RESEARCH ARTICLE

Assessing site productivity based on national forest inventory data and its dependence on site conditions for spruce dominated forests in Germany

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Abstract

Aim of study: (i) To estimate site productivity based on German national forest inventory (NFI) data using above-ground wood biomass increment (ΔB) of the stand and (ii) to develop a model that explains site productivity quantified by ΔB in dependence on climate and soil conditions as well as stand characteristics for Norway spruce (*Picea abies* (L.) Karst.).

Area of study: Germany, which ranges from the North Sea to the Bavarian Alps in the south encompassing lowlands in the north, uplands in central Germany and low mountain ranges mainly in southern Germany.

Material and methods: Biomass increment of the stand between the 2nd and 3rd NFI was calculated as measure for site productivity. Generalized additive models were fitted to explain biomass increment in dependence on stand age, stand density and environmental variables.

Main results: Great part of the variation in biomass increment was due to differences in stand age and stand density. Mean annual temperature and summer precipitation, temperature seasonality, base saturation, C/N ratio and soil texture explained further variation. External validation of the model using data from experimental plots showed good model performance.

Research highlights: The study outlines both the potential as well as the restrictions in using biomass increment as a measure for site productivity and as response variable in statistical site-productivity models: biomass increment of the stand is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. However, it entails the difficulty of how to deal with the influence of management on stand density.

Additional keywords: Site index; site potential; biomass increment; statistical model; climate.

Introduction

How to best summarize site productivity in one measure has been a crucial question in forestry (Skovsgaard & Vanclay, 2008; Bontemps & Bouriaud 2014). The most widely used measure is the height-age site index (SI), i.e. an expected or realized stand height at a given reference age (Assmann, 1961). Height has the advantages that it can be measured directly and that it is generally not much affected by management (Wenk *et al.*, 1990). In fact, SI is so well-established in forest research and practice, that it is often taken as the true productivity rather than simply an indicator that

may or may not reflect the site potential (Skovsgaard & Vanclay, 2008). This belief is based on Gehrhardt's first refinement of Eichhorn's rule stating that the relationship between total volume production of a tree species and stand height is identical for all site indices known as general yield level. But later he refined this relationship by specifying different relationships between total volume production and stand height for each site index referred to as a special yield level. Evaluating experimental plots of Norway spruce in Southern Germany, Assmann found that the total volume production of stands of the same age and SI can still vary ± 15 % in dependence on site characteristics.

This leads to the so-called subdivided special yield level (Pretzsch, 2009). These findings of Assmann, that SI does not completely capture site productivity, motivated us to use a measure for site productivity that comprises more aspects of productivity than mere height and to relate it to site conditions. As Assmann established the theory of the subdivided special yield level investigating experimental plots of Norway spruce (one of the most common and economically important tree species in Germany), we focus on this species as well. Our study is based on German national forest inventory (NFI) data.

Numerous studies model the relationship between site conditions and site productivity based on NFI data. Mostly SI is the measure of site productivity (*e.g.* Seynave *et al.*, 2005; Albert & Schmidt, 2010; Nothdurft *et al.*, 2012), but a variety of other measures has been used as well, *e.g.* stand basal area increment (Charru *et al.*, 2010; Charru *et al.*, 2014) or mean annual volume increment (Gustafson *et al.*, 2003; Condés & García-Robredo, 2012). Watt *et al.* (2010) compared two models for *Pinus radiata* productivity in dependence on site characteristics. In the first model SI is the response variable, in the second model productivity is expressed as the mean annual increment at a standard age for a standard density predicted from a stand basal area growth model and auxiliary relations for height and volume. Wang *et al.* (2005) estimated net primary productivity (NPP) of forest ecosystems in China from inventories and modelled it in dependence on site conditions.

NPP encompasses the entire production of organic substances (i.e. net biomass growth) as well as the turnover (of plant organs or entire individuals) in a given time period (Pretzsch, 2009). However, as root biomass, turnover of plant organs and investments in reproduction can only be approximate estimates using NFI data, including these components introduces a lot of uncertainty into NPP estimations. Therefore, in order to estimate site productivity we chose the physiological measure above-ground wood biomass increment (ΔB) of the stand.

Using experimental plots the focus often is on total volume production. But as the history of stand development of NFI plots is not known, total volume (or biomass) production cannot be estimated. In contrast to total volume (or biomass) production, ΔB is strongly influenced by stand density and stand age. On the one hand ΔB can be limited by stand structure and density, on the other hand it can be limited by site conditions. Thus, actual ΔB and potential ΔB must be distinguished (Kahle, 2015). Actual ΔB is the realized ΔB under the current stand structure, density and age. Potential ΔB is the capability of the site to produce

biomass, irrespective of how much of this potential is utilized under the current stand structure and density (Skovsgaard & Vanclay, 2008). It is determined by site conditions and thus reflects site potential. As most forests in Germany are managed, ΔB estimated from NFI data will generally not correspond to potential ΔB. Thus, a central aspect is how to take stand density into account (Bontemps & Bouriaud, 2014). Besides stand density, stand age has a strong influence on ΔB and has to be taken into account when assessing site potential.

Inspired by the idea that based on NFI data direct productivity-environment relationships can be established when taking stand density effects into account (Bontemps & Bouriaud, 2014), this study investigates whether the use of ΔB is a feasible way to do so and whether there is an additional benefit in using ΔB as a complementary measure to SI for site productivity. Main aim of the study was to estimate site productivity based on German NFI data and develop a model that explains site productivity in dependence on site conditions for Norway spruce. We validated the model using an independent dataset from experimental plots. Our research questions were: (1) What stand variables explain the variability in ΔB for a given site index? (2) How can the strong influence of stand density on ΔB best be dealt with? (3) Can actual and potential ΔB be differentiated based on NFI data? (4) How is the influence of site conditions on ΔB?

Material and Methods

Study area

Germany ranges from the North Sea to the Bavarian Alps in the south encompassing lowlands in the north, uplands in central Germany and low mountain ranges mainly in southern Germany. 30 % of the area is covered by temperate forests. In the northwest and the north the climate is oceanic, whereas in the east there is a strong continental influence. In central and southern Germany the climate varies from moderately oceanic to continental. The Alps and some low mountain ranges have a mountain climate with lower temperatures and higher precipitation.

Data

National Forest Inventory Data

To estimate biomass increment data of the second (2002) and third (2012) NFI were used. NFI in Germany is based on a permanent nationwide 4 km × 4 km grid. Each grid point in forest area is the center of an angle-count sampling (BMELV, 2011). There are trees that

were included in the angle-count sampling (basal area factor 4) in NFI 3 but had not been thick enough to be included in NFI 2. Other trees were measured for the NFI 2 but were missing in the NFI 3. Diameter at breast height (dbh) and height of these trees were predicted for the middle of the period between NFI 2 and NFI 3 (Jenkins *et al.*, 2001; Dahm, 2006) using the function of Sloboda (Riedel *et al.*, 2017). Thus, plots where thinning occurred between the inventories are included in our dataset. However, plots where all trees that had been surveyed in NFI 2 were missing in NFI 3 due to harvest or mortality were excluded. For the study plots with a basal area proportion of spruces ≥ 70 % and stand age (calculated as mean of the age estimations of the sample trees weighted by the stem numbers per ha that they represent) between 30 and 150 years were selected. Plots where the climate signal is likely to be confounded by extreme soil characteristics (gley soils, pseudogley soils and moor soils) were discarded. Finally, 3830 plots remained for analysis.

Above-ground wood biomass was estimated using species-specific functions of dbh and height. We chose the functions of Zell (2008), as they were developed based on German NFI data. The functions estimate total above-ground wood biomass, i.e. comprise both stem wood biomass as well as branch biomass. The increment of above-ground wood biomass per year was determined for each tree as the difference between NFI 3 and NFI 2 divided by the period length. These values were extrapolated to 1 ha and summed up at plot-level resulting in one ΔB assigned to each plot (Jenkins *et al.*, 2001; Dahm, 2006). In summary, ΔB represents total above-ground wood biomass net growth of the stand, i.e. turnover of plant organs is not considered. A detailed description of how ΔB is derived based on the angle-count sample is presented in Appendix 1.

The stand density index of Reineke (SDI) (Reineke, 1933; Zeide, 2005) with an exponent of -1.605 was used as a measure of stand density. As tree species differ in their requirements of growing space, SDI values are species specific. In order to allow comparisons between different species or to use the SDI for mixed stands, it is necessary to weight the SDI. For each species the 95-percentile of the SDI distribution of pure stands was determined. Weighting factors were calculated dividing the 95-percentile value of spruce (used as reference species) by the 95-percentile value of the respective tree species. For each NFI plot species specific SDI values were multiplied by the weighting factors and then summed up to the overall SDI of the respective plot. A detailed description of the calculation of the SDI is presented in Appendix 2. Statistical values of the NFI data are summarized in Table 1.

Table 1. Characterization (minimum, maximum, mean, standard deviation) of the NFI plots (n = 3830) used for modelling.

Parameter	Min	Max	Mean	SD
Mean diameter (cm)	9.9	70.5	32.5	9.9
Dominant height (m)	4.9	48.9	29.9	5.3
Stand age (yr)	30	150	71	27
SDI	59	2325	984	350
Biomass (t ha^{-1})	16	862	292	109
ΔB (t ha^{-1} yr^{-1})	0.2	24.8	9.0	4.1

Environmental Data

Regionalized daily climate (Böhner *et al.*, 2018) and soil data (von Wilpert *et al.*, 2017) are available at the NFI plots. Based on the daily climate data, for each NFI plot annual values of the climate variables presented in Table 2 were calculated and then averaged over the measurement period between NFI 2 and NFI 3.

The relationship between the variability in ΔB and stand variables

In order to address the first research question (What stand variables explain the variability in ΔB for a given site index?), we explored the variation in ΔB not already explained by SI. We aimed at identifying the stand and tree characteristics that differ between plots of greater and lesser ΔB but of the same SI: Is greater productivity mainly due to greater stem numbers or do stem numbers not differ that much, but trees are thicker and radial growth of single trees is faster? First, for each plot SI was determined by estimating the top height and extrapolating it to age 100 applying the Chapman-Richards function (Brandl *et al.*, 2018). Second, a generalized additive model (GAM) was fitted explaining ΔB in dependence on SI (package mgcv (Wood, 2011) in R 3.3.2 (R Core Team, 2016)). Stand age was included as additional covariate in order to account for the influence of age on ΔB. The residuals of this model correspond to the variation in ΔB not explained by SI and age. Third, we divided the residuals in quartiles and tested if stand and tree parameters differed significantly between the quartiles using Kruskal Wallis and post-hoc Nemenyi-Test (significance level p = 0.01), as the data were not normally distributed. On plot level we considered SDI, stem number (N), standing above-ground wood biomass and quadratic mean diameter (dg), on single tree level we considered height, dbh and relative dbh increment, i.e. dbh increment between NFI 2 and NFI 3 divided by the dbh measured at NFI 2. Relative dbh increment was only assessed for trees measured at both inventories. In order to be able to

Table 2. Overview of environmental variables (abbreviation, unit, minimum, maximum, mean, standard deviation) for the NFI plots used in the study.

Parameter	Abbreviation	Unit	Min	Max	Mean	SD
Mean annual temperature	T_yr	°C	3.6	11.4	8.2	1.1
Mean temperature May to Sept.	T_5to9	°C	9.8	18.3	14.8	1.2
Mean temperature warmest quarter	T_wq	°C	11.9	20.1	16.5	1.2
Max. temperature warmest month	Tmax_wm	°C	17.6	27.7	23.5	1.5
Mean temperature coldest quarter	T_cq	°C	-5.1	3.3	-0.5	1.2
Min. temperature coldest month	Tmin_cm	°C	-9.5	-1.1	-5.1	1.4
Temperature seasonality (standard deviation *100)	T_sd	°C*100	598	788	693	39
Temperature annual range (Tmax_wm–Tmin_cm)	T_range	°C	23.6	32.3	28.6	1.6
Annual precipitation sum	P_yr	mm	504	2589	1036	301
Precipitation sum May to Sept.	P_5to9	mm	251	1364	490	151
Precipitation sum warmest quarter	P_wq	mm	165	886	315	99
Precipitation seasonality (coefficient of variation)	P_cv		43	65	52	4
Evapotranspiration (Penman-Monteith) May to Sept.	ETpm_5to9	mm	269	504	407	37
Available water capacity of the first 60 cm	AWC	mm	78	202	138	21
Base saturation of the first 60 cm	BS	%	1	100	30	26
Clay content of the first 60 cm	clay	%	1	53	19	9
Silt content of the first 60 cm	silt	%	1	74	40	12
Sand content of the first 60 cm	sand	%	1	96	41	19
C/N-ratio of the first 60 cm	CN		7	34	15	3

compare height and dbh of trees of varying ages height and dbh had to be rescaled: A 95%-quantile regression was applied describing height or dbh respectively as a fourth order polynomial of age. Then, each tree's height or dbh respectively was divided by the predicted 95%-quantile of height or dbh respectively at the tree's age resulting in a relative measure independent of age.

Details on the methodology are given in Appendix 3.

Modelling site productivity from site conditions

We modelled ΔB in dependence on site and stand characteristics using generalized additive models with a gamma error distribution and log-link function. A variety of climate and soil variables was offered to variable selection (Table 2). Climate variables comprise annual precipitation sum (P_yr), summer precipitation (P_wq), precipitation during growing season (P_5to9), mean annual temperature (T_yr), summer temperature (T_wq, Tmax_wm), temperature during growing season (T_5to9), winter temperature (Tmin_cm, T_cq) as well as temperature variability (T_sd, T_range). Soil parameters include base saturation (BS), soil texture variables (clay, silt, sand), C/N-ratio (CN) and available water capacity (AWC) of the first 60 cm. We selected the best model of all possible combinations of explanatory variables using AIC as criterion. Combinations including highly

correlated variables (Dormann *et al.*, 2013) had been discarded beforehand.

ΔB strongly depends on stand density. Stand density itself depends both on thinning regime and environmental conditions, since favorable sites allow a greater stand density than unfavorable sites (Pretzsch, 2002). We wanted to find a measure of site productivity that is independent of forest management and solely reflects differences in site quality. Stand density could be included as covariate into the model and set to a fixed value for predictions. But as stand density is not independent of site quality, it weakens the explanatory power of the environmental variables. Therefore, we tried to separate the effect of environmental conditions from the effect of forest management on stand density. Our approach follows the methodology applied to experimental plots when characterizing density on plots of varying thinning grades on the same site. Density of a given stand is expressed by the ratio of the basal area of the stand and the maximum basal area observed on the same site (Pretzsch, 2002). Regarding NFI plots as a huge experimental design we identified plots of similar site conditions using k-means clustering. The k-means method partitions the observations into a specified number of groups (i.e. clusters) so that the sum of squares from the observations to the assigned cluster centers is minimized. Based on a comprehensive set of climatic (P_yr, P_wq, P_cv, T_yr, T_wq, Tmin_cm,

T_sd, ETpm_5to9) and soil variables (BS, AWC, silt, sand, CN) observations were assigned to 21 clusters using the algorithm of Hartigan & Wong (1979) and trying 1000 initial random sets of cluster centers. The optimal number of clusters had been determined according to the Bayesian information criterion for expectation-maximization, initialized by hierarchical clustering for parameterized Gaussian mixture models using the R package mclust (Scrucca *et al.*, 2016). For each cluster, interpreted as one experimental plot with a set of comparable site conditions but different thinning grades, the 95-percentile of the SDI distribution (SDI$_{95}$) was determined. Again we chose the 95-percentile instead of the maximum in order not to give potential outliers too much influence. Still, SDI$_{95}$ is interpreted as the maximum SDI that can be reached under the corresponding site conditions. Then, for each NFI plot the ratio of its SDI and the SDI$_{95}$ of the corresponding cluster was calculated resulting in a relative density (RD) that reflects the effect of thinning on density. ΔB can then be explained by RD, age and the environmental variables.

Validation

The model's predictive performance was evaluated by calculating root mean squared error (RMSE) based on a 10-fold cross validation (data splitting train data : test data = 9 : 1) (*e.g.* Mellert *et al.*, 2016). Besides, we checked for systematic errors by determining the slope of a least squares regression without intercept of observed ΔB against predicted ΔB both at the scale of the linear predictor, i.e. the log scale (*e.g.* Dolos *et al.*, 2015).

For external validation independent data of 78 long-term experimental plots on 14 locations in Bavaria were available. From these data the increment periods which were close to the inventory periods of the NFI were used. Table 3 comprises the stand characteristics of the experimental plots.

Results

The relationship between the variability in ΔB and stand variables

In the data there was a clear trend to larger quadratic mean diameter (dg), dbh, standing biomass and ΔB with increasing SI. Thus, in general greater ΔB coincided with higher SI. However, there was considerable variation in ΔB that was not explained by SI and stand age. This residual variation could be related to stand variables (Table 4): Differences in ΔB were largely

Table 3. Characterization of the experimental plots (n = 78) used for validation; stand age, mean height and mean diameter are obtained from the last survey.

Parameter	Min	Max	Mean	SD
Stand age (yr)	20	118	44	22
Mean height (m)	9.1	39.1	21.8	6.2
Mean diameter (cm)	11.5	52.7	26.8	9.0
Mean annual temperature (°C)	7.0	9.0	8.2	0.7
Temperature seasonality (°C*100)	706	754	726	15
Precipitation sum warmest quarter (mm)	245	427	338	66
Base saturation of the first 60 cm (%)	5	100	41	26
Sand content of the first 60 cm (%)	9	64	28	18
C/N-ratio of the first 60 cm	7	25	17	6

due to differences in stand density (Fig. 1a). Sites with greater ΔB generally had a higher stem number per ha, whereas there was no clear trend for quadratic mean diameter. Standing above-ground wood biomass significantly differed between the quartiles of the distribution of the residuals and showed an increasing trend. Trees on sites with greater ΔB but same SI did not have greater single tree diameters on average, but relative dbh increments were higher (Fig. 1b). There was no clear trend in single tree heights. Thus, in general, at a given SI greater ΔB was mainly due to greater stand density: Production was higher, because stem number and standing biomass was higher. In addition, faster dbh-growth contributed to the greater ΔB.

ΔB in dependence on site conditions

The final model can be described with:

$$\Delta B_{act} = \exp \left(f(RD) + f(age) + f(T_{yr}) + f(P_{wq}) + f(T_{sd}) + f(BS) + f(sand) + f(CN) + \varepsilon \right) \quad [1]$$

where f denotes a regression spline (Table 5).

ΔB strongly depends on stand density and stand age, but plausible effects of site conditions can be fitted as well (Fig. 2). Relative density (RD) has a strong, approximately linear positive effect. ΔB decreases with increasing stand age from 30 years onwards (for model fitting plots with stand ages between 30 and 150 years were used). ΔB increases with rising mean annual temperatures (T_yr). The increase is stronger in the low and medium temperature range, whereas the slope flattens at higher temperatures. The effect of precipitation is smaller. Low summer precipitation (P_wq) clearly limits ΔB. As above a value of about

Table 4. Detailed results of the comparison between the 4 quartiles of the distribution of the residuals; Larger residuals go in line with greater ΔB at a given site index and stand age; significance levels are p = 0.05 (*), p = 0.01 (**) and p = 0.001 (***); trend denotes whether there is an increasing (+) or decreasing (-) trend with greater ΔB or whether the data exhibit no clear trend (+-); same letters denote groups that do not differ significantly.

Parameter	Significance	Trend	1. quartile	2. quartile	3. quartile	4. quartile
dbh	***	+-	a	a	b	b
height	***	+-	a	b	c	a
rel. dbh inc.	***	+	a	b	c	d
SDI	***	+	a	b	c	d
N	***	+	a	b	c	d
dg	***	-	a	ab	bc	c
biomass	***	+	a	b	c	d

800 mm confidence intervals become very wide, no conclusions should be drawn from the subsequent curve progression. ΔB is reduced at both extremes of temperature seasonality (T_sd). Optimum ΔB is reached at medium base saturation (BS), whereas high base saturation has a negative effect on ΔB. To a lesser extent low base saturation reduces ΔB as well. Low sand content (sand) has a positive effect on ΔB, whereas the effect of very high sand content is negative. ΔB decreases nearly linearly with rising C/N ratio.

Validation

Cross-validation resulted in a RMSE of 1.996 t ha^{-1} yr^{-1}. The slope of the regression of observed against predicted ΔB was nearly 1 (0.988). External validation of the model with an independent data set revealed that differences in ΔB can be predicted quite reliably (Fig. 3). The R² of the linear relationship is 0.753. RMSE was 1.652 t ha^{-1} yr^{-1}.

Discussion

ΔB as a measure for site productivity

As the trend to structurally diverse mixed stands and thinning from above reduces the informative value of SI (Pretzsch, 2009), it makes sense to look for complementary measures of site productivity (Bontemps & Bouriaud, 2014). We chose above-ground wood biomass increment (ΔB): On the one hand, ΔB encompasses height and dbh increment as well as stand density, and on the other hand it is feasible to
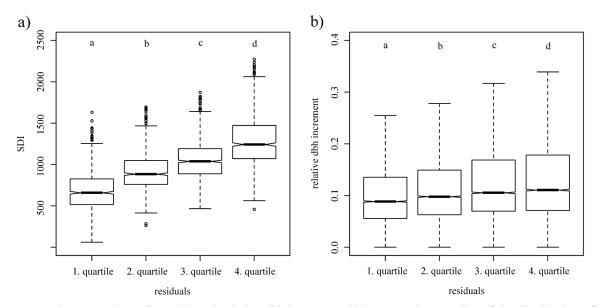

Figure 1. Comparison of SDI (a) and relative dbh increment (b) between the quartiles of the distribution of the residuals. Larger residuals go in line with greater ΔB at a given site index and stand age.

Table 5. Detailed summary of the site productivity model (edf: estimated degrees of freedom).

	Estimate	Standard error	T statistics	p value
intercept	2.119	0.004	571.335	$< 2 \times 10^{-16}$
	edf	Ref. df	F statistics	p value
f(RD)	8.124	8.799	755.645	$< 2 \times 10^{-16}$
f(age)	3.188	3.993	684.052	$< 2 \times 10^{-16}$
f(T_yr)	4.533	5.651	15.338	2.69×10^{-16}
f(P_wq)	4.896	6.033	12.314	8.22×10^{-14}
f(T_sd)	3.139	3.944	11.509	4.03×10^{-9}
f(BS)	2.669	3.335	8.364	8.12×10^{-6}
f(sand)	7.302	8.314	5.328	6.79×10^{-7}
f(CN)	1.256	1.474	15.427	6.65×10^{-6}
Adjusted R²		0.758		
RMSE		1.996 (t ha⁻¹ yr⁻¹)		
slope (observed against predicted ΔB)		0.988		

estimate ΔB based on NFI data. We preferred ΔB to volume increment for two reasons: First, it constitutes a physiological measure. Second, wood density is taken into account which facilitates the comparison between different species. The downside of the use of ΔB is that its calculation draws on assumptions about allometric relationships between different tree compartments. In comparison to stem volume increment, this leads to higher uncertainty in the estimated productivity measure.

ΔB serves as an indicator or proxy of site productivity. Therefore, when interpreting our results, we relate them to productivity. However, it has to be kept in mind that there are more aspects to net primary productivity like below-ground biomass growth and turnover of plant organs that are not taken into account. Both the allocation of NPP to different tree components as well as the turnover depend on stand density and stand age. For instance, declining woody biomass increment towards older ages does not necessarily mean that NPP is declining in the same way, but it likely reflects a change of allocation between stem biomass and the rest of the tree. This has to be kept in mind when interpreting the results.

Sites with similar SI and stand age showed noticeable variation in biomass increment: Greater ΔB was mainly due to higher stem numbers, reinforced by larger relative dbh increments. If more productive sites at similar SI and age differ more in stem number and only to a lesser degree in diameters from less productive ones, site productivity is better captured looking at ΔB of the stand than at the increment of single trees alone or mere stand height. It has to be kept in mind that this effect was found for sites of similar SI and is not a general principle. When looking at the entire data set i.e. the whole range of site indices and ages there is a clear trend to larger dg with increasing SI. The differences in productivity at same SI cannot immediately be traced back to differences in site conditions and thus be interpreted as subdivided specific yield levels, as most forests in Germany are managed and therefore differences in stand density leading to differences in productivity are mainly due to thinning. Still, maximum stand density i.e. carrying capacity on a given site depends on site conditions (Pretzsch, 2002). Favorable sites would show greater dbh increment than unfavorable sites given the same stand density. But as forest owners might tend to keep higher stem numbers at favorable sites, better site conditions are sometimes not expressed as much in greater dbh increment but in higher stand density. Thus, exploring the relationship between the variability in ΔB and stand variables at a given SI and stand age emphasized the importance of adequately dealing with stand density when modelling ΔB. Therefore, we differentiated between management effects and environmental effects on stand density by calculating a relative density in the modelling approach. This allowed us to develop a model that separates the effects of thinning from the effects of site conditions on productivity. Of course, this is an idealization as the effects of thinning regime and site quality can never be separated completely and there are many influences on stand density not encompassed by the explanatory variables used in this study. We modelled ΔB in dependence on age, relative stand density and environmental variables in one step and can predict potential ΔB by setting the relative density and age to reference values, just as height can be modelled in dependence on age and environmental variables in
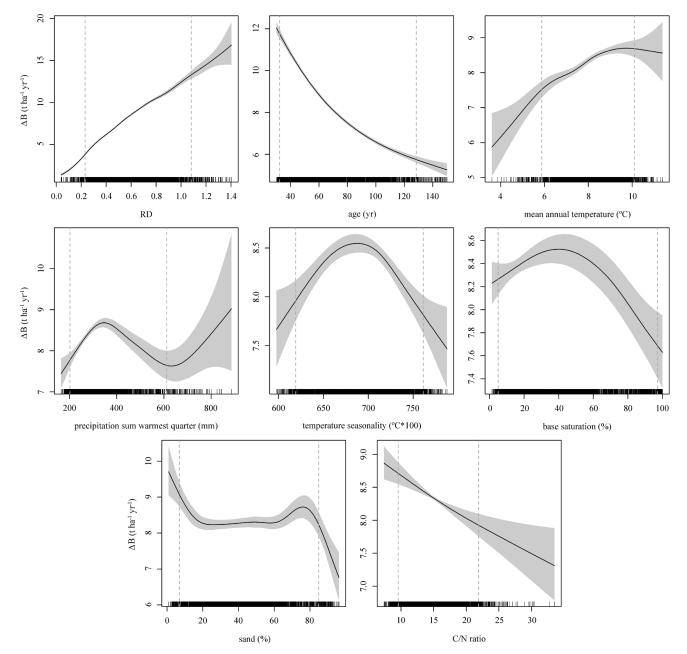
Figure 2. Effects of explanatory variables (RD, age, mean annual temperature, precipitation sum warmest quarter, temperature seasonality, base saturation, sand content and C/N ratio) on ΔB when the other variables are set to their means (table 1 and table 2). Grey areas comprise 95% pointwise prognosis intervals; a rug plot shows the distribution of the covariate; the vertical dashed lines mark the 2.5 and 97.5% quantiles of the covariate's distribution.

one step and SI can be predicted by setting age to a reference age (*e.g.* Brandl *et al.*, 2014; Vallet & Perot, 2016). Actual ΔB can be predicted by setting the relative density and age to the current values of the given plot. An alternative approach would be to first estimate a productivity measure detrended from age and density effects and in a second step model this detrended productivity index in dependence on environmental variables (*e.g.* Watt *et al.*, 2010; Charru *et al.*, 2014), which is in analogy with the approach of first deriving

the SI of a stand, i.e. detrending height of the age effect, and then modelling SI in dependence on environmental variables (*e.g.* Albert & Schmidt, 2010).

ΔB in dependence on site conditions

Overall the model shows a high goodness of fit and validation on an independent data set showed that it reliably predicts differences in ΔB. The effects of age and relative density on ΔB in the model are clear and
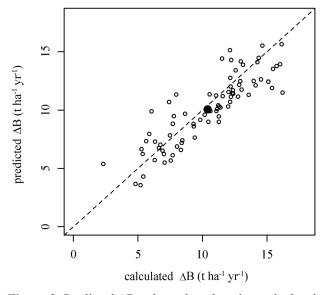
Figure 3. Predicted ΔB values plotted against calculated ΔB values for the experimental plots. The solid black dot represents the mean values of the validation dataset. The dashed line marks the 1:1 relation.

ecologically plausible: Since stand density is directly connected to leaf biomass (Pretzsch *et al.*, 2014b), dense stands reach maximum leaf area and thus maximum light interception (Zeide, 2001). Therefore, it makes sense that productivity increases with increasing stand density. This result is in contrast to Pretzsch (2006) who found a unimodal optimum relationship between stand density and growth. This contradiction might be due to our use of NFI data instead of data of experimental plots. As most German forests are managed the proportion of unthinned NFI plots with such high stand densities as to cause reductions in growth is too small to influence the model effect.

One would expect net primary productivity for a given stand to increase until an age of about 50 years and then decline again due to the changing balance between gross primary productivity and respiration during stand development (Barnes *et al.*, 1998). But in this study ΔB declines monotonously with stand age within the age range considered (30 until 150 years). On the one hand, this might indicate that the age dependence of aboveground wood biomass increment differs from the age dependence of NPP due to changes in allocation with age. On the other hand, it can be explained by our use of cross-sectional data instead of time series, i.e. we did not follow the trajectory of one stand through time. Plots of the same age can differ in their developmental stage (Mehtätalo, 2004). Replacing age by dominant height as an indicator for developmental stage reveals the expected pattern with an increase in ΔB at low dominant heights followed by a slow decline at greater heights (not shown). Still, in order to compare and

predict site productivity it is preferable to use stand age in the model (Mehtätalo, 2004).

Adding climate and soil parameters as explanatory variables renders plausible effects on ΔB. On a global scale aboveground NPP is relatively low in cold and dry climates and rapidly rises as both temperatures and water availability increase (Barnes *et al.*, 1998). This global-scale pattern can also be observed on a German scale, although we are looking at ΔB here. Temperature regime and water supply clearly are limiting factors, and as both increase, productivity rises. The most influential environmental factor in our study is mean annual temperature. This is consistent with other current studies. For instance, Pretzsch *et al.* (2014a) concluded that mainly rising temperatures and extended growing seasons increase growth. Kauppi *et al.* (2014) identified the spatial and temporal variation of growing degree days as the main causal factor affecting variations in forest growth. At the high end of the temperature range the increase of ΔB with rising temperatures slows down and approximates a more or less constant level. One might expect a decline at very high temperatures due to drought stress (Dolos *et al.*, 2015). However, due to high risks and adapted forest management spruce dominated stands in Germany simply do not occur in sufficient numbers at very high temperatures in order to clearly detect such an effect. On a global scale water supply is a crucial variable constraining biomass (Stegen *et al.*, 2011). The effect of precipitation in our study is rather weak, as water is, except in extreme drought years, not generally the growth limiting factor in our data set (spruce dominated NFI plots in Germany): Annual precipitation of 92 % of the plots exceeds the threshold value of 800 mm given by Mayer (1992) for the optimum growth range. Still, ΔB decreases when summer precipitation is low. Within the same climate ΔB differs, since it is influenced by soil properties, species composition and the stage of ecosystem development (Barnes *et al.*, 1998). The effect of base saturation on ΔB follows an optimum relationship. On acidic soils the supply of basic cations reduces growth, whereas on calcareous sites Ca-K-antagonism (Rehfuess, 1990) and immobilization of phosphor (Mellert & Ewald, 2014) can occur. Low sand content has a positive effect on ΔB, whereas high sand contents affect ΔB negatively. The effect of sand content might both reflect effects of nutrient and water supply. Soils with high sand content often have a low available water capacity and are poor in nutrients.

The proportion of explained variance by environmental variables is small, but therein comparable with other studies (*e.g.* Condés & García-Robredo, 2012; Charru *et al.*, 2014). If we could look at total volume production the effect of site conditions on productivity

would be accumulated over the whole life of the stand. The same applies to stand height. Differences in site conditions cannot be reflected as distinctly in ΔB between a time span of 10 years. For instance, when looking at a rather short time span, it is more likely that weather variability between the years does not reflect average climate conditions and thus blurs the effect of climate on growth. However, this time span in combination with corresponding climate data allows to assess short-term growth response, which can also be perceived as an advantage of this approach. Environmental data are regionalized and thus introduce uncertainty into the analysis. Environmental influences on forest growth must be summarized into a few quantifiable factors. It is no wonder that their effect is small considering the complexity of tree growth. Complex interactions between site conditions and forest management, extreme events as well as genetic variability may greatly affect productivity.

Comparisons with studies about site factors influencing biomass (*e.g.* Chave *et al.*, 2003; Keith *et al.*, 2009; Stegen *et al.*, 2011) are only possible to a certain degree, as biomass and biomass growth may react differently to environmental influences. For instance, an extension of the growing season will increase biomass growth as long as water supply is not limiting. Forest biomass may stay the same, since trees only move faster along their life's trajectory and die at a younger age, but self-thinning lines remain constant (Pretzsch *et al.*, 2014a).

Benefit of using ΔB

Productivity is often estimated based on height information alone (*e.g.* Seynave *et al.*, 2005; Albert & Schmidt, 2010; Nothdurft *et al.*, 2012), thus taking only the vertical aspect of productivity, i.e. height growth, into account. The results of this study illustrate the importance of the horizontal aspect of productivity, i.e. diameter increment and the strongly correlated branch increment as well as stand density, as sites that do not differ significantly in SI and age can still differ in productivity. Recent analyses of Norway spruce stands in Bavaria (Southern Germany) based on NFI data could be interpreted in the light of these findings: Based on NFI data similar site indices are estimated for the two Bavarian forest eco-regions Swabia and Spessart. A SI-model based on Bavarian NFI data also predicts similar site indices for these two regions (Brandl *et al.*, 2014). However, in forestry practice Swabia is generally considered the better site for spruce. Looking at our data we found that sites of similar stand age (Spessart 80 years, Swabia 76 years) and SI (Spessart 36.7 m, Swabia 36.4 m) in Swabia indeed have greater

above-ground wood biomass (Spessart 296 t ha^{-1}, Swabia 403 t ha^{-1}) and show greater above-ground wood biomass increment (ΔB) (Spessart 7.8 t ha^{-1} yr^{-1}, Swabia 9.9 t ha^{-1} yr^{-1}). In contrast to the mentioned SI-model our model predicts significant differences in productivity. Actual ΔB can be predicted using actual stand density and age (Spessart 8.4 t ha^{-1} yr^{-1}, Swabia 10.4 t ha^{-1} yr^{-1}). Setting a fixed age (*e.g.* 80 years) and a fixed relative stand density (*e.g.* 0.7) potential ΔB can be predicted (Spessart 8.7 t ha^{-1} yr^{-1}, Swabia 9.5 t ha^{-1} yr^{-1}) resulting in a difference of 9.2 % due to climate and soil. Potential ΔB cannot be compared to the measured values, but reveals differences in site potential. This example illustrates the benefit of not only looking at SI but also at ΔB when assessing site productivity.

Conclusion

As the use of SI as an indicator for site productivity is not unquestioned, we looked for a more direct measure of productivity that can be estimated based on NFI data. ΔB of the stand is a comprehensive measure of site potential as it incorporates both height and basal area increment as well as stem number. ΔB entails the difficulty of how to deal with the influence of stand density and stand age which we explored in the study. However, there is the advantage of encompassing at once a stand's productivity in the response variable with no need to consider the question of different yield levels later on. We conclude that the stand-alone use of ΔB as a measure for site potential is not recommendable, because many assumptions are needed when dealing with the effect of stand density. Still, considering both traditional SI and ΔB might result in a more accurate picture of site potential as there are sites that do not differ significantly in SI, but still differ in productivity. Using ΔB as response it was possible to fit plausible effects of site conditions. These effects are small in comparison to the effects of stand structure. Still, connecting ΔB with climatic variables allows predictions of productivity for future climatic scenarios.

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