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Competition, tree age and size drive the productivity of mixed forests of pedunculate oak, beech and red oak

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ABSTRACT

In order to understand the relationship between tree diversity and forest productivity, it is crucial to understand what is going on at the level of individual trees, since each tree responds to the prevailing environmental conditions and interacts with his neighbours. We explored tree interactions in 53 forest plots in northern Belgium (*TREEWEB* platform) containing all possible combinations of pedunculate oak, beech and red oak. We cored 307 trees and determined the average annual basal area increment for the last 10 years for each sampled tree. We investigated the importance of neighbourhood competition, tree age an size for tree-level growth and then scaled up the species-specific tree growth to stand-level productivity. By exploring how competition, tree age and size varied along the studied gradient of tree species richness, we were able to explain the observed species-specific tree level and stand-level growth along the tree species richness gradient. We found no relationship between tree species richness and forest productivity, due to contrasting growth patterns of the three species along the richness gradient: the growth of pedunculate oak decreased, growth of beech was constant and growth of red oak increased along the tree species richness gradient. Increased heterospecific competition was the main reason for the observed lower growth of pedunculate oak in mixtures, whereas variation in tree age and size along the studied tree species richness gradient were the main drivers for the observed growth patterns of beech and red oak. Species-specific age differences along the tree species richness gradient could be linked with the species composition. We observed a multi-aged stand structure with the light-demanding pedunculate oak being older than the more shade-tolerant beech and red oak, probably a consequence of management interventions needed to enable long-term coexistence of light-demanding and shade-tolerant species. Our study highlights that the management history of mature forests may influence diversity-productivity relationships and should therefore be taken into account during the analysis.

1. Introduction

Mixed forests, i.e. forests consisting of multiple tree species, are widely thought to provide higher biomass production, which is both an important indicator of ecosystem functioning and a valuable ecosystem service of forests (Gamfeldt et al., 2013; van der Plas et al., 2016). Although a global meta-analysis found that mixed-species stands were on average 24% more productive than the average monocultures of the given species (Zhang et al., 2012), patterns vary considerably between studies. Diversity-productivity relationships in forest ecosystems can be positive (Chamagne et al., 2017; Liang et al., 2016; Paquette and Messier, 2011; Vilà et al., 2013, 2007), neutral (Nguyen et al., 2012; Vilà et al., 2003) and even negative (Conte et al., 2018; Jacob et al., 2010; Szwagrzyk and Gazda, 2007). In order to understand diversity-related differences in forest productivity, it is crucial to understand what is going on at the level of individual trees (Chen et al., 2016). Trees respond to the prevailing environmental conditions and interact with their neighbours. Focusing on individual trees will thus help in gaining insight into interactions between trees, such as competition, complementary use of resources and facilitation that are likely mechanisms underlying differences in productivity of mixtures compared to monocultures (Forrester, 2014; Pretzsch et al., 2017).

Aboveground competition for light is a major determinant of forest structure and growth (Jucker et al., 2014; Morin et al., 2011). Higher

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light use is often suggested as an explanation for the higher growth in mixtures (Pretzsch and Schütze, 2009). Different tree species may indeed occupy different parts of the forest's canopy space, which may increase light capture at stand-level in mixed forests (Sapijanskas et al., 2014). For example, trees of species that differ in maximum tree height and shade tolerance can distribute their foliage in complementary vertical profiles (Forrester et al., 2017), thereby increasing a stand's canopy packing and use of incoming light (Jucker et al., 2015). At the tree level, individuals can be highly plastic and adjust their crown morphology to the local biotic or abiotic environment (Barbeito et al., 2014; Li et al., 2014). Differences in shading caused by neighbouring crowns of different species could affect the tree's architecture, which could in turn affect its light capture efficiency and growth (Sapijanskas et al., 2014). For example, Bayer et al. (2013) found that beech trees surrounded by heterospecific neighbours showed a more shallow branch angle, further crown extension and denser crown space filling than beech trees surrounded by conspecific neighbours, and Metz et al. (2013) showed that the growth response of beech was less negatively affected by interspecific competition compared with intraspecific competition. Next to competition for light, belowground competition for water is also an important determinant of tree growth (Coomes and Grubb, 2000). When water availability becomes limited, for example during drought periods, neighbouring trees compete more strongly for water, which can result in decreased growth (Gómez-Aparicio et al., 2011). Tree growth in mixtures can be higher than in monocultures during periods of drought (Lebourgeois et al., 2013), but the opposite has also been observed, i.e. a more negative impact of drought on trees growing in mixtures as compared to trees growing in monocultures (Grossiord et al., 2014). Differences among the species studied or in local environmental conditions might play a role in explaining these inconsistent results. Light availability is thought to be the main limiting factor for tree growth in temperate forests, compared to more water-limited Mediterranean forests and nutrient-limited boreal forests (Toïgo et al., 2018) and positive interactions among plants have been hypothesised to gain importance if resources are limited (cf. the stress gradient hypothesis, Bertness and Callaway, 1994).

The current knowledge on diversity-productivity relationships in forests has been obtained through different complementary scientific approaches (Baeten et al., 2013). Experimental forestry trials comparing monocultures with two-species mixtures of common merchantable tree species have existed for many decades (Pretzsch, 2005). Large-scale tree species diversity experiments with more than two species richness levels and a larger pool of species have been installed more recently (Scherer-Lorenzen et al., 2005; Paquette et al., 2018; www.treedivnet.ugent.be). The oldest of these experiments was planted in 1999, so the trees are still young and the observed relationships might differ considerably from those in mature forests. Furthermore, these experimental tree communities consist of even-aged stands, thus the age structure and canopy architecture often differs from those in naturally established forests (Scherer-Lorenzen et al., 2005). Mature forests of contrasting tree species diversity have been studied observationally using either data from regional or national forest inventories (Vilà et al., 2013) or from study plots that have been carefully selected along a tree species diversity gradient in existing forests to maximally control for confounding factors such as soil conditions and forest history (e.g., the FunDivEUROPE exploratory platform: Baeten et al., 2013). Mature forests studied in observational and exploratory designs have established spontaneously or through silvicultural management and may vary in stand development and structure. Light-demanding tree species generally establish first, followed by more shade-tolerant tree species that establish under shelter. In mixed forests, age differences between species differing in shade tolerance can thus be expected. Given the importance of tree age and size in affecting tree growth (Aakala et al., 2013), it is important to also consider tree age and size as potential drivers affecting diversity-productivity relationships in mature forests. To our knowledge, including tree age has hardly been done so far. Tree ring width series are useful to gain insight into the role of tree age in biodiversity-productivity relationships in forests.

We used tree increment cores from mature temperate forests in northern Belgium (*TREEWEB*, De Groote et al., 2017) to study the effects of tree species richness on tree growth. We looked at three tree species important for wood production in Europe: the native pedunculate oak and beech and the non-native red oak. Red oak is non-native in Europe and is considered an invasive species with potentially disruptive effects on the ecosystems it invades (e.g. Riepsas and Straigyte, 2008). Therefore, knowledge on long-term interactions of red oak with native species, although still limited, is valuable. The collected increment cores enabled us to investigate the growth of individual trees and to look at the role of tree age. This study aimed to determine (1) how tree growth is affected by conspecific and heterospecific competition and how this competition changes along the species richness gradient, (2) how tree characteristics that affect tree growth such as tree age and size vary along the species richness gradient and (3) how tree-level growth scales up to the stand-level so as to increase our understanding of the observed diversity-productivity patterns at stand-level.

2. Materials and methods

2.1. Study area

The *TREEWEB* platform is a network of 53 plots in mature forests situated in a 450 km^2 window in northern Belgium (De Groote et al., 2017). The temperate climate is characterized by a average annual temperature of 9.5 °C and an annual precipitation of 726 mm distributed evenly over the year (1980–2010, Royal Meteorological Institute of Belgium). All forests have a similar land-use history (continuously forested since at least 1850), are located on a relatively dry, sandy loam soil and showed no signs of recent forest management. The plots are monocultures, two-species mixtures and three-species mixtures containing all possible combinations of pedunculate oak (*Quercus robur* L.), beech (*Fagus sylvatica* L.) and red oak (*Quercus rubra* L.), with six to eight replicates per tree species combination. The design of the *TREEWEB* platform avoids complete dilution: all species are present at all diversity levels so that increasing species diversity is not confounded with a decreasing abundance of one particular tree species. The diversity of the plots was maximized by selecting plots with high evenness of tree species abundances, thus avoiding mixtures with strong monoculture signature because one species is dominant (cf. Baeten et al., 2013). Admixture of non-target tree species was accepted as long as the summed basal area of the admixed species was $< 5\%$ of the total basal area. The plots were 30 m × 30 m large and surrounded by a buffer zone of 10 m wide with a similar forest composition and structure, to avoid edge effects. The plots were fully characterised in spring 2015. All trees with a diameter at breast height larger than 15 cm of which the crown covered part of the plot were identified to species and their coordinates were measured. We characterised each tree by recording the diameter at breast height, height and crown base height, i.e. height of the crown's lowest primary branch. In addition, we quantified the crown dimensions of each tree by four-point vertical crown projection. The plots had an average stem density of 183 trees/ha (100–444 trees/ha) and an average basal area of 39 m^2/ha (25–55 m^2/ha). The topsoil was sampled in all plots for determination of soil texture and chemical analysis of pH, total carbon and nitrogen, and exchangeable potassium, calcium, magnesium and aluminium. More detailed information about the setup of the *TREEWEB* platform and the plot inventory can be found in De Groote et al. (2017) and more detailed information on the soil sampling in De Groote et al. (2018).

2.2. Tree core data

We collected bark-to-pith increment cores (using a 5.15 mm