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The relative importance of environmental drivers and their interactions on the growth of Norway spruce depends on soil unit classes: A case study from Saxony and Thuringia, Germany

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ABSTRACT

In forest management and science it is important to determine the drivers of tree growth and to quantify their relative importance with regard to forest site characteristics. The growth of individual trees depends on complex interactions of biotic and environmental drivers. Controlling the influence of biotic drivers (e.g. interspecific competition and bark beetles) is the main concern of forest management. However, large uncertainties emerge from environmental drivers and their impacts on tree growth. The aim of this study is to quantify the relative importance of environmental drivers (climate, soil, and terrain attributes) on the growth of Norway spruce trees (*Picea abies* (L.) Karst.). For that purpose, the relative basal area increment of individual spruce trees was modelled with a Boosted Regression Tree (BRT) approach. The approach is particularly suitable, since BRT quantify the relative predictor importance, taking nonlinearities and predictor variable interactions into consideration. We assume distinct differences in the growth responses to environmental drivers on three main soil unit classes (cambisol, podzol and waterlogged soils) in Saxony and Thuringia, Germany. The results of this study clearly demonstrate the importance of soil properties (available water capacity and sand content of the soil) on the growth of Norway spruce trees. Terrain attributes and water availability are crucial for Norway spruce growth on cambisol, podzol and waterlogged soils. Moreover, interactions among environmental drivers are more relevant on sites with cambisol as compared to podzol or waterlogged soils. Considering interactions between environmental drivers in the model led to significant differences in the identification of important environmental drivers. This observation was consistent among soil unit classes, especially for environmental drivers associated with water availability. Thus, the implementation of the results in growth models of high spatial resolution will support decision making in forest management, e.g. through identifying proper regions for spruce development and risk control.

1. Introduction

The long-term objective of forest management in Saxony and Thuringia (Germany) is to maintain forest functions, such as timber use, forest conservation and recreational functions (Eisenhauer et al., 2016). Norway spruce (*Picea abies* (L.) Karst.) is one of the main tree species in Saxony and Thuringia and covers a forest area of 30–50%. With an increasing frequency of heat waves, storm damages and pathogens, health and productivity of Norway spruce stands is simultaneously decreasing (Ciais et al., 2005, Biedermann et al., 2019). In order to control the nature-based disaster risk and to develop forest management strategies it is important to determine the drivers of Norway spruce growth and to quantify their relative importance with regard to forest site characteristics. The growth of individual trees depends on complex interactions between biotic and environmental drivers (e.g. Spiecker, 1999, Pretzsch, 2009). These complex interactions are rarely included in site-productivity models, especially considering environmental drivers related to terrain, soil and climate characteristics. Forest management considers or buffers the effects of biotic drivers, e.g. through thinning strategies. However, large uncertainties emerge from environmental

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drivers and their effects on tree growth. Therefore, this study seeks to gain further insight in the relative importance of environmental drivers on the growth of Norway spruce trees.

Norway spruce occurs in a wide range of areas: from high mountain ridges to the valleys in pure and mixed stands on a wide variety of soil types, terrain attributes and climatic conditions (Schmidt-Voigt, 1986). It is an ideal modeling species due to the heterogeneity of site characteristics and the high abundance in forest areas. Thus, multiple studies observed the growth of Norway spruce trees in relationship to environmental drivers in site productivity models, i.e. climate, terrain and soil attributes. These studies confirm that water availability significantly limits spruce growth (Neumann, 2001, van der Maaten-Theunissen et al., 2012, Pretzsch et al., 2014, Šrámek et al., 2019) as a result of high temperatures and low precipitation amounts (Brandl et al., 2014). The drought-sensitivity of Norway spruce is related to site elevation (i.e. altitude above sea level), where growth is temperature-limited on high elevated sites and water-limited on low-elevated sites (Ellenberg & Leuschner, 2011). In mountain areas, growth is negatively correlated with slope but positive with solar radiation (Rohner et al., 2016). Additionally, growth of Norway spruce substantially relies on nutrient availability (Albert & Schmidt, 2012, Mellert & Ewald, 2014). Soil properties determine tree growth, particularly due to different water holding capacities that buffer adverse growth conditions (Kirchen et al., 2017). These examples demonstrate that growth of Norway spruce depends on complex relationships between climate conditions, water availability and soil nutrients (Kirchen et al., 2017). As a consequence, it is rather unlikely that a single environmental driver adequately captures the spatio-temporal complexity of tree growth mechanisms (Brandl et al., 2014). It is therefore crucial to observe interactions between environmental drivers to achieve a higher accuracy of site-productivity models (Kohnle et al., 2014, Rohner et al., 2018) and thus a better understanding of spruce growth.

Several environmental drivers jointly influence trees growth in natural forest systems. While most environmental drivers directly influence tree growth (e.g. solar radiation on crown and leave development), numerous indirect and interlinked influences significantly affect tree growth, primarily via soil and terrain attributes (e.g. water availability and nutrient supply). For dendroecologists, that is the primary reason to select proper sampling sites close to the ecological limits of tree growth. Therewith, a single growth regulator distinctly controls the tree growth and linear correlation approaches are suitable to estimate the strength of relationships (Fritts, 1976). Analyses along environmental gradients are popular to study the influence of multiple predictors on tree growth. For instance, the interlinked effect of temperature and precipitation has been frequently studied along altitudinal gradients (van der Maaten-Theunissen et al., 2012; Hartl-Meier et al., 2014; Wernicke et al., 2020). Additionally, multiple regression approaches are appropriated methods to unravel the joint influences of different predictors on tree growth (Cook & Kairiukstis, 1990). Usually, site-productivity models incorporate the interaction of environmental drivers. Thereby, non-linear relationships and interactions of large-scale forest inventory data are considered as well (Albert & Schmidt, 2010, Rohner et al., 2018). Contrary, a much more holistic approach with multiple possible interactions between a response variable, climate, soil and other potential growth-limiting properties is reported in few studies (Aertsen et al., 2012, Brandl et al., 2014, Chakraborty et al., 2019). Important interactions were identified between temperature and precipitation (Albert & Schmidt, 2010, Brandl et al., 2014, Rohner et al., 2018), between temperature and drought among different soil characteristics (Chakraborty et al., 2019), as well as between soil type and nutrients (Aertsen et al., 2012). These studies revealed the importance of interactions among environmental drivers on tree growth. However, a quantification of the importance of interactions in site-productivity models is still lacking. Therefore, we applied a boosted regression tree (BRT) approach on increment data of the German national forest inventory (NFI, Thünen-Institute, 2019). BRT is a machine learning technique that explicitly includes all relevant interactions between environmental drivers.

We examined the impact of the main environmental drivers, such as climate, terrain and soil attributes, on the basal area increment of spruce trees and modeled spruce growth separately for three common soil unit classes of Saxony and Thuringia (cambisol, podzol and water influenced soils). These soil unit classes differ substantially in their water holding capacity and nutrient availability (Amelung et al., 2018) but also in terms of the applied silvicultural strategies (Blanckmeister and Hengst, 1971). For example, spruce stands at lower mountain ranges are often characterized by water influenced soil types since water shortage is a distinct problem at lower altitudes, where Norway spruce was planted outside its natural habitat. Hence, we expected that spruce growth responds differently on various environmental drivers dependent on the soil unit class.

The overall aim of this study was to quantify the importance of individual environmental drivers and to highlight the relevance of interactions between soil, terrain and climate attributes in a site-productivity model. Our BRT- approach pursued three main hypotheses: [i] the most important environmental drivers for Norway spruce growth and their interactions include soil unit class; [ii] considering interactions among environmental drivers lead to an increasing accuracy in site productivity models; [iii] interactions of environmental drivers that indicate water limitation are crucial to consider in site-productivity models of Norway spruce.

2. Material and methods

2.1. Study area and data acquisition

Decadal tree growth data originated from the repeated sampling campaigns of the German national forest inventory (NFI) 2002 and 2012 within the federal states of Thuringia and Saxony, Germany. Forest data were sampled on a 2.83 × 2.83 km grid in Saxony and a 4 × 4 km grid in Thuringia, applying consistent angle count sampling (Thünen-Institute, 2019). The climate in Thuringia and Saxony varies from arid lowlands to the humid mountain ranges of the Ore Mountains and the Thuringian Forest (highest elevation: Fichtelberg = 1215 m a.s.l., Großer Beerberg = 983 m a.s.l., respectively). Yearly mean temperature and precipitation sums ranged on average between 11.8 and 15.9 °C and 370–648 mm, respectively for the years 2002–2012.

We developed a site productivity model to gain further insight in the dependency of the basal area increment of Norway spruce to environmental drivers. The basal area increment was derived from the comprehensive databases of the NFI 2002 and 2012 (Thünen-Institute, 2019). We calculated relative basal area increment (BAI_{rel}) per tree by dividing the BAI (2002–2012) with the basal areas of trees measured during the NFI 2002. To use the BAI_{rel} as the response variable in the site-productivity model was important to account for the relationship between the increment from 2002 to 2012 and the size variability among trees, also known as allometric relationship between size and growth (Anfodillo et al., 2013). Thus, we filtered the forest inventory data with respect to comparable allometric relationships (comparable tree sizes and ages), due to predominantly capture the environmental drivers in the response variable (BAI_{rel}) instead of allometric relationships. In total, BAI_{rel} of 8019 trees from Saxony and Thuringia were included in the model. In this study, we use the terms spruce and Norway spruce interchangeable.

Data of environmental drivers were gathered from multiple sources (Table 1). Climate data (daily temperature and precipitation values) were derived from the regional climate information system (ReKIS, 2019), a database comprising interpolated climate data originating from long-term climate station records, covering the entire study region on 1 × 1 km raster cells. The mean temperature and the precipitation sums were calculated for growing seasons. The growing seasons were calculated annually for each cell of the ReKIS raster by applying the adjusted

Table 1
Environmental drivers used as predictor variables in the BRT models. Mean ± standard deviations of the environmental drivers per soil unit classes are summarized in Table S2.

Environmental driver	Abbreviation	Unit	Data source
Temperature mean	Temp	°C/growing season	ReKIS
Precipitation sum	Precip	mm/growing season	ReKIS
Standardized precipitation index	SPI		ReKIS
Solar radiation	soldir	kWh m^{-2}	SAGA-GIS
Topographic wetness index	TWI		SAGA-GIS
Available water capacity	AWC	cm^3_{H2O} cm^{-3}_{Soil}	NFI
Sand content of the soil	Sand	%	NFI
Species fraction	Spec_frac	%	NFI

formula of von Wilpert (1990). Hence, the first day of the growing season represents the average day of year including (a) the first day when a 7-day temperature mean exceeds 10 °C and (b) the first day of year when the moving windows exceeds 10 °C for 5 consecutive days. The growing season ends with the day of year when the temperature of a 7-day moving window falls below 10 °C for 5 consecutive days with the latest possible day of year being day 279 (October 5th).

The standardized precipitation index (SPI) is used to identify precipitation surpluses (i.e. humid conditions) and shortages (i.e. drought periods). The SPI is based on monthly precipitation sums from the ReKIS database and was calculated by applying the R-function “spi” from the R-package SPEI (Begueria & Vicente-Serrano, 2017). To account for the relevance of drought on the growth of spruce trees, we calculated the SPI based on the precipitation sums of 18 months prior to the focal month. Monthly SPI-values were averaged for the entire study period for each ReKIS-raster cell. The SPI is standardized and ranges between −2 to +2 standard deviations. Negative SPI-values describe sites that experienced drought and positive SPI identify sites that experienced humid conditions (McKee et al., 1993).

Terrain attributes are important drivers to quantify tree growth in site-productivity models (Ou et al., 2019, Seltmann et al., 2019). Owing to the drought sensitivity of spruce trees, we were particularly interested in terrain information that characterize water availability. Based on a digital elevation model (grid-cell size: 10 m), we computed the topographic wetness index (TWI) and the topographic solar radiation (soldir) via SAGA-GIS (“System for Automated Geoscientific Analyses”; Böhner & Selige, 2006, Conrad et al., 2015). The TWI describes the potential water availability of a site in relation to the up-slope area and the slope angle. High TWI values are related to downslope sites and valleys, where water availability is highest (Beven & Kirkby, 1979, Moore et al., 1991, Böhner & Selige, 2006). The topographic solar radiation combines information about the slope direction, the slope position and a lumped atmospheric transmittance (Böhner and Antonic, 2009; Hofierka and Suri, 2002; Wilson and Gallant, 2000).

A comprehensive data set of soil parameters along the NFI sampling points is subject to ongoing research. However, the importance of soil properties on spruce growth motivated us to implement at least the data of the available water capacity (AWC) and grain sizes in the BRT. AWC values were inferred from the database presented in Schmidt-Walter et al. (2019). Grain sizes were implemented to achieve at least some indication for the water holding capacity of the respective soils (large amounts of sand represent weak holding capacities and vice versa).

We also included a measure of forest mixture, i.e. species fraction per NFI-sampling point, to capture information about competition and thus light and nutrient regime as well as forest management strategy.

2.2. Statistical analysis

Boosted regression trees (BRT) were applied to quantify the relative importance of environmental drivers and their interactions on the growth of spruce trees. To test the relevance of different soil unit classes, we build individual BRT models for cambisol, podzol and water logged soils (WLS). BRT is a machine learning algorithm and a further development of classic CART models (classification and regression tree models; Hastie et al., 2009). A BRT-model divides the data set of the response variable into groups of predictor variables (environmental drivers) where each group represented a branch of a regression tree. This modeling step was repeated multiple times (i.e. at least 1000 trees are built in a BRT as a rule of thumb; Elith et al., 2008), where the first tree was based on the original data and all subsequent trees on the residuals of the predecessor(s). Each of the trees combined a set of predictor variables that explained BAI_{rel}. The selection of an environmental driver to this combined set allowed a quantification of the relative importance deduced from the relative count it was selected by the BRT.

BRTs are characterized by their strong predictive performance and are independent to nonlinearity and heteroscedasticity of the input data. Therewith, BRTs are recommended model approaches for comprehensive, differently scaled ecological datasets (De’ath, 2007, Elith et al., 2008). Three model parameters influence the predictive performance of BRT and must be adjusted in a process of model development: (1) the learning rate, (2) tree complexity and the (3) bag fraction. The (1) learning rate (lr) controls the fractions of the data that are modeled in each tree, i.e. smaller learning rates lead to more trees within a BRT model. (2) Tree complexity (tc) determines the interaction depth within the BRT model, e.g. tc = 1 implies that only one (i.e. solely the most important environmental driver) is used in each modeling step, while the two most important environmental drivers and their interactions are used to model the dependent variable with tc = 2. Thus, tc represents a proxy for the interactions level that is used to model the dependent variable. Each BRT model was calculated for tc = 1 to tc = 5 in order to test hypothesis [ii]. Testing the predictive performance of BRT with an increasing number of tc-values provides insight in the relevance of interactions among predictor variables (environmental drivers). Our approach is not to evaluate interactions between 5 environmental drivers but to focus on the most important interaction between 2 drivers. In each BRT-modeling step with tc ≥ 2, one of the environmental drivers has the highest explanation power. This means, a hierarchy is build up, from most to least important environmental driver and their interactions. In order to interpret these interactions ecologically meaningfull, it is most convenient to focus on the pair of environmental drivers with the highest interaction importance, even if more predictor variables were used to generate the modeling results. Relative interaction importance was calculated within the BRT based on Friedman’s H-statistic (Friedman & Popescu, 2005) to assess the relative strength of interaction effects in non-linear models. Additionally, by comparing the relative importance of environmental drivers among models with different tc (e.g. tc = 1 and tc = 3) we observed the extent of interaction importance per environmental driver. The (3) bag fraction (bf) represents the fraction of training data that was randomly selected in each modeling step.

In the process of model development we tested the optimal combination of lr (tested options: lr = 0.01, 0.005, 0.001, 0.0005, and 0.0001) and bf (tested options: bf = 0.5, 0.6, and 0.7) by comparing the prediction error of various model setups. Results of these tests for all soil classes converged for ideal lr and bf values at lr = 0.1 and bf = 0.7. To account for the stochastic behavior of the BRT-algorithm, we computed the BRT model (lr = 0.1; bf = 0.7) 100 times, observing different tc-values to quantify the importance of interactions (tc = 1, 2, 3, 4, and 5).

We calculated analysis of variance with Tukey post hoc test to evaluate the relevance of interactions by comparing the explained deviances of BRT among models with different tc-values. In like manner, we examined the effect of interactions on the variable importance of the environmental drivers of the different BRTs (tc = 1 to tc = 5). The significance levels was set to α = 0.05.

All analyses were conducted within the R-environment 3.6.1 (R Core

Team, 2019), using the packages 'dismo' (Hijams et al., 2017) and 'gbm' (Greenwell et al., 2019).

3. Results

We identified various relevant drivers for BAI_{rel} of Norway spruce trees among soil unit classes. The environmental drivers with the highest average relative contribution to BAI_{rel} were TWI, temperature and precipitation on cambisol soils (32.3%, 25.7%, and 9.8%; respectively); TWI, solar radiation and SPI on podzol soils (31.9%, 26.6%, and 12.9%; respectively); and TWI, AWC and temperature on WLS (20.6%, 17.4%, and 13.5%; respectively; Fig. 1).

The explained deviations differed significantly between models with increasing interaction depth for all soil unit classes (cambisols: $F(4,495) = 13311$, $p < 0.0001$; podzol: $F(4,495) = 2446$, $p < 0.0001$; WLS: $F(4,495) = 26612$, $p < 0.0001$) (Fig. 2). BRT with tc = 1 explained a significantly smaller amount of deviation than with tc = 2 or higher for all soil unit classes (Tukey post-hoc test: $p < 0.0001$; for all soil classes). These results highlighted that the consideration of interactions between environmental drivers in site productivity models enhanced model accuracy and thus predictive performance.

To quantify the importance of interactions, we calculated the difference between the relative variable importance of the BRT-models without (tc = 1) and with variable interactions (tc = 3). We found that TWI had –23.8% (tc1 = 14.0%, tc3 = 37.8% relative importance) and −6.3% (tc1 = 16.2%, tc3 = 22.5% relative importance) lower relative importance on cambisol and WLS in BRT with tc = 1 than with tc = 3. This means that TWI was underestimated on these soil unit classes in BRT without the consideration of interactions. On podzol, TWI revealed only a 0.4% higher relative importance in BRT with tc = 1 as compared to BRT with tc = 3. Furthermore, we observed a decreasing influence (-14.5%) of the relative importance of AWC without interaction in comparison to a three-way-interaction on cambisol and an increasing influence of solar radiation on podzol (+16.5%; Fig. 3; Fig. S2). These results show that considering interactions between environmental drivers in site-productivity models has the potential to enhance the explanation power and to provide more detailed environmental – growth relationships.

It has been demonstrated that particularly TWI, temperature and precipitation controlled BAI_{rel} of Norway spruce (Rohner et al., 2016, 2018, Schmidt-Walter et al., 2019). Our results, however, indicated a rather non-uniform and highly variable influence of the mentioned main drivers (TWI, temp, prec) on BAI_{rel} of spruce, stocking on the three soil

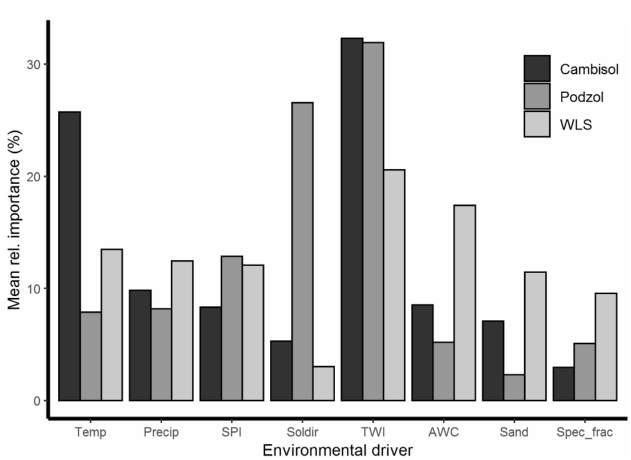

Fig. 1. Mean relative importance of environmental drivers on BAI_{rel} per soil unit class (cambisol, podzol and WLS: waterlogged soils). The mean relative importance values result from 100 model repetitions of BRT across tree complexity values tc = 1 to tc = 5. Abbreviations of environmental drivers are presented in Table 1.

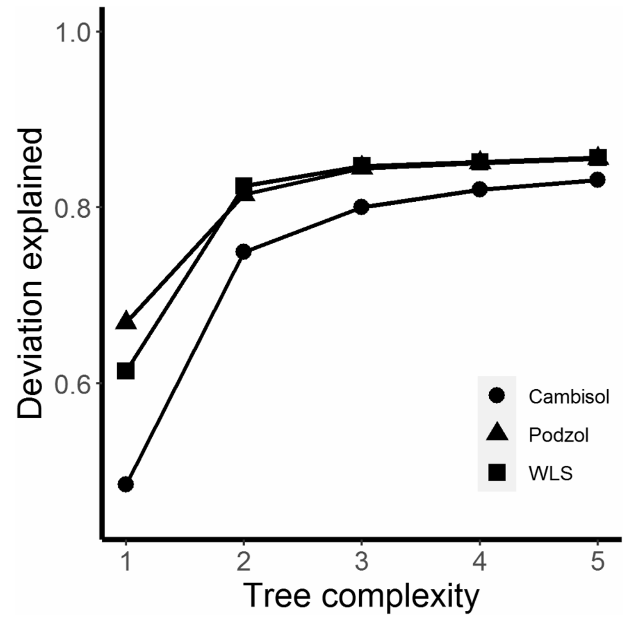

Fig. 2. Relationship between tree complexity (tc) and mean explained deviation of the BRT-model repetitions (n = 100) per soil unit class (cambisol, podzol and WLS: waterlogged soils). The increased explained deviations from tc = 1 to tc = 2 mean that BRT considering an interaction between two predictor variables (tc = 2) have a higher explanatory power than those without the consideration of interactions (tc = 1). Thus, interactions between predictor variables are more relevant on cambisol soils as compared to podzol soils and WLS.

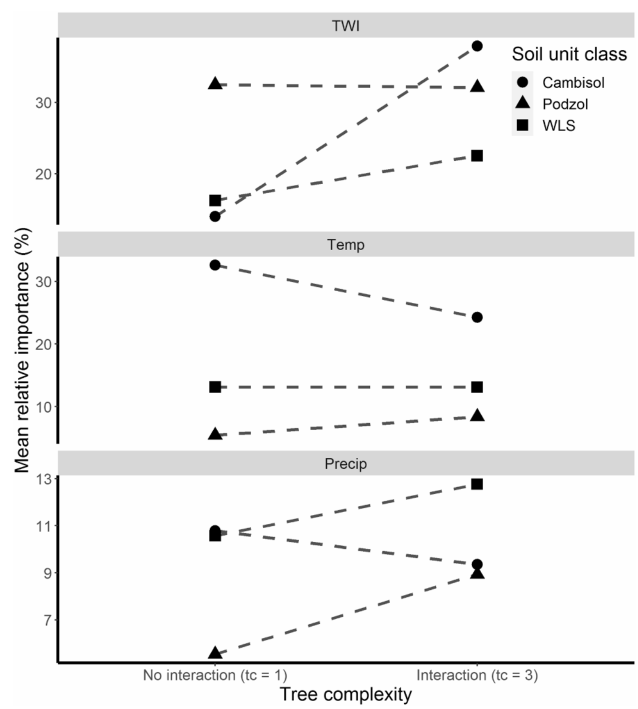

Fig. 3. Effect of BRT with interactions (tc = 3) on the variable importance of significant growth drivers of Norway spruce per soil unit class as comparison to BRT without interactions (tc = 1). The abbreviations of environmental drivers are explained in Table 1. Mean relative importance of the three focal environmental drivers is higher when considering interactions in the model (tc = 3) with the exception of TWI on podzols and precipitation on cambisols.

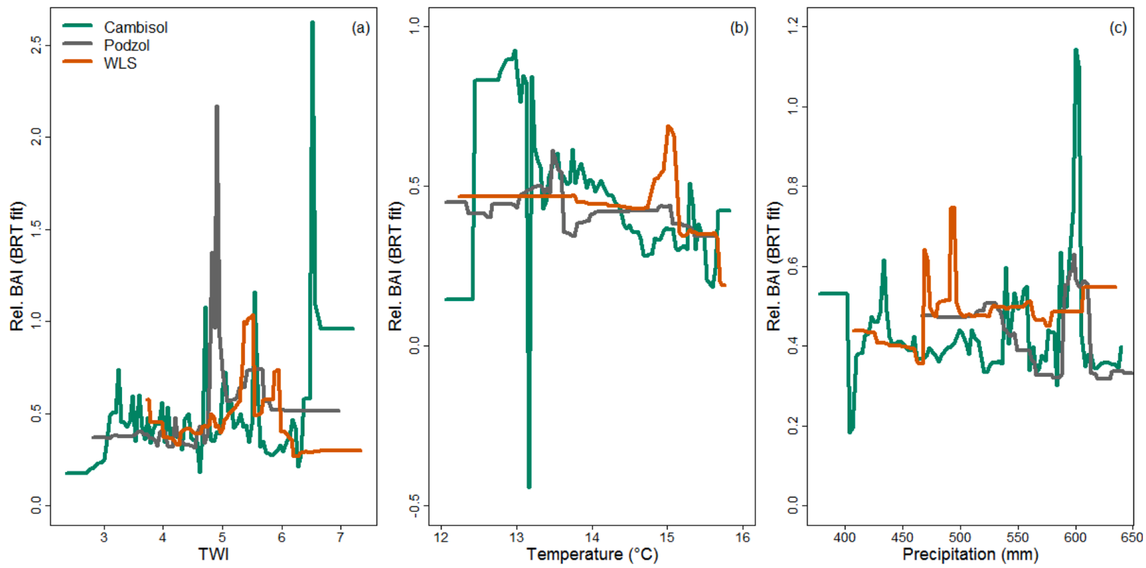

Fig. 4. Fitted BAI_{rel} values in relationship to (a) TWI, (b) temperature mean and (c) precipitation sum during the growing season per soil unit class (color code). The figure shows a varying response of spruce BAI_{rel} to similar environmental drivers, dependent on the respective soil unit class.

unit classes (Fig. 4, Fig. S1). The illustrated results considered a three-way interaction (tc = 3) due to model accuracy purposes (for further details we refer to Fig S1).

A consecutive increase in TWI induced a positive growth response of BAI_{rel} for trees on cambisols and a distinct BAI_{rel} response for trees stocking on podzols characterized by an intermediate TWI ~ 5. On WLS, optimal TWI conditions were observed between TWI = 5–6, even though the response was generally less pronounced than on cambisol and podzol (Fig. 4a). Moreover, spruce BAI_{rel} decreased on cambisols with rising temperatures. On podzol soils, the response of BAI_{rel} was less pronounced as compared to the response on cambisol soils with an optimum BAI_{rel} at approximately 13.5 °C. On WLS, highest BAI_{rel} were inferred for trees on sites with a temperature of ca. 15 °C (Fig. 4b). Further, we observed a positive relationship of spruce BAI_{rel} with increasing precipitation sums on cambisol and podzol soils. On WLS, BAI_{rel} revealed the strongest response on sites with precipitation sums between approximately 460–500 mm (Fig. 4c). Thus, the relative importance and therein the effect of various environmental drivers on BAI_{rel} depends on the respective soil unit class. The most important interactions between environmental drivers differed in dependence to soil unit class (Table 2). To model BAI_{rel}, we found that decadal temperature sums and AWC were most important on cambisols, TWI and SPI on podzols and the interaction between sand content and SPI on WLS (Fig. 5a–c, respectively).

Highest BAI_{rel} was observed on sites with cambisol soils and an interaction between low temperatures and high values of AWC (Fig. 5a). On podzol soils the highest BAI_{rel} was observed on sites with intermediate TWI and high SPI-values, i.e. under humid conditions (Fig. 5b). Low sand contents on WLS indicated high BAI_{rel} on sites with intermediate SPI-values. Increased spruce growth was also observed on WLS-sites that were characterized by an elevated sand concentration under humid condition, i.e. high SPI-values (Fig. 5c). These results indicate

Table 2
Average relative interaction importance between the two most important environmental drivers per soil unit class (BRT with tc = 3). Bold interactions are presented in Fig. 5. Abbreviations: the reader is referred to Table 1.

Soil unit class	Env. driver	Temp	Prec	SPI	Soldir	TWI	AWC	Sand	Spec_fraq
Cambisol	Temp	–	0.11	0.9	0.02	**0.82**	0.19	0.07	–
Cambisol	Prec	–	–	0.03	–	0.04	0.09	0.47	–
Cambisol	SPI	–	–	–	–	0.01	0.11	0.01	0.01
Cambisol	Soldir	–	–	–	–	0.05	0.07	–	–
Cambisol	TWI	–	–	–	–	–	0.25	0.16	–
Cambisol	AWC	–	–	–	–	–	–	0.01	0.03
Cambisol	Sand	–	–	–	–	–	–	–	–
Cambisol	Spec_fraq	–	–	–	–	–	–	–	–
Podzol	Temp	–	–	–	–	0.12	0.01	0.01	–
Podzol	Prec	–	–	–	–	0.12	–	–	–
Podzol	SPI	–	–	–	–	**0.14**	–	–	0.03
Podzol	Soldir	–	–	–	–	–	0.01	0.01	–
Podzol	TWI	–	–	–	–	–	0.06	0.01	–
Podzol	AWC	–	–	–	–	–	–	–	–
Podzol	Sand	–	–	–	–	–	–	–	–
Podzol	Spec_fraq	–	–	–	–	–	–	–	–
WLS	Temp	–	–	–	–	–	0.01	0.05	–
WLS	Prec	–	–	–	–	0.02	–	0.04	–
WLS	SPI	–	–	–	–	0.01	0.04	**0.18**	–
WLS	Soldir	–	–	–	–	–	0.01	0.01	–
WLS	TWI	–	–	–	–	–	–	0.12	0.02
WLS	AWC	–	–	–	–	–	–	–	0.02
WLS	Sand	–	–	–	–	–	–	–	0.01
WLS	Spec_fraq	–	–	–	–	–	–	–	–

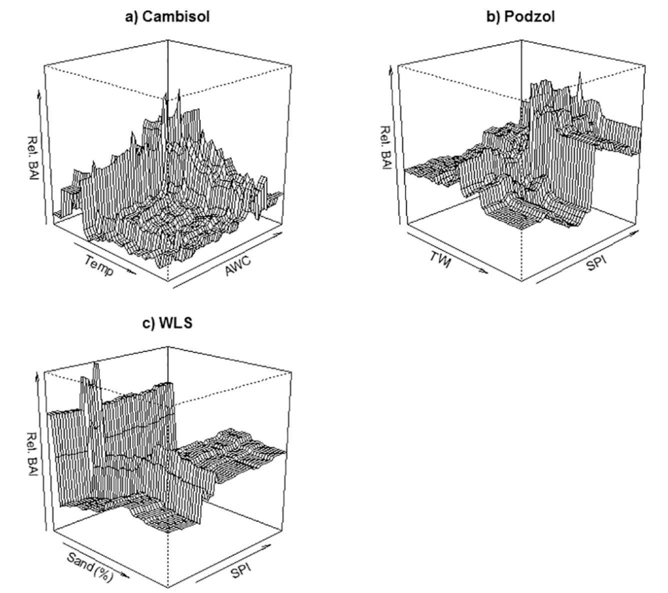

Fig. 5. Interaction plots presenting the two most relevant interactions of environmental drivers on spruce BAI_{rel} (Rel. BAI) per soil unit class (a) cambisol-, (b) podzol and (c) waterlogged soils (WLS; for all soil unit classes: BRT with tc = 3). Abbreviations: the reader is referred to Table 1.

that interactions between environmental drivers depend on the respective soil unit class, highlighting that some environmental drivers with low relative importance (e.g. sand content) are relevant explanatory variables in interaction with another environmental driver (e.g. SPI).

4. Discussion

The primary aim of this study was to depict important environmental drivers for Norway spruce BAI_{rel} on three soil unit classes by applying a site-productivity model based on BRT. Our analyses of the NFI data resulted in two conclusions about the growth of spruce trees in Saxony and Thuringia, Germany. First, terrain attributes and water availability revealed the highest relative variable importance to explain spruce growth on all three soil unit classes but with varying responses of spruce growth. Second, we found strong evidence that interactions among the environmental drivers significantly influence the BAI_{rel} among all three soil unit classes. Most important interactions were observed among environmental drivers influencing the water availability of Norway spruce.

First, terrain attributes (TWI and solar radiation) showed highest relative importance on Norway spruce BAI_{rel} across the three observed soil unit classes in Saxony and Thuringia, Germany. It has been demonstrated that particularly TWI, temperature and precipitation controlled BAI_{rel} of Norway spruce (Rohner et al., 2016, 2018, Schmidt-Walter et al., 2019). Our findings are also consistent with recent studies using machine learning approaches that identified terrain attributes (Ou et al., 2019) and the water balance in the soil (Brandl et al., 2016) as most important drivers for tree growth. These observations are also consistent with studies using linear or additive modeling approaches, showing that terrain and soil moisture attributes (Seynave et al., 2005, Rohner et al., 2018, Rabbel et al., 2018) but also climatic drivers are most relevant for tree growth (Albert & Schmidt, 2010, Hlásny et al., 2017, Chakraborty et al., 2019). Forest management strategies apply these relationships. For example, spruce stands were cultivated on sites with higher levels of water availability, especially under warmer climate conditions in Saxony and Thuringia (Wagenknecht & Belitz, 1959, Eisenhauer et al., 2016). Examinations of NFI-data documented an overall positive effect of increasing water availability and temperature on spruce growth (Albert & Schmidt, 2010, Brandl et al., 2014, Rohner et al., 2018, Chakraborty et al., 2019).

Growth responses of Norway spruce to environmental drivers depend strongly on differences between soil unit classes. The observed soil unit classes differ in their soil structure, in the ability to store resources, in the possible rooting habitat for spruce trees and thus in their potential to provide water, which is a crucial environmental driver for Norway spruce growth (Pretzsch et al., 2014, Kirchen et al., 2017, Šrámek et al., 2019). The most distinct differences in the growth response among the three soil unit classes were revealed with mean temperature, precipitation sums and TWI. The non-uniform response of spruce growth to TWI on sites with cambisol (e.g. several BAI_{rel}-peaks as response to TWI, Fig. 4a) could be influenced by the high abundance of cambisol soils that cover a wide ecological range in Saxony and Thuringia (78% of observed trees were found on cambisol, 12% on WLS, and 10% on podzol). Thus, the variability of site conditions may be larger on cambisols as compared to podzols and WLS, e.g. in terms of terrain, water availability and climate conditions (Moldenhauer et al., 2013). In this perspective, podzols are supposed to be the main soil class at sandy sites that are characterized by TWI $\sim$ 5. That implies an increased drought sensitivity and positive response to high precipitation amounts of the stocking trees, due to the weak water holding capacity of podzols. WLS are characterized by highest water holding capacities among the three soil unit classes and provide a suitable habitat for Norway spruce in lower mountain ranges where average temperatures are greater as compared to sites at higher elevations. Thus, spruce has higher BAI_{rel} on WLS-sites with high average temperatures, whereas the BAI_{rel} response on warm temperatures on cambisols is opposite. These sites with high average temperatures are found in the lower mountain ranges in Saxony and Thuringia, i.e. outside of the natural habitat of spruce trees. Cambisol soils occur primarily in higher elevations on sites with low temperatures, i.e. within the natural habitat of spruce trees (Ellenberg, 1988).

Spruce growth on cambisol and podzol soils increases with increasing TWI, i.e. BAI_{rel} was higher on mid- and down-slope sites as compared to up-slope or mountain ridge sites. Because of water runoff, water availability on up-slope sites is frequently lower as compared to mid- and down-slope sites. Thus, water limitation and subsequently growth suppression is higher on upslope and mountain ridge sites as compared to mid- and down-slope positions. Interestingly, we revealed a peak in BAI_{rel} for podzol sites at mid-slope position. This result was surprising because podzol soils have a lower water holding capacity as compared to cambisol soils (Amelung et al., 2018) and thus were expected to foster high levels of BAI_{rel} on down-slope sites. The different growth responses per environmental driver confirm that it is important to consider soil properties in site-productivity models. Further studies are required to investigate specific characteristics of soil-growth heterogeneity in forest systems.

Second, our results strongly corroborated the consideration of predictor-interactions in site-productivity models. We found a higher model accuracy and detailed insights in the importance of environmental drivers on tree growth when considering at least 2 interactions. This is in line with recent studies using machine learning algorithms describing the importance of interactions between climate, site conditions and competitive effects on tree growth (Chakraborty et al., 2019, Ou et al., 2019). But model accuracy did not further increase in models where 3 or more interactions were considered. It means that interactions between 3 or more environmental drivers explain spruce growth as good as interactions between 2 environmental drivers. This finding can be related to the classic niche theory, stating that growth of an organism depends only on few important drivers (Fritts, 1976, Stine, 2019) out of the combined influences of the habitat (i.e. the multitude of environmental and biotic drivers; Hutchinson, 1957). Our findings confirmed that especially the joint influence of climate and soil properties induce even stronger responses of tree growth as compared to the pure single effect of climate or soil property. These findings are related to results from tree-interaction studies from Switzerland (Chakraborty et al., 2019), underlying the complexity of forest ecosystems.

Climatic drivers were more relevant as compared to soil characteristics due to indirect effects, i.e. interactions with soil parameters (Chakraborty et al., 2019). Similarly, when considering interactions we found an increase in relative importance of TWI, mean temperature and precipitation sums in seven out of nine models of different soil unit classes. Some important processes that influence tree growth, above all the water availability, result from complex interactions between environmental drivers and show temporal and spatial heterogeneity. Drought as the most important limitation for spruce growth (Bréda et al., 1995, Pretzsch & Dieler, 2010) depends on multiple environmental and biotic factors, e.g. temperature, precipitation, terrain attributes, altitude, soil type, forest structure and species mixing (e.g. Bouriaud & Popa, 2009, van der Maaten-Theunissen et al., 2012, Rötzer et al., 2017). In addition to drought, recent studies emphasized primarily the relevance of temperature interactions with water availability (Brandl et al., 2014, Ou et al., 2019), interactions of climatic drivers with elevation gradients (van der Maaten-Theunissen et al., 2012) and interactions of climatic drivers with competition (Piutti & Cescatti, 1997, Wright et al., 2018). Thus, the consideration of interactions between various environmental drivers in site-productivity models helps to gain a better understanding of tree growth, especially with higher spatial precision and in relation with forest community dynamics.

Our results show that interactions between environmental drivers are crucial to model the site-productivity of Norway spruce trees on different soil unit classes. The strong influence of interactions on sites with cambisol soils and the overall underestimation of water-availability drivers in models that do not consider interactions was striking, especially given the emphasis on the high relevance of these drivers in existing published literature about the growth of Norway spruce. The documented relevance of interactions between environmental drivers and their soil unit class – dependency suggest that site-productivity models may further improve the prediction ability of Norway spruce growth pattern, e.g. in studies that observe drought scenarios. Based on the presented analytical framework using the comprehensive data sources of the NFI we suggest incorporating site-specific details and interactions between environmental drivers in site-productivity models. Furtheron, the relevance of biotic drivers (e.g. competition) should be predicted based on the resulting interactions of our model, e.g. the competitive changes that result during thinning strategies. Forest management strategies aim to identify optimal growth regions for Norway spruce in dependency of changing environmental conditions (e.g. through climate change) with the long-term objective to secure the growth potential and control the nature-based disaster risk of Norway spruce on large forest areas in Saxony and Thuringia.

CRediT authorship contribution statement

Christian Torsten Seltmann: Conceptualization, Methodology, Data curation, Formal analysis, Writing - original draft. **Jakob Wernicke:** Writing - review & editing, Conceptualization. **Rainer Petzold:** Writing - review & editing, Conceptualization. **Martin Baumann:** Writing - review & editing, Conceptualization. **Kristian Münder:** Funding acquisition, Supervision. **Sven Martens:** Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118671.

References

Aertsen, W., Kint, V., De Vos, B., Deckers, J., van Orshoven, J., Muys, B., 2012. Predicting forest site productivity in temperate lowland from forest floor, soil and litterfall characteristics using boosted regression trees. Plant Soil 354, 157–172. https://doi.org/10.1016/j.ecolmodel.2010.01.007.

Albert, M., Schmidt, M., 2010. Climate-sensitive modelling of site-productivity relationships for Norway spruce (Picea abies (L.) Karst.) and common beech (Fagus sylvatica L.). For. Ecol. Manage. 259 (4), 739–749. https://doi.org/10.1016/j.foreco.2009.04.039.

Albert, M., Schmidt, M., 2012. Standort-Leistungs-Modelle für die Entwicklung von waldbaulichen Anpassungsstrategien unter Klimawandel. Archiv für Forstwesen und Landschaftsökologie 46 (2), 57–71.

Amelung, W., Blume, H.-P., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., Wilke, 2018. Scheffer/Schachtschabel Lehrbuch der Bodenkunde. Springer Spektrum, Berlin.

Anfodillo, T., Carrer, M., Simini, F., Popa, I., Banavar, J.R., Maritan, A., 2013. An allometry-based approach for understanding forest structure, predicting tree-size distribution and assessing the degree of disturbance. Proc R Soc B 280, 20122375. https://doi.org/10.1098/rspb.2012.2375.

Begueria, S., Vicente-Serrano, S.M., 2017. SPEI: Calculation of the standardised precipitation-evapotranspiration index. R package version 1.7. https://CRAN.R-project.org/package=SPEI.

Beven, K.J., Kirkby, M.J., 1979. A physically-based variable contributing area model of basin hydrology. Hydrol. Sci. Bullet. 24 (1), 43–69.

Biedermann, P.H.W., Müller, J., Grégoire, J.C., Gruppe, A., Hagge, J., Hammerbacher, A., Hofstetter, R.W., Kandasamy, D., Kolarik, M., Kostovcik, M., Krokene, P., Sallé, A., Six, D.L., Turrini, T., Vanderpool, D., Wingfield, M.J., Bässler, C., 2019. Bark beetle population dynamics in the anthropocene: challenges and solutions. Trends Ecol. Evolut. 34 (10), 914–924. https://doi.org/10.1016/j.tree.2019.06.002.

Böhner, J., Selige, T., 2006. Spatial prediction of soil attributes using terrain analysis and climate regionalisation. In: Boehner, J., McCloy, K.R., Strobl, J. (Eds.), SAGA – Analysis and Modelling Applications, Goettinger Geographische Abhandlungen, Goettingen, pp. 13–28.

Blanckmeister, J., Hengst, E., 1971. Die Fichte im Mittelgebirge. Neumann Verlag, Radebeul.

Böhner, J., Antonic, O., 2009. Land surface parameters specific to topo-climatology. In: Hengl, T., Reuter, H.I. (Eds.), Geomorphometry – Concepts. Software, Applications.

Bouriaud, O., Popa, I., 2009. Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. Trees 23, 95–106.

Brandl, S., Falk, W., Klemmt, H.J., Stricker, G., Bender, A., Rötzer, T., Pretzsch, H., 2014. Possibilities and limitations of spatially explicit site index modelling for spruce based on national forest inventory data and digital maps of soil and climate in Bavaria (SE Germany). Forests 5, 2626–2646. https://doi.org/10.3390/f5112626.

Brandl, S., Falk, W., Mette, T., Tötzer, T., Pretzsch, H., 2016. Standortsensitive Modellierung der Produktivität. DVFFA - Sektion Ertragskunde, Beiträge zur Jahrestagung 89–101.

Bréda, N., Granier, A., Barataud, F., Moyne, C., 1995. Soil water dynamics in an oak stand. Plant Soil 172, 17–27. https://doi.org/10.1007/BF00020856.

Chakraborty, D., Jandl, R., Kapeller, S., Schueler, S., 2019. Disentangling the role of climate and soil on tree growth and its interaction with seed origin. Sci. Total Environ. 654, 393–401. https://doi.org/10.1016/j.scitotenv.2018.11.093.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesalal, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533. https://doi.org/10.1038/nature03972.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for automated geoscientific analyses

(SAGA) v. 2.1.4. Geosci. Model Dev. 8, 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015.
Cook, E.R., Kairiukstis, L.A., 1990. Methods of Dendrochronology – Applications in the Environmental Sciences. Springer, Dordrecht. http://doi.org/10.1007/978-94-015-7879-0.
De'ath, G., 2007. Boosted trees for ecological modeling and prediction. Ecology 88 (1), 243–251. https://doi.org/10.1890/0012-9658(2007)88[243:BTFEMA]2.0.CO;2.
Eisenhauer, D.R., Gemballa, R., Petzold, R., Wolf, H., Schlutow, A., Otto, L.F., Baier, P., 2016. Klimarisiken und Anpassungsmöglichkeiten für Fichten- und Kiefernforste in Sachsen. In: Eichhorn, J., Guericke, M., Eisenhauer, D.-R. (Eds.), Waldbauliche Klimaanpassung im regionalen Fokus: Sind unsere Wälder fit für den Klimawandel? oekom Verlag, München.
Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.
Ellenberg, H., Leuschner, C., 2011. Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgard.
Ellenberg, H., 1988. Vegetation Ecology of Central Europe, fourth ed. Cambridge University Press, Cambridge.
Friedman, J.H., Popescu, B.E., 2005. Predictive learning via rule ensembles. Ann. Appl. Stat. 2 (3), 916–954. Sept. 2008.
Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London, New York, San Francisco.
Greenwell, B., Boehmke, B., Cunningham, J., GBM-Developers, 2019. gbm: Generalized boosted regression models, R-package version 2.1.5, https://CRAN.R-project.org/package=gbm.
Hartl-Meier, C., Dittmar, C., Zang, C., Rothe, A., 2014. Mountain forest growth response to climate change in the Northern Limestone Alps. Trees 28 (3), 819–829.
Hastie, T., Tibshirina, R., Friedman, J., 2009. The Elements of Statistical Learning. Springer Science and Business Media, New York.
Hijams, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. dismo: Species dristribution modeling. R-package version 1.1-4, https://CRAN.R-project.org/package=dismo.
Hlásny, T., Trombik, J., Bošeľa, M., Merganič, J., Marušák, R., Šebeň, V., Štěpánek, P., Kubišta, J., Trnka, M., 2017. Climatic drivers of forest productivity in Central Europe. Agric. For. Meteorol. 234–235, 258–273. https://doi.org/10.1016/j.agrformet.2016.12.024.
Hofierka, J., Suri, M., 2002. The Solar Radiation Model for Open Source GIS: Implementation and Applications. International GRASS users conference in Trento, Italy.
Hutchinson, G.E., 1957. Cold Spring Harb. Symp. Quant. Biol. 22 (2), 415–427.
Kirchen, G., Calvaruso, C., Granier, A., Redon, P.O., Van der Heijden, G., Bréda, N., Turpault, M.P., 2017. Local soil type variability controls the water budget and stand productivity in a beech forest. For. Ecol. Manage. 390, 89–103. https://doi.org/10.1016/j.foreco.2016.12.024.
Kohnle, U., Albrecht, A., Lenk, E., Ohnemus, K., Yue, C., 2014. Zuwachsttrends im Spiegel langfristiger Versuchsflächen in Südwestdeutschland. Allgemein Forst- und Jagdzeitung 185, 97–117.
McKee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. In: Anaheim, C.A. (Ed.), Preprints, Eighth Conference on Applied Climatology. American Meteorological Society, pp. 179–184.
Mellert, K.H., Ewald, J., 2014. Nutrient limitation and site-related growth potential of Norway spruce (Picea abies [L.] Karst) in the Bavarian Alps. Eur. J. Forest Res. 133 (3), 433–451. https://doi.org/10.1007/s10342-013-0775-1.
Moldenhauer, K.-M., Heller, K., Chliffard, P., Hübner, R., Kleber, A., 2013. Influence of Cofer Beds on Solpe Hyrology. In: Kleber, A., Terhorst, B. (Eds.), Mid-Latitude Slope Deposits (Cover Beds). Developments in Sedimentology, vol. 66, pp. 127–152.
Moore, I.D., Grayson, R.B., Ladson, A.R., 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. Hydrol. Process. 5 (1).
Neumann, U., 2001. Zusammenhang von Witterungsgeschehen und Zuwachsverlaufen in Fichtenbestanden des Osterzgebirges. Forstwissenschaftliche Beitrage Tharandt, Verlag Eugen Ulmer, Stuttgart.
Ou, Q., Lei, X., Shen, C., 2019. Individual tree diameter growth models of larch–spruce–fir mixed forests based on machine learning algorithms. Forests 10, 187. https://doi.org/10.3390/f10020187.
Piutti, E., Cescatti, A., 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can. J. For. Res. 27 (3), 277–284. https://doi.org/10.1139/x96-176.
Pretzsch, H., 2009. Zur Verteilung des Zuwachses zwischen den Bäumen eines Bestandes und Abhängigkeit des Verteilungsschlüssels von den Standortbedingungen. Allgemeine Forst- und Jagdzeitung 181 (1), 4–13.
Pretzsch, H., Dieler, J., 2010. 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, 355–369.
Pretzsch, H., Rötzer, T., Matyssek, R., Grams, T.E.E., Häberle, K.H., Pritsch, K., Kerner, R., Munch, J.C., 2014. Mixed Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica [L.]) stands under drought: from reaction pattern to mechanism. Trees 28, 1305–1321. https://doi.org/10.1007/s00468-014-1035-9.
R Core Team, 2019. R: A language and environmenta for statistical computing. R foundation for Statistical computing, Vienna, Austria. https://www.R-project.org/.
Rabbel, I., Neuwirth, B., Bogena, H., Diekkrüger, B., 2018. Exploring the growth response of Norway spruce (Picea abies) along a small-scale gradient of soil water supply. Dendrochronologia 52, 123–130. https://doi.org/10.1016/j.dendro.2018.10.007.
ReKIS: Regionales Klimainformationssystem für Sachsen, Sachsen-Anhalt und Thüringen, 2019. http://141.30.160.224/fdm/rekisViewer.jsp#menu-1 (accesses on 01. July 2019).
Rötzer, T., Biber, P., Moser, A., Schäfer, C., Pretzsch, H., 2017. Stem and root diameter growth pf European beech and Norway spruce under extreme drought.
Rohner, B., Weber, P., Thürig, E., 2016. Bridging tree rings and forest inventories: how climate effects on spruce and beech growth aggregate over time. For. Ecol. Manage. 360, 159–169. https://doi.org/10.1016/j.foreco.2015.10.022.
Rohner, B., Waldner, P., Lischke, H., Ferretti, M., Thürig, E., 2018. Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. Eur. J. Forest Res. 137, 29–44. https://doi.org/10.1007/s10342-017-1087-7.
Schmidt-Walter, P., Ahrends, B., Mette, T., Puhlmann, H., Meesenburg, H., 2019. NFI 2012 water budgets and drought stress indicators database. Göttingen 2018. Open Agrar Repositorium. https://doi.org/10.3220/DATA/20181108-095429.
Schmidt-Vogt, H., Jahn, G., Vogellehner, D., 1987. Die Fichte, Band 1: Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften.Verlag paul Parey, Hamburg, Berlin.
Seltmann, C.T., Wernicke, J., Münder, K., Martens, S., 2019. Einzelbaumweise Zuwachsmodellierung der Fichte im sächsischen Mittelgebirge mit boosted regression trees. DVFFA – Sektion Ertragskunde. Beiträge zur Jahrestagung 115–126.
Seynave, I., Gégout, J.C., Hervé, J.C., Dhôte, J.F., Drapier, J., Bruno, É., Dumé, G., 2005. *Picea abies* site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. Can. J. For. Res. 35 (7), 1669–1678. https://doi.org/10.1139/x05-088.
Spiecker, H., 1999. Overview of recent growth trends in European forests. Water Air Soil Pollut. 116, 33–46. https://doi.org/10.1023/A:1005205515952.
Šrámek, V., Neudertová Hellebrandová, K., Fadrhonsová, V., 2019. Interception and soil water relation in Norway spruce stands of different age during the contrasting vegetation seasons of 2017 and 2018. J. Forest Sci. 65, 51–60. https://doi.org/10.17221/135/2018-JFS.
Stine, A.R., 2019. Global demonstration of local Liebig's law behavior for tree-ring reconstructions of climate. Paleoceanogr. Paleoclimatol. 4, 203–216. https://doi.org/10.1029/2018PA003449.
van der Maaten-Theunissen, M., Kahle, H.P., van der Maaten, E., 2012. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. Ann. Forest Sci. 70, 185–193. https://doi.org/10.1007/s13595-012-0241-0.
von Wilpert, K., 1990. Die Jahrringstruktur von Fichten in Abhängigkeit vom Bodenwasserhaushalt auf Pseudogley und Parabraunerde. Institut fur Bodenkunde und Waldernahrungslehre, Freiburg.
Wagenknecht, E., Belitz, G., 1959. Die Fichte im nordostdeutschen Flachland. Neumann Verlag; Radebeul, Berlin.
Wernicke, J., Körner, M., Möller, R., Seltmann, C.T., Jetschke, G., Martens, M., 2020. The potential of Generalized Additive Modelling for the prediction of radial growth of Norway spruce from Central Germany. Dendrochronologia. https://doi.org/10.1016/j.dendro.2020.125743.
Thünen-Institute, 2019. Dritte Bundeswaldinventur - Ergebnisdatenbank, https://bwi.info (accessed on 01 July 2019).
Wilson, J.P., Gallant, J.C., (Eds.), 2000. Terrain Analysis – Principles and Applications. New York, John Wiley & Sons.
Wright, M., Sherriff, R.L., Miller, A.E., Wilson, T., 2018. Stand basal area and temperature interact to influence growth in white spruce in southwest Alaska. Ecosphere 9 (10), e02462. https://doi.org/10.1002/ecs2.2462.