig. 2: Sample plots on the geologic map of East Bavaria (1:500000, GLA 1996). Numbers refer to sample plot numbers in Tab. 2 and 3.

Stand ID	N total (N class 1,2,3,4)	Age range (yrs)	Max height (m)	Site index (m)	Dbh range (cm)	Dbh incr. 1999-2002 (cm/yr)
Spruce						
1 LA	1 (1,-,-)	78	36.0	38.4-40.5	55.0	0.846
3 LM	3 (1,1,2,-)	33-37	20.4	22.3-22.8	14.5-25.6	0.430-0.862
4 LJ	2 (-,1,1,-)	24-27	16.6	41.2-45.2	12.8-18.8	0.352-1.152
6 KA	5 (-,2,1,2)	60-73	26.0	28.8-28.9	13.7-34.5	0.104-0.528
7 KM	4 (1,1,2,-)	39-45	19.3	28.3-30.9	14.4-27.0	0.320-0.482
8 KJ	3 (1,1,1,1)	31-33	13.1	28.3-31.4	10.4-15.2	0.224-0.502
11 MM	5 (-,4,1,-)	48-56	24.7	32.5-32.9	20.2-30.4	0.270-0.570
12 MJ	4 (1,1,2,1)	32-35	21.0	37.4-40.7	13.5-24.1	0.116-0.576
13 GrJ	4 (1,1,2,-)	29-32	18.7	39.0-39.5	13.2-21.8	0.372-0.784
14 GrM	4 (2,-,2,-)	42-46	27.4	38.1-41.7	19.2-44.3	0.248-1.348
15 GnA	3 (2,1,-,-)	121-127	42.9	35.2-37.7	48.4-73.8	0.500-0.756
Pine						
18 LM	4 (1,1,2,-)	85-87	31.7	29.9-31.4	32.1-41.9	0.084-0.304
19 LJ	4 (1,-,2,1)	45-47	24.2	33.1-34.9	16.1-35.9	0.142-0.528
20 LA	4 (-,1,2,1)	84-85	31.3	31.3-31.7	25.9-43.7	0.052-0.418
21 KM	4 (1,2,1,-)	58-59 (97)	24.2	29.9-30.0	19.1-36.9	0.132-0.420
22 KJ	2 (1,1,-,-)	29-30	17.3	32.0-35.2	16.6-18.6	0.348-0.596
23 KA	3 (1,1,1,-)	164-166	29.0	23.4-24.3	32.6-53.4	0.100-0.244
27GnA	5 (2,1,2,-)	107-116	31.8	26.7-28.3	29.7-51.8	0.050-0.224
28 GnJ	5 (-,2,3,-)	42-44	23.4	31.9-33.4	19.4-35.9	0.196-0.596
29 MJ	5 (-,2,2,1)	33-38	18.8	29.6-31.4	14.0-22.5	0.232-0.722
30 MA	3 (2,-,1,-)	117-120	31.6	27.8-27.9	38.6-54.7	0.046-0.140
31 MM	1 (-,-,-,1)	96	18.9	17.2-22.6	21.7	0.042
32 GrM	2 (-,-,1,1)	141	21.4	17.2-19.0	15.1-22.9	0.150-0.248
33 GrA	1 (-,-,1,-)	125	25.2	21.4-23.3	31.2	0.130
34 GrJ	3 (-,2,1,-)	27-28	15.0	29.3-31.3	12.9-18.5	0.454-0.726
Beech						
2 LA	4 (-,1,2,1)	100-116	31.1	26.8-26.9	27.0-41.1	0.122-0.522
3 LM	4 (-,2,2,-)	65-70	21.8	25.9-23.1	13.9-28.1	0.220-0.744
9 MA	4 (1,1,2,-)	84-94	34.6	33.8-34.0	20.9-41.1	0.096-0.308
11 MM	5 (-,2,2,1)	59-67	26.2	32.1-33.2	14.0-28.0	0.126-0.540
12 MJ	2 (2,-,-,-)	39-46	17.9	30.6-31.6	15.1-20.0	0.328-0.360
13GrJ	4 (-,2,2,-)	49-52	18.2	28.2-29.8	13.1-19.8	0.206-0.446
14 GrM	5 (-,2,1,2)	46-47	21.1	34.5-36.9	14.7-26.2	0.124-0.428
25 KA	4(2,1,1,-)	44-53	21.6	32.1-33.9	17.3-26.1	0.336-0.684
26 KJ	4 (-,2,2,-)	47-49	24.5	37.9-37.9	15.1-25.2	0.392-0.586

Tab. 1: Sample tree characteristics. Site index given as expected mid tree-height at age of 100 yrs. Reference yield table for spruce: Assmann and Franz (1965), for beech: Schober (1967), for Scots pine: Wiedemann (1943). Since the sample number of each plot allowed only a rough stand height estimate, we listed two site indices based on the following assumptions: (a) the maximum height represents the top 100 height, and (b) the average tree height of site classes 1-3 represents the midtree height. The indices typically differ no more than +/- 2 m

4= suppressed (Kraft 1884). After a preliminary data analysis the final sample collective was reduced to 10 Norway spruce stands with N = 41 trees, 14 Scots pine stands with N = 46 trees and 10 European beech stands with N = 36 trees. Tab. 1 gives an overview of site stratification and sample tree characteristics. Tab. 2 summarises important site properties. The stem analyses were part of a larger sampling design to estimate the range of mineral contents in different tree organs (DBU project „Nähr-

Stand ids	Tree species	Growth region	Substrate	Altitude (m a.s.l.)	T. veg (T.a) 1971- 2000 (°C)	P. veg (P.a) 1971-2000 (mm)	T. veg (T.a) 2003 (mm)	P. veg (P.a) 2003 (mm)
13, 14	PA, FS	10.4	loamy sandy skeleton-rich Cambisols/ Podisols on Granite	695	13.1 (6.3)	440 (950)	15.8 (6.9) ¹	262 (505) ¹
15	PA	10.4	loamy sandy skeleton-rich Cambisols/ Podisols on Gneiss	720-750	12.9 (6.1)	450 (950)	15.8 (6.9) ¹	262 (505) ¹
32, 33, 34	PS	10.3	sandy skeleton-rich Cambisols/ Podisols on Granite	485	14.7 (7.5)	405 (805)	17.2 (8.2) ²	341 (712) ²
27, 28	PS	10.3	medium to profound loamy sandy Cambisols on Gneiss	420-485	14.7 (7.6)	415 (805)	17.2 (8.2) ²	341 (712) ²
21, 22, 23, 25, 26	PS, FS	9.1	sandy to clayey Cambisols/ Pseudogleys on Upper Cretaceous	385-430	15.0 (7.8)	320-350 (610-680)	16.3 (7.5) ³	219 (456) ³
12	PA, FS	6.2	(loamy-) sandy, skeleton-rich Rendzinas/ Cambisols on Upper Jurassic	450	15.1 (7.9)	340 (675)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
9, 11	PA, FS	6.2	loamy to clayey Cambisols on Upper Jurassic	470	15.0 (7.9)	345 (685)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
29, 30, 31	PS	6.2	loamy-silty Luvisols/ Cambisols on Upper Jurassic	485	15.0 (7.8)	315 (615)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
6, 7, 8	PA	6.2	medium-profound loamy, partly stoney Cambisol on Upper Cretaceous	510	14.9 (7.7)	350 (710)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
4	PA	6.2	loamy to clayey Cambisols on Loess	480	15.0 (7.8)	332 (674)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
1, 2, 3	PA, FS	6.2	(very) profound silty loam Cambisol, locally pseudogleyic on Loess-loam	470	15.0 (7.9)	330 (660)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵
18, 19, 20	PS	6.2	sandy to silty-loamy Cambisol from Loess-loam	430-450	15.4 (8.1)	325 (630)	17.3 (8.5) ⁴ 18.8 (9.5) ⁵	273 (449) ⁴ 205 (448) ⁵

Tab. 2: Site characteristics of the sample stands. Tree species: PA = *Picea abies*, PS = *Pinus sylvestris*, FS = *Fagus sylvatica*. Growth region according to AK Standortkartierung (1985). T.veg and P.veg are temperature and precipitation during the vegetation period May-Sep, T.a and P.a annual averages/ sums. Site information on the climate 1971-2000 was derived from high resolution maps of the monthly mean temperature and precipitation (Zimmermann et al. 2007). The values for 2003 were obtained from two DWD- and three ICP Level-II meteorological stations: 1= Flossenbürg (Level-II), 2= Oberveichtach (DWD), 3= Bodenwöhr (Level-II), 4= Riedenburg (Level-II), 5= Regensburg (DWD). Soil data were obtained from the Bavarian forest site information system BaSIS of the Bavarian State Institute of Forestry LWF.

stoffentzug im Rahmen der Holzernte“ (Pretzsch et al. 2014). As the data set was originally collected for different aims, it has no balanced experimental design as would be desirable for our aims. Differences in drought reaction between social classes are possibly disturbed by regional, site or stand properties. However, (1) as shown in Tab. 2, the 2003-drought was an outstanding extreme event at all sites, and (2) the social classes are randomly distributed between the sites, so that disturbing factors will presumably only produce a larger variance but no bias. Unfortunately, the high costs of stem analyses make the collecting of a large data set under ceteris paribus conditions very difficult. Tree discs were extracted in seven heights: (1) 0.3 m abv.grd, (2) 1.3 m abv.grd, (3) halfway between (2) and (4), (4) 1m below crown insertion, (5) 1m above crown insertion, halfway between (5) and (7), (7) 7 cm diameter limit. After sample preparation, the tree rings of each disc were measured in the four cardinal directions

(deviations due to presence of branches or fissures possible) with a Digital Positioner. The ring-width measurements were averaged disc-wise using the software TS-APWin Scientific 4.65 (© Rinntech 2002-2010). The synchrony was checked between the disc averages for each tree and between the dbh-discs of all trees per sample plot using the Cross-Date function in TSAP-Win. Stem analyses allow avoiding problems with missing tree rings since synchrony can be assured from other measurements on the same disc and other discs. Missing tree rings occurred only occasionally in the final years of suppressed trees and only in discs of the lower stem. An R routine of the former stem analysis program "Stamma" (Knorr 1987) allowed calculating the diameter increment at different relative heights. Since tree height increases between the years, also the relative heights change, e.g. if a 10 m tall tree gains 0.5 m in height, the 10 % height changes from 1 m to 1.05 m.

Measures and statistics

From the diameter increment we calculated our target parameter basal area increment BAI at each sampled height as in Sterba (1981). To compare BAI along the stem axis for trees of different height, diameter and increment the data needed to be scaled. To make different heights comparable, the BAI was interpolated in 10 % intervals between 0 and 100 % of the total tree height (at harvest). We use the notation BAI10 for the BAI at 10 % height, BAI50 for the BAI at 50% height etc. To make different absolute increments comparable, for each individual tree, the BAI of the stem at height h was scaled to the BAI10:

$$rBAI = BAI(\text{height } h) / BAI10 \quad (\text{Eq. 1})$$

where rBAI stands for relative BAI (1 = 100 %). Note that the 10 % height as our reference height is different from Sterba (1981) who fixed it to the absolute height of 1.3 m above ground, i.e. at breast height. In our case, this is important since we compare stem shapes of trees of different absolute heights (c.f. Hohenadel 1936 in Prodan 1965). For the BAI10, we use either the BAI10 of each separate period like in Sterba (1981) (Eq. 2) or the pre-drought BAI10 of 1999-2002 as a common reference period (Eq. 3):

$$rBAI.intra = BAI(\text{height } h, \text{ period } p) / BAI10(\text{period } p) \quad (\text{Eq. 2})$$

$$rBAI.inter = BAI(\text{height } h, \text{ period } p) / BAI10(1999-2002) \quad (\text{Eq. 3})$$

Since the 7 cm limit for the uppermost disc lies typically at heights between 50-80 % (depending on tree size), data for the basal area increment in the upper 60-90 % height interval are rare. However, from Fig. 1 we expect changes in the increment pattern to manifest already at 10-50 % height (above 1.30 m). Hence, the ratio BAI50 vs BAI10 can serve as a measure for the stem increment allocation. Like in eq. 2 we can scale the ratio of the drought year 2003 and the post-drought 2004-2007 to the ratio of the

pre-drought period 1999-2002. If, in the drought or post-drought, the increment loss at 10 % height, $rBAI_{10}(\text{period } p)$, is as strong as at 50 % height, $rBAI_{50}(\text{period } p)$, the ratio BAI_{50}/BAI_{10} is 1, and the stem increment pattern did not change relative to the pre-drought period. According to Sterba 1981, this is to be expected for suppressed trees (cf. Fig. 1). If the increment loss of the $rBAI_{10}$ is stronger than of the $rBAI_{50}$, the ratio BAI_{50}/BAI_{10} is > 1 , and the stem increment pattern changed towards a more acrotone increment relative to the pre-drought period. According to Sterba 1981, this is to be expected for (pre)dominant trees (cf. Fig. 1).

The periodic $rBAI(\text{period } p)$ of the 10 % and 50% height and the ratio BAI_{50}/BAI_{10} were statistically analysed for their dependence on the trees' social class by means of (a) Spearman's (rank) correlation, and (b) Welch's test for equal means. Spearman's rank correlation describes monotonous trends in ordinal scaled data (values from 1 to +1). Significance levels are tested according to Best & Roberts (1975). The Welch test can be understood as an analysis of variance relaxing the necessity of equal variances (Welch 1951). All calculations and graphics were done in R 3.1.2 (R Development Core Team 2014).

Results

Fig. 3 displays the basal area increment BAI of spruce, pine and beech in 10 % height intervals along the stem axis relative to the reference BAI at 10 % height (denoted BAI_{10}) for the social classes 1-4. The upper row uses BAI_{10} of the pre-drought period 1999-2002 as common reference (Eq. 3) while the lower row sets the BAI_{10} of each separate period (Eq. 2). Fig. 4 displays the BAI_{10} , BAI_{50} and the ratio BAI_{50}/BAI_{10} of drought year 2003 and post-drought 2004-2007 scaled to the respective values of the pre-drought period 1999-2002. The corresponding statistics are summarised in Tab. 3.

Spruce: Of the three species considered, spruce reacts strongest to the 2003-drought reducing its BAI_{10} to 65% – more or less equal in all classes (Fig. 3a, 5a.1). In class 1-3, the upper stem reacts weaker reducing BAI_{50} to 80 % of the pre-drought level leading to a more acrotone increment (Fig. 3a/b, 5a). In class 1-3, the BAI_{10} recovers to 80 % of the before-drought level, and the BAI_{50} to 100 % in class 1-3 (Fig. 3a, 5b.1/2), thereby maintaining a more acrotone increment than before the drought (Fig. 3b, 5b.3). In class 4, recovery of BAI_{10} and BAI_{50} differs. While BAI_{10} recovery is in the same range as in class 1-3, the BAI_{50} of 2 out of 4 trees further drops, thereby dragging the mean BAI_{50} to 70 % (Fig. 3a, 5b.1/2). Statistically, due to the large variability, the stem increment pattern as quantified by the ratio BAI_{50}/BAI_{10} is more class-sensitive than the increment losses at the individual heights $rBAI_{10}$ and $rBAI_{50}$. For the post-drought ratio, the Welch-test indicates significant differences between the classes (Tab. 3).

Pine: Pine reacts most variable to drought. Average basal area loss in 2003 is generally

Species	Stat. Test	Drought 2003			Post Drought 2004-2008		
		rBAI10	rBAI50	BAI10/BAI50	rBAI10	rBAI50	BAI10/BAI50
Spruce	ps (p-value)	-0.09 (0.56)	0.03 (0.86)	-0.262 (0.098(,))	-0.04 (0.79)	-0.13 (0.43)	-0.197 (0.217)
	Welch	0.792	0.971	0.317	0.377	0.598	0.008**
Pine	ps (p-value)	-0.360 (0.014*)	-0.358 (0.015*)	0.07 (0.65)	-0.400 (0.006**)	-0.252 (0.090(,))	0.08 (0.59)
	Welch	0.133	0.048*	0.3631	0.068(,)	0.049*	0.147
Beech	ps (p-value)	-0.25 (0.14)	-0.23 (0.18)	-0.01 (0.97)	-0.328 (0.051(,))	-0.18 (0.30)	0.07 (0.71)
	Welch	0.509	0.180	0.349	0.261	0.224	0.466

Tab. 3: Statistics of the Basa area increment BAI at 10 % and 50 % height (BAI10 and BAI50) and the ratio BAI50/BAI10 during the drought year 2003 and post drought 2004-2007 compared to the pre drought reference 1999-2002. <ps> for Spearmans rank correlation coefficient with subsequent significance according to Best & Roberts (1975), <Welch> for test for equal means according to Welch (1951).

weaker than in spruce with a BAI10 reduction of 15 % and BAI50 reduction of 5 % (Fig. 3c, 5c.1/2). But also the differences between the classes are stronger: increment loss increases from class 1 to class 4 (Fig. 4c.1/2). While class 1 trees barely reacted, class 4 trees react strongest reducing BAI10 and BAI50 to 59 % and 68 %, respectively. Unlike spruce, where as in Sterba (1981) dominant class 1-3 trees proved a slightly more acrotone BAI in the drought year and suppressed class 4 trees not, in pine, pre-dominant class 1 trees did not change their increment pattern while co-/ dominant class 2-3 and unexpectedly also suppressed class 4 trees shifted towards a more acrotone increment (Fig. 3d, 5c.3). BAI10 and BAI50 recover in all classes. The average BAI recovery in class 1 trees reaches 119 % and 127 % of the pre-drought level for BAI10 and BAI50, respectively; class 4 trees stay behind at 74 % and 82 % of the pre-drought level for BAI10 and BAI50, respectively (Fig. 3c, 5d.1/2). The more acrotone increment allocation of class 2-4 continued in the post drought period; the increment pattern of class 1 remained unchanged (Fig. 3d, Fig. 4d.3). Statistically, differences between the classes are significant for the strength of the increment reaction in the BAI10 and BAI50 but not for their ratio, i.e. the increment pattern did not change significantly.

Beech: At first glance, the beech increment pattern resembles spruce more than pine, yet the drought reaction is weaker and recovery stronger. An increase in the drought reaction from class 1 to 4 is weak (Fig. 3e, 5e1/2), but while class 1-3 recover to almost 100% (BAI10 slightly more than BAI50), class 4 trees further decrease their basal area increment: BAI10 from 76 % to 73 %, BAI50 from 72 % to 63 % (Fig. 3e, 5f.1/2). The increment pattern remains almost unchanged (Fig. 3f, 5e/f.3). Like for pine, differences between the classes are stronger for the rBAI10 or rBAI50 than for the ratio BAI50/BAI10; the increment pattern did not change significantly.

Discussion

By means of stem analyses Sterba (1981) showed that dominant spruce trees reacted to drought with an increased acrotone stem increment while suppressed trees did

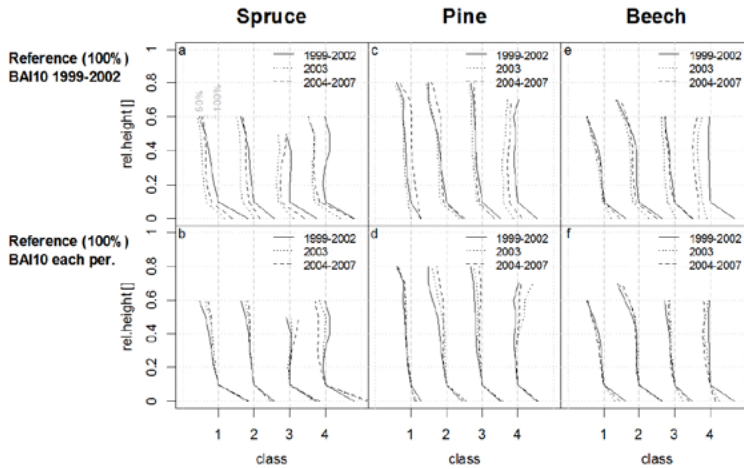


Fig. 3: Basal area increment BAI in 10 % height intervals of spruce, pine and beech in pre-drought 1999-2002, drought 2003 and post-drought 2004-2007, (upper row a/c/e) relative to the BAI10 of the pre-drought period 1999-2002, (lower row b/d/f) relative to the BAI10 within each period (as in Sterba 1981). Tree number in spruce class 1, 2, 3, 4 = 10, 13, 14, 4; tree number in pine class 1, 2, 3, 4 = 9, 13, 19, 5; tree number in beech class 1, 2, 3, 4 = 5, 13, 14, 4.

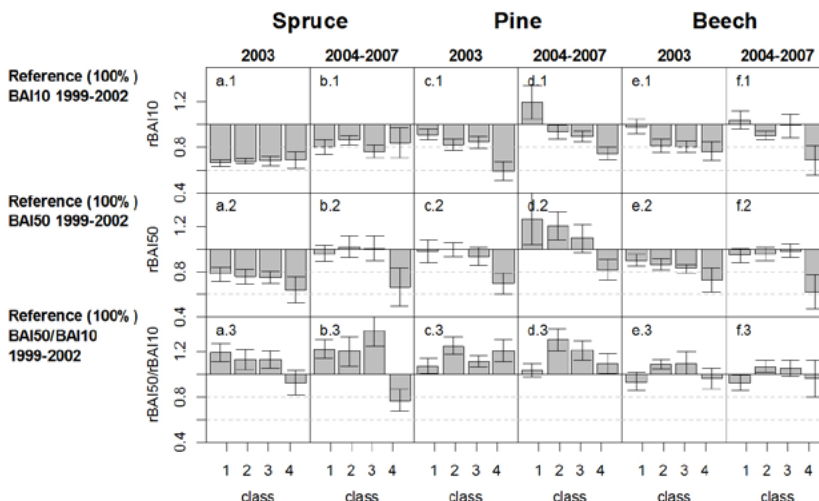


Fig. 4: Basal area increment BAI10 and BAI50 and ratio BAI50/BAI10 of spruce, pine and beech in drought 2003 and post-drought 2004-2007 relative to BAI10 and BAI50 and ratio BAI50/BAI10 of the pre-drought 1999-2002. Tree number in spruce class 1, 2, 3, 4 = 10, 13, 14, 4; tree number in pine class 1, 2, 3, 4 = 9, 13, 19, 5; tree number in beech class 1, 2, 3, 4 = 5, 13, 14, 4.

not react (c.f. Fig. 1). It was left open whether the suppressed trees were less affected by drought or whether their already strong acrotone allocation expressed some sort of mechanical or physiological limit. In terms of forestry practice, Sterba (1981) pointed out that an alteration of stem shape leads to biased stem taper estimates and hence volume calculation. This is certainly true, yet, unless the stress frequency

and/ or intensity change over a longer time span the effect on stem taper is probably not grave. We will focus our discussion on how stress-induced changes in the stem allocation relate to our understanding of how forest trees cope with drought stress.

Our data set of 123 stem analyses originated from different stands and beyond spruce also included pine and beech. The strength of the 2003 drought led to a drop in BAI10 (at 10 % height) of 35 % in spruce and 20 % in pine and beech. The loss in BAI50 (at 50 % height) was generally weaker with 25 % in spruce, 5 % in pine and 15 % in beech. Yet, although the stem increment shifted towards a more acrotone allocation, the changes and also the differences between the classes were much less pronounced than described by Sterba (1981) for spruce. Only spruce behaved as expected: increment in the dominant classes 1-3 became stronger acrotone while in suppressed class 4 not. In pine and beech, the loss in BAI10 and BAI50 during drought increased from dominant to suppressed trees, but no significant changes occurred in stem increment pattern. Post-drought recovery in 2004-2007 was for all three species stronger for dominant than for suppressed trees. The patterns in increment distribution and class dependency persisted.

By scaling the stem increment in 2003 against the pre-drought period, we are able to compare shifts in the increment pattern and the strength of the drought reaction. It can be seen that class 1 in pine and beech which did not change their increment pattern also reacted less strong to the drought than the other classes (BAI10 loss of 10 % and 2 %, respectively). In spruce, where the class 1 increment pattern did change, the BAI10 loss of 35 % was equally high as in the other classes. The shift in increment pattern obviously also depends on the strength of the drought reaction which is strongly species-specific. In this respect, the allocation changes are in accordance with other drought tolerance rankings of forest trees (Zang et al. 2011; other authors like Niinemets et al. 2006 regard Scots pine as far more drought tolerant). Literature whether dominant or suppressed trees react stronger to drought is usually based on ring width analysis with contrary results (e.g. Pichler and Oberhuber 2007, Linares et al. 2010 contra Zang et al. 2011, Mérian and Lebourgeois 2011). In our data, differences in the drought reaction between the classes were little in spruce and beech, but during the recovery, it were the class 4 trees that stayed behind, and in some of their individuals the drought seems to have triggered a continuing decline. Scots pine possessed a strong gradient in drought reaction and recovery from class 1 to 4, which might be due to its taproots which give dominant trees preferential access to deeper water storage (Schütt and Stimm 2014). Whether the growth impulse of Scot pine in the years 2004-2007 is related to the drought in 2003 remains uncertain.

Even if the changes in increment pattern were weak compared to Sterba (1981), all species reduced stem increment stronger in the basal than the upper stem section. Literature (Sterba 1981, 1984, Athari and Kramer 1983, Pretzsch et al. 2010) indicates that not only drought, but also other stress sources trigger a shift in the increment pattern in favour of the crown's stem section. This phenomenon is frequently exp-

lained by the auxin model of tree growth (Schweingruber 1996, Sundberg et al. 2000) where the apical production of auxin favors the cambial activity in the upper stem in stress years. The molecular mechanisms behind the tapering of xylem conduits are just beginning to be understood (Anfodillo et al. 2012, Nilsson et al. 2008). Effectively, a prioritisation of radial growth in the upper stem section reduces xylem resistance and alleviates water tension in the upper canopy (Breda et al. 2006, Matyssek et al. 2011, p. 167, Eilmann et al. 2009). In this light, it would be expected that rather European beech as the more anisohydric species with low stomatal drought sensitivity would invest into the upper stem, and not the isohydric spruce which reacts with early stomata closure to drought (McDowell et al. 2008, Breda et al. 2006, Pretzsch et al. 2013). Still, we do not know whether beech and pine change towards a more acrotone allocation if drought conditions become more severe. Cochard et al. (1996; for poplars) and Nardini et al. (2013; for six Mediterranean broadleaf species) showed that anisotropic species actually go to the point where they risk hydraulic failure with partial or even complete desiccation of the upper crown. Obviously, there is no simple explanation of the increment distribution from tree hydraulics, especially, since other stress sources trigger similar allocation changes: simple competition (which shows directly in the different stem taper of dominant and suppressed trees), complex forest dieback (Athari and Kramer 1983), insect pests (Sterba 1984), elevated ozone (Pretzsch 2010).

In the end, we cannot offer a simple explanation for trees' allocation patterns under drought stress. The most promising steps may lie in a better understanding of the cambial regulation of xylem generation from the tree top to the bottom (Aloni and Zimmermann 1983, Sundberg et al. 2000, Anfodillo et al. 2012). Stem analyses complement such studies on a superior hierarchical level as year rings resolve the cambial activity in annual time steps. They retrace the entire age of the tree and reveal how strong stem increment allocation varies in dependence of climate and other factors.

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