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Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands

Julia Juchheim *, Christian Ammer, Peter Schall, Dominik Seidel

Department of Forest Ecology and Silviculture of the Temperate Zones, Faculty of Forest Science, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

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A B S T R A C T

Silvicultural success in achieving, among other management goals, maximum productivity strongly depends on knowledge of the relationship between stand density and the resulting growth response of a stand. However, there are still controversial discussions whether wood production can be enhanced by silvicultural thinning or reaches its maximum in unmanaged forest stands if time plays no role. Moreover there is no universal answer whether structural diversity promotes or reduces productivity. In the present study we applied terrestrial laser scanning (TLS) to investigate the relationship between three-dimensional space filling, forest management intensity, productivity and conventional measures of structural diversity. We examined 35 beech-dominated forest plots along a gradient of management intensity in three regions of Germany. We found that space filling in leaf-on condition increased with management intensity, particularly in the shaded crown. Increased space filling in the shaded crown due to tree removals also resulted in higher stand productivity. We conclude that an increased space filling in the shaded canopy of managed European beech stands is responsible for the compensation of production losses in the upper canopy due to thinning activities. Conventional measures of structural diversity were not sensitive to the applied silvicultural activities. We also found no relationship between structural diversity described by conventional measures and stand productivity.

1. Introduction

For decades forest management aimed at optimizing growth and yield in a stand under given environmental conditions and tree species compositions (Pretzsch, 2005; Puettmann et al., 2015). Silvicultural success in achieving, among other management goals, maximum productivity strongly depends on knowledge of the relationship between management type and intensity, leading to a certain forest structure and the resulting growth response of a stand (e.g. Röhrig et al., 2006).

An important management tool to control stand development and stability is the thinning intensity. It affects the density of a stand and temporarily reduces the competition enforced on the remaining trees. As a result it has a strong impact on stand structure and tree growth, but also on the response to stressors such as drought (Ammer, 2017). Finally, thinnings may increase the revenue of forest management (Knoke, 1998; Mäkinen and Isomäki, 2004). Therefore, relating tree growth to stand density plays a pivotal role in forest management. Of particular importance was the identification of the optimal density for a given management goal. That is why Zeide (2004) called "forestry the science of density optimization". If one aims at maximized stand level productivity optimal density is usually addressed as the basal area at which the annual basal area increment reaches the maximum on a given site (cf. Assmann, 1970). Langsæter (1943) was among the first researchers who postulated a relationship between volume increment and stand density. Based on long-term thinning experiments in European beech (*Fagus sylvatica* L.) stands Assmann (1970) found evidence for this hypothesis. More specifically, he identified a hump-shaped relationship between stand density and productivity. As long as the increased growth responses of favored trees outweigh the negative effects which may be associated with the removal of trees, the productivity curve is ascending; when the positive and the negative effects are in balance it reaches a peak and when the negative effects predominate the curve declines. Assmann (1970) explained this finding with the positive effects of thinning on the growth of the remaining trees due to increased resource availability. However, the existence of an 'optimal density' was questioned in the past (Curtis et al., 1997) and was shown to be depending on species identity, age and site fertility (Pretzsch, 2005). Moreover, there are still controversial discussions whether wood production can be enhanced by silvicultural thinning or reaches its maximum in unmanaged forest stands if time plays

* Corresponding author.
E-mail address: jjuchhe@gwdg.de (J. Juchheim).

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no role (Pretzsch, 2005; Seidel et al., 2015). Another feature determining tree and stand growth is the thinning type. Contrasting thinning types such as thinning from above (removing co-dominant trees) or thinning from below (removing mainly suppressed trees) strongly impact stand structure. It is well known that repeated removals of overstorey trees lead to a higher resource availability for mid- and understorey trees and result in more heterogeneous stand structures than thinnings from below which cause a structural homogenization (Röhrig et al., 2006). However, as for thinning intensity it is controversially discussed whether or not structural diversity results in higher (Lei et al., 2009; Dănescu et al., 2016) or lower stand growth (Liang et al., 2007; Long and Shaw, 2010; Ryan et al., 2010; Luu et al., 2013; Soares et al., 2016).

For practical convenience, in forestry the intensity of thinning activities is commonly quantified by the amount or proportion of basal area removed. Basal area can easily be measured and controlled in the field and is widely used as a measure to identify the optimal density, e.g. for maximum timber production. It does however not provide insight into the physiological explanation for productivity differences, e.g. the actual presence or absence of photosynthetically active plant material or the amount of available light in a stand. Other stand characteristics, for example leaf area, which are related to tree vitality, control light interception, carbon assimilation and transpiration (Lendzion and Leuschner, 2008) and affect productivity more directly. However, difficulties in determining characteristics like leaf area in the field hampered their wide application. To gain a deeper understanding of the relationship between stand density and productivity Harry et al. (1964) introduced the idea of 'crowding'. Crowding however changes with tree size and average distance among trees (Assmann, 1970; Zeide, 2005). A meaningful alternative to crowding is Reinecke's stand density index (SDI; Reineke, 1933). This index relates the actual stand density to a theoretical maximum stocking density and is independent from age, diameter, site quality, and other variables (Zeide, 2005). As an alternative to density measures indices of structural complexity, such as the Gini coefficient of diameters or the Shannon index of diameters (e.g. Dănescu et al., 2016), were used to investigate the structure-productivity relationship. So far, there is no universal answer and it is controversially discussed whether structural diversity promotes or reduces productivity (Ishii et al., 2004, Dănescu et al., 2016; Soares et al., 2016).

A more meaningful quantitative measure to explain how management intensity affects stand density and how this feeds back to productivity may be the amount of space occupied by tree components, i.e. space filling. Unfortunately, the inaccessibility, sheer size and structural complexity of a forest stand hindered most approaches to address the actual space filling, meaning the three-dimensional density that takes into account all above-ground tree compartments including the leaves, at different stand densities.

Today, terrestrial laser scanning (TLS) is available as a powerful tool to measure comprehensive spatial structures in complex environments such as forests with reasonable effort (e.g. Watt and Donoghue, 2005; Dassot et al., 2011; Liang et al., 2016; Seidel et al., 2016a). The ground-based perspective of TLS allows for a detailed representation of the forest from the ground up to the canopy, especially if data from a large number of scan positions is combined (e.g. Danson et al., 2007). The technology also proved useful to determine the actual three-dimensional space filling of forests (Seidel et al., 2013).

The present study applied TLS in beech-dominated forests to investigate the relationship between three-dimensional space filling, forest management intensity, productivity and conventional measures of structural diversity. Our hypotheses are that (i) space filling, productivity and structural diversity are affected by management intensity, (ii) stand productivity increases with space filling but not with structural diversity described by conventional measures.

2. Materials and methods

2.1. Study sites

The investigation was conducted within the framework of the Biodiversity Exploratories (www.biodiversity-exploratories.de), a long-dated and large-scaled project for biodiversity research (Fischer et al., 2010). The study plots of the Biodiversity Exploratories are located in three regions across Germany: the Biosphere Reserve Swabian Alb in the South-western part of Germany, the National Park Hainich and its surrounding areas in Central Germany and the UNESCO Biosphere Reserve Schorfheide-Chorin in the North-eastern part of Germany (Table 1).

For our study we selected 35 beech-dominated forest plots along a gradient of management intensity. We classified forest management intensity by using the silvicultural management intensity indicator (SMI; Schall and Ammer, 2013). The indicator consists of two components, the risk of stand loss which is mainly driven by the tree species, and the relative stand density. It scales from 0 to 1. The first component quantifies the age dependent survival probabilities due to natural hazards at or before a reference age (180 years), while the second refers actual stand biomass to biomass carrying capacity of the site, calculated from yield tables. Both components are tree-species specific and reflect the central forest management decisions: choice of tree species and control of stand density (Schall and Ammer, 2013). The selected plots represent the main beech forest management types in Central Europe and comprise unmanaged stands and managed uneven-aged and even-aged stands. In order to reduce the effect of age and species diversity on space filling and stand productivity we selected stands with the developmental stage of mature timber (90–180 years old) and absent or low admixture of other tree species than beech (proportion of beech on total basal area: 70–100%).

2.2. Terrestrial laser scanning and sampling design

Around the center of each plot an area of 45 m × 45 m was scanned with a Faro Focus 3D (Faro Technologies Inc., Lake Marry, USA) terrestrial laser scanner. The scanner was mounted at breast height (1.3 m) on a tripod and covered a field of view of 360° and 305° in horizontal and vertical direction respectively. The angular step width was set to 0.035°, resulting in about 44.4 million measurements per scan. Scans were conducted in summer 2014 and

Table 1
Summary of climatic and edaphic properties of the study plots. MAP = mean annual precipitation; MAT = mean annual temperature; N = number of investigated plots. For more detailed information about the research plots see Fischer et al. (2010).

	Swabian Alb	Hainich-Dün	Schorfheide-Chorin
Location	SW Germany	Central Germany	NE Germany
Elevation (m a.s.l.)	460–860	285–550	3–140
MAP (mm)/ MAT (C°)	700–1000/6–7	500–800/6.5–8	500–600/8–8.5
Dominant soil type forest	Eutric Cambisol	Luvisol	Dystric Cambisol
Investigated forest types	Mature even-aged forest (N = 5); unmanaged forest (N = 3)	Mature even-aged forest (N = 5); unmanaged forest (N = 7); uneven-aged forest (N = 5)	Mature even-aged forest (N = 5); unmanaged forest (N = 5)