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Species and soil effects on overyielding of tree species mixtures in the Netherlands

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ABSTRACT

A growing number of studies provides evidence that mixed-species forests often have higher stand productivity than monospecific forests, which is referred to as overyielding. In this study, we explored how the combination of species and soil conditions affect overyielding in terms of periodic annual volume increment (PAIV) in Dutch forests. We studied Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.), and silver birch (*Betula pendula* Roth) growing in four two species combinations (Douglas-fir–common beech, Scots pine–pedunculate oak, pedunculate oak–-common beech, and pedunculate oak–silver birch) from 398 long-term permanent field plots all over the Netherlands. We found that the Douglas-fir–common beech and Scots pine–pedunculate oak mixtures always showed overyielding. This overyielding was largely attributed to the Douglas-fir in the former mixture and to the pedunculate oak in the latter mixture, respectively. In both cases, overyielding was stronger at poor soils than at rich soils. The pedunculate oak–common beech mixtures overyielded at poor soils and underyielded at rich soils, which was attributed to the response of the common beech. Overyielding was not observed for the pedunculate oak–silver birch mixtures, irrespective of soil conditions. The results do not support our hypothesis since overyielding was not always driven by fast-growing light-demanding species. Overyielding was stronger for evergreen–deciduous species combinations, suggesting that differences in leaf phenology are a major driver of overyielding. Secondly, our results imply that overyielding is much stronger at poor soils than at rich soils, which is in line with the prediction of the stress-gradient hypothesis. We conclude that the growth of one species benefits from the admixture species, particularly in evergreen–deciduous species mixtures and that soils affect the extent of overyielding as studied in the Netherlands.

1. Introduction

Forest management practices often have turned traditional monoculture stands into mixed stands in Europe over the last decades (Bravo-Oviedo et al., 2014), not only because mixed stands increase biodiversity and ecosystem services of forests (van der Plas et al., 2016), but also because they can be more stable, resilient and productive than monospecific stands (Vilà et al., 2013; Jucker et al., 2014b; Lu et al., 2016; Thurm et al., 2016b; del Río et al., 2017). The phenomenon of a higher production in mixed stands compared to pure stands is also referred to as overyielding.

A mechanism that is often proposed for explaining overyielding is niche complementarity in resource use by the different species. Divergence in shade tolerance, crown architecture, leaf phenology and root distribution may play a main role in this (Kelty, 1992; Tilman et al., 2001; Forrester and Albrecht, 2014; Pretzsch et al., 2014; Pretzsch et al., 2015). If two species in the mixture differ in both shade tolerance and leaf phenology, trees of fast-growing, light-demanding species may transmit sufficient light through their canopy to allow shade-tolerant species to grow underneath, and total leaf life span may be elongated, leading to greater light use over a whole year (Forrester et al., 2017). Such overyielding would be stronger if the two species also differ in root depths, for example shallow-rooted species mixed with deep-rooted species. In this case, the total acquisition of soil water

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and nutrients in a forest could be raised (Forrester et al., 2010; Reyer et al., 2010; Brassard et al., 2013; Pretzsch et al., 2013b). However, complementary resource use may decline over time when trees of both species grow taller and occupy more space, both aboveground (Cavard et al., 2011) and belowground (Ma and Chen, 2017). Such a decline was however not observed in temperate Dutch forests, probably because forest management (notably thinning) keeps stands below a maximum stand basal area and density, and reduces competition and allows for complementary resource use (Lu et al., 2016). Yet, it remains largely unclear how different tree species contribute to overyielding of mixed forest stands, and whether such overyielding is affected by soil conditions.

Some studies found that in two-species mixed stands, both species contributed to overyielding (del Río and Sterba, 2009; Condés et al., 2013; Pretzsch et al., 2013a) while others reported that only one species was responsible for overyielding (Vallet and Pérot, 2011; Huber et al., 2014; Toïgo et al., 2015; Thurm and Pretzsch, 2016). These contrasting results may be due to differences in species composition, with different or similar traits between the species, and to other factors affecting species interactions, such as site conditions with different growth-limiting factors. In a previous study, we found that differences in the leaf phenology between evergreen and deciduous species and, to a lesser extent, shade tolerance are important factors for overyielding at stand level (Lu et al., 2016). In general, more shade-tolerant species tend to be slower growing than light-demanding species, leading to a stand with different canopy layers. Owing to size-asymmetric competition for light, trees of fast-growing species will rapidly win the height growth competition with trees of slow-growing species, but the slow-growing species may persist in the understory because they are more shade tolerant (Oliver and Larson, 1996; Jucker et al., 2014a). Since trees of slower growing species remain shorter, trees of faster growing species encounter more free space aboveground, their crowns occupy more space and full growth rates that may exceed those of trees in monoculture stands, where more individuals of the same fast-growing species compete for the same space. In contrast, the trees of the slow-growing species are shaded by the individuals of the fast-growing species in the mixtures, and will therefore show slower growth rates than trees in monoculture stands. In other words, the overyielding is not only because trees of slow-growing species occupy space that cannot be occupied by trees of the fast-growing species, but also because trees of fast-growing species show higher growth rates in mixtures than in monocultures of the same species. We therefore expect that dominant, fast-growing species will overyield, and that suppressed, more slowly growing species will actually under yield in mixtures when comparing to single species stands.

This overyielding effect may vary on different site conditions. There are two dominant viewpoints describing these changes. The stress-gradient hypothesis states that species interactions shift from competition in favourable environments to facilitation in harsh environments (Bertness and Callaway, 1994). Following this, overyielding would be stronger on poor sites than on rich sites, because species facilitate each other to improve the soil resource availability. Several studies found overyielding on poor sites and underyielding on rich sites (Pretzsch et al., 2013a; Pretzsch et al., 2015; Toïgo et al., 2015). However, the resource-ratio hypothesis states that competition for light on rich soils switches to competition for soil resources on poor soils (Tilman, 1985). On rich soils where soil water and nutrients supplies are adequate, stands can develop large leaf areas but competition for light will also increase, so overyielding would be stronger if the mixed species have complementary light use (Forrester, 2014). On poor soils, limited availability of nutrients or water will limit growth and trees in mixtures are then expected to compete more fiercely for belowground resources. Yet, when this results in less leaf production and lower light interception, this may leave less room for light complementarity and positive mixture effects would lessen (Tilman, 1985; Jucker et al., 2014a). Indeed, several studies report that overyielding increased under better site conditions (Forrester et al., 2013; Jucker et al., 2014a; Sterba et al., 2014; Thurm and Pretzsch, 2016), because trees in mixtures invested more into stem growth (Thurm et al., 2016a) and crown development (Dieler and Pretzsch, 2013; Jucker et al., 2014a; Williams et al., 2017) than in monocultures. Thus, the impact of soil on overyielding is still ambiguous and debated.

In this study, we investigated how overyielding depends on the combination of mixed species at species level and how it changes with soil conditions in Dutch forests. First, we hypothesized that the faster growing and more light-demanding species would dominate the slower growing and more shade-tolerant species in mixed-species stands, and that the resulting stratified canopies and the subsequent partitioning of the light would cause overyielding by complementary light use. Second, we expected that this overyielding effect would be stronger on poor soils than on rich soils, according to the stress-gradient hypothesis, because one species improves the soil resource availability for the other species or allows for complementary soil resource use. Third, following the resource-ratio hypothesis, the overyielding would be stronger on rich soils, owing to that rich soils allow for a denser forest canopy with possibilities for complementary light use, particularly when species differ in shade tolerance or leaf phenology. We evaluated our hypotheses by analysing five species (Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.), and silver birch (*Betula pendula* Roth)) growing in Douglas-fir–common beech, Scots pine–-pedunculate oak, pedunculate oak–common beech, and pedunculate oak–silver birch mixtures and their respective monocultures from 398 long-term permanent field plots all over forest area of the Netherlands.

2. Methods

2.1. Study site and species

We compared the growth of the species in mixtures with their respective monocultures using long-term measurements from permanent field plots in the Netherlands, maintained by the Forest Ecology and Forest Management Group of Wageningen University. In this study, we analysed the species mixture effect on stand productivity on different soils for five tree species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), common beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.), and silver birch (*Betula pendula* Roth) growing in monocultures and mixtures of Douglas-fir–common beech, Scots pine–pedunculate oak, pedunculate oak–common beech, and pedunculate oak–silver birch. Hereafter, the five species and monocultures are written as Douglas-fir, beech, pine, oak and birch, and the four mixtures accordingly as Douglas-fir–beech, pine–oak, oak–beech and oak–birch, respectively. The shade tolerance index for Douglas-fir, beech, pine, oak and birch is 2.78 ± 0.18, 4.56 ± 0.11, 1.67 ± 0.33, 2.45 ± 0.28 and 2.03 ± 0.09, respectively. The increasing values correspond with increasing shade tolerance (Niinemets and Valladares, 2006). There are 314 plots of pure stands and 84 plots of mixed stands with stand ages ranging from 6 to 265 years. Most plots were regularly thinned. For information on plot distributions and thinning history, see Lu et al. 2016).

The study plots were located throughout the Netherlands. Dutch climate is moderate maritime with a mean annual temperature of 10.8 °C with cool winters (average temperature in December–February of 2.5 °C) and mild summers (average temperature in June–August of 15.9 °C). The mean annual rainfall is around 800 mm and is evenly distributed throughout the year (KNMI, 2015). Plot characteristics and