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Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands

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ABSTRACT

Recent studies show that mixed species forests sometimes have higher stand productivity than monospecific forests, which we refer to as overyielding. Yet, results for temperate forests are ambiguous, possibly because forests differ in local site conditions, thinning history and forest age. In line with the niche complementarity hypothesis, we expect stronger overyielding for forests with species differing in both leaf phenology (evergreen or deciduous) and shade tolerance. We also hypothesize that overyielding will decrease with stand development because of decreasing resource availability. We compared 4 two-species mixtures with their corresponding monospecific stands from long-term field measurements in the Netherlands. The mixtures were Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)–common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.)–common oak (*Quercus robur* L.), common oak–common beech, and common oak–silver birch (*Betula pendula* Roth). Overyielding was observed in 2 of the 4 mixtures: Douglas-fir–common beech mixtures had 35.9% and 36.7% higher volume growth relative to Douglas-fir and common beech monocultures, respectively; Scots pine–common oak mixtures had 20.3% and 31.2% higher volume growth relative to Scots pine and common oak monocultures, respectively, on average over time. Furthermore, overyielding was relatively constant for the two mixtures through stand development. This result was robust after accounting for possible effects of site quality and thinning history, where site quality contributed independently to stand productivity and thinning history had no effect. No significant overyielding effects were observed for the two deciduous mixed stands, i.e. common oak–common beech and common oak–silver birch. Mixing tree species in temperate forests resulted in overyielding for evergreen–deciduous species mixtures, but not for deciduous–deciduous species mixtures. This indicates that leaf phenology contributes to overyielding effects. Overyielding was higher in the Douglas-fir–common beech mixtures than the Scots pine–common oak mixtures, which coincides with a stronger contrast in shade tolerance between Douglas-fir and common beech and thus stronger complementarity. Our results support the complementarity hypothesis and imply that such mechanisms are maintained with stand development. It therefore appears that mixing evergreen with deciduous species with contrasting shade tolerance is a valid management strategy for increasing diversity and productivity of temperate forests in the Netherlands.

1. Introduction

Over the past decade, forest stands dominated by single species (monospecific stands or monocultures) have been converted to stands co-dominated by multiple species (mixed stands, or mixtures) in Europe, as mixed stands are considered more resistant and resilient to disturbances than monocultures (Bravo-Oviedo et al., 2014; Gazol and Camarero, 2016) and may provide higher levels of multiple ecosystem services (Gamfeldt et al., 2013). Both theory and data suggest that mixed stands can be more productive than monocultures, which is also referred to as overyielding (Morin et al., 2011; Zhang et al., 2012; Vilà et al., 2013; Jucker et al., 2014b; Zhang and Chen, 2015); however, the evidence for overyielding is mixed since other studies document that mixtures are not more productive than monospecific stands (Bouillet et al., 2013; Epron et al., 2013; Forrester and Albrecht, 2014). It could be that overyielding effects in existent forests are masked by other factors, such as variable soil conditions, forest management history and competitive interactions (Pretzsch et al., 2015b), which all vary across plots and change with stand age.

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A possible key mechanism contributing to overyielding is complementary resource use in which divergent crown architectures, crown phenology and root distributions may play a main role (Forrester and Albrecht, 2014; Pretzsch et al., 2014, 2015a). In mixtures, tree species with divergent architectures may occupy different spaces and partition light capture. When young growing stands close their canopy, trees of light-demanding species may transmit sufficient light through their canopy, so that trees of shade-tolerant species can survive and grow in their shade, leading to greater use of a limited resource such as light (complementarity). Several studies have reported where species differ in shade tolerance were more productive than monocultures (Morin et al., 2011; Jucker et al., 2014a; de-Dios-García et al., 2015; Toïgo et al., 2015). Such overyielding may even be strengthened when tree species in mixtures also differ in their crown phenology, such as deciduous and evergreen species, and thus in their light capture over a year. Another frequently mentioned mechanism underlying overyielding is mixing species with shallow roots and those with deep roots, which enhances the acquisition of nutrients and water (Forrester et al., 2010; Reyer et al., 2010; Brassard et al., 2013; Pretzsch et al., 2013b). Yet, there is still little evidence that mixtures where species differ in shade tolerance, leaf phenology, or root distributions will overyield (Forrester and Pretzsch, 2015). Moreover, most of existing studies compared the effect of species mixing on overyielding under different site quality and climatic conditions (the spatial mixture effect), and some studies documented that overyielding happened on poor soils and underyielding on rich soils because of complementarity effect (Pretzsch et al., 2013a, 2015a; Toïgo et al., 2015). Little information is available for long-term mixture effect (the temporal mixture effect) in forests, as most previous studies did not account for stand age.

Stand productivity decreases after canopy closure when leaf area index peaks, probably because the increasing costs of maintaining living wood and hydraulic limitations reduce the net primary productivity (Ryan et al., 1997). When trees grow taller and gradually occupy more space, both below-ground and above-ground, mixing effect may shift and overyielding may become weaker which might result from changes in resource capture and interspecific interactions among species with stand development (Cavard et al., 2011). Long-term repeated measurements from the same plots to study the effect of species mixing provide information about how species interactions change as stands develop (Forrester and Pretzsch, 2015). Previous findings show that aboveground wood production is more stable through time in mixed-species stands than pure stands (Cardinale et al., 2007; Jucker et al., 2014b; Drössler et al., 2015). However, mixing effect with stand development on productivity is still hardly known because most studies used protocols that removed possible stand age impacts, using for example dominant height and quadratic mean diameter or quadratic mean diameter at age of 50 and 100 years from yield table as surrogates of age (Pretzsch et al., 2010, 2015a; Condés et al., 2013). This approach masks possible age effects on overyielding, which might result from changes in resource capture and interspecific interactions among species with stand development. A further complication to testing and understanding of overyielding in mixed forests is forest management history such as thinning. Yet, in the European context, species interactions are continuously affected by forest management practices. Apart from stand age, forest management history is thus considered a key factor, and accounted for by using protocols that calculated productivity either in fully stocked stands (Pretzsch et al., 2013a, 2015a), or by removing stands that were managed in the last five years from the analysis to minimize possible management effects (Jucker et al., 2014b; Toïgo et al., 2015). Therefore, by using these protocols to remove impacts of stand age and forest management, these studies may mask possible trends in age effects and thinning regime on productivity and, indirectly, possible overyielding.

In this study, we asked what is the effect of species mixture on stand productivity and dynamics over time. First, in line with the niche complementarity hypothesis (Kelty, 1992; Tilman et al., 2001), we expect that mixing tree species that differ in both leaf phenology and shade tolerance would overyield most strongly because of complementary resource use by the different species. Everything else being equal, evergreen–deciduous species mixed stands may thus be more productive than deciduous–deciduous species mixed stands, and overyielding impacts are expected to increase with increasing differences in shade tolerance (or light requirements) between the species in the mixed forest. Second, we expect overyielding to decrease with stand development because fully growing stands take all resource and limit resource partitioning. However, in thinned stands, resource partition may maintain with age and thus offset trends in overyielding. We evaluated our hypotheses by comparing 4 two-species mixtures (Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)–common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.)–common oak (*Quercus robur* L.), common oak–common beech, and common oak–silver birch (*Betula pendula* Roth)) with the respective monocultures of the same species from 410 permanent field plots in Dutch forests. In this study, we use the term overyielding to refer to higher production in mixed stands relative to the corresponding pure stands, without taking the species proportions explicitly into account. This definition of overyielding is in agreement with some studies (Jucker et al., 2014b), but not with studies that account for species proportions in mixed stands (Kelty, 1992; Condés et al., 2013; Pretzsch et al., 2013a).

2. Methods

2.1. Study site and species

We used the growth and yield data, maintained by the Forest Ecology and Forest Management Group of Wageningen University (FEM), which are derived from permanent field plots in the Netherlands, to investigate the effect of species mixing on stand productivity and dynamics with stand development. The database includes 135 mixed-species and 1311 monospecific stands all over the Netherlands (see Appendix A for a description of FEM growth and yield database from permanent field plots). The Netherlands has a moderate maritime climate created by predominant southwest winds, and the mean annual temperature is 10.8 °C with cool winter (average temperature in December–February is 2.5 °C) and mild summer (average temperature in June–August is 15.9 °C). The mean annual rainfall is around 800 mm and is evenly distributed throughout the year (KNMI, 2015).

In this study, we compared the productivity in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)–common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.)–common oak (*Quercus robur* L.), common oak–common beech, and common oak–silver birch (*Betula pendula* Roth) mixtures with their corresponding monospecific stands. The stands comprised plots surveyed up to 15 times. The oldest records date back to 1929 and the most recent one to 2011. Stand ages ranged from 6 to 265 years. The measurement intervals varied from 1 to 16 years, depending on the age of the trees (Table 1). All trees with sufficient height (circa > 1.3 m) were measured for their diameter at breast height (dbh). Tree variables, e.g. dbh and height, were measured for almost all trees in each survey. For the few missing trees, we used models to estimate dbh and height (see Appendix A).