



# How does neighbourhood tree species composition affect growth characteristics of oak saplings?



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## ABSTRACT

Recent research into positive effects of species diversity has renewed interest into mixing tree species in managed forests. Mixing tree species may have positive effects on productivity and other forest ecosystem functions, while also reducing the impact of extreme weather events or disease – both expected to become worse in the context of global change. In particular saplings are very vulnerable to attacks by pathogens and positive effects at this stage may play a substantial role in shaping later forest dynamics, biomass yields and other ecosystem services. While positive effects of mixing tree species have been found, which species were mixed specifically had large impact on the results and it was often unclear just how these interactions work and what their impact is on tree physiology.

In this study, we investigated the impact of local neighbourhood tree species composition on various above- and belowground growth characteristics of four year old oak (*Quercus robur* and *petraea*) saplings in two sites with contrasting abiotic conditions. To evaluate specific mechanisms underlying composition effects, we attempted to link these characteristics to the degree of oak powdery mildew infections and shading cast by local neighbourhood trees, two important factors influencing oak sapling survival and growth. Our results showed no impact of neighbourhood tree species richness, but there were strong effects of species identity on dry biomass production and total leaf area in an abiotically more favorable site. These effects of species presence were related to a strong negative impact of powdery mildew and the degree of shading, both affected differently by different tree species. Effects of composition, mildew and shading were much weaker in the abiotically less favorable site, but we could not disentangle this effect from a difference in oak species. Our results suggest that admixing certain tree species can have considerable positive impact. Mixing of species on an individual basis can be generally recommended, particularly if high impact specialist pathogens such as oak powdery mildew are to be expected. However, differences in juvenile growth rates need to be taken into account, as they may lead to strong adverse effects of shading.

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## 1. Introduction

Mixed tree species composition in managed forests has been a contentious topic since the dawn of modern forestry in the 18th century. As modern forestry initially revolved around the sustainable optimization of wood and biomass production, mono-specific stands of highly productive (often coniferous) species quickly

became the norm (Pretzsch, 2005; Scherer-Lorenzen, 2014). Recently, worries concerning global loss of biodiversity and research into positive effects of biodiversity on the functioning of ecosystems have reinvigorated this discussion (Cardinale et al., 2012; Hillebrand and Matthiessen, 2009; Hooper et al., 2005; Zhang et al., 2012). Case studies, analyses into forest inventory data and meta-analyses showed positive effects of mixing tree species on the functioning of forest ecosystems (Liang et al., 2016; Paquette and Messier, 2011; van der Plas et al., 2016; Vilà et al., 2007; Zhang et al., 2012).

Mechanisms proposed in an attempt to explain these positive effects of mixing tree species include complementarity of resource use in time and/or space (Morin et al., 2011; Ratcliffe et al., 2015) or through facilitation such as hydraulic lift (Zapater et al., 2011) or

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nitrogen fixation (Forrester et al., 2006). Mixing tree species has also been associated with decreased pressure of pests and pathogens, mitigating their negative impact and reducing the risk of catastrophic infestation episodes (Hantsch et al., 2013; Jactel et al., 2005; Jactel and Brockerhoff, 2007). Similarly, mixing species may also hedge against other calamities such as severe droughts, wildfires or spring frost through a portfolio effect of variant susceptibilities (Isbell et al., 2009; Van de Peer et al., 2016). Direct facilitation by neighbouring trees is also possible here, for instance by reducing physical transmission rates of pathogens (Peacock et al., 2001) or tempering the local microclimate (Eränen and Kozlov, 2008; Gómez-Aparicio et al., 2004; Hantsch et al., 2014). This has been of particular interest as the various abiotic and biotic processes giving rise to the Anthropocene, such as greenhouse gas emissions and the spread of invasive species, are expected to increase the frequency and severity of such extremes (Niinemets, 2010; Spathelf et al., 2014).

One of the most critical phases of tree development is the sapling stage, when trees are more accessible to herbivores and have less reserves to compensate for growth- and assimilation-impairing processes such as spring frost, drought and diseases (Barton and Hanley, 2013; Sobek et al., 2009). Under these stressful conditions, facilitation between organisms may be promoted as suggested by the Stress Gradient Hypothesis (SGH, Bertness and Callaway, 1994) and indications that this might be the case have been found in practice in various ecosystems, including forests (He et al., 2013; Paquette and Messier, 2011; Toïgo et al., 2015). While different methodologies between SGH and diversity experiments make it difficult to compare or extrapolate results, these findings do suggest that plant interactions could shift to become more positive along stress gradients. This would have repercussions for the assessment of diversity effects, as the potential for facilitation is likely to be greater in more diverse stands. Here, size asymmetry due to different growth rates allows for sheltering effects (Castagneyrol et al., 2013; Eränen and Kozlov, 2008; Smit et al., 2006) and different susceptibilities (often resistance) to pests or pathogens reduces their potential populations and likelihood to encounter hosts (Guyot et al., 2013; Sobek et al., 2009).

Such mitigating effects of facilitation in the sapling stage may have repercussions for future tree vitality and growth, as effects of stress can carry over to later years (Bert et al., 2016; Marçais and Desprez-Loustau, 2012). For example, the biotrophic oak powdery mildew fungus (*Erysiphe* sp.) infects the leaves of oaks (*Quercus* sp.) reducing leaf lifespan and photosynthesis (Hajji et al., 2009). Besides a negative impact on growth rates, it is responsible for substantial mortality in young oak saplings, who lack the reserves to compensate for these productivity losses while struggling in competition with other trees and understorey species (Bert et al., 2016; Marçais and Desprez-Loustau, 2012; Pap et al., 2012). As powdery mildew is a host-specific disease which requires asexual spore production during the growing season for maximal infection rates (Feau et al., 2012), reducing the availability of hosts and increasing the frequency of 'dead ends' for the spores may limit the disease's impact in more tree species rich stands. Supporting findings for this mechanism have been found (Dillen et al., 2016; Hantsch et al., 2013), as well as for similar diseases such as leaf rusts (Peacock et al., 2001). Size asymmetry between smaller oak saplings and sheltering pioneer species of similar age might mitigate negative effects of wind or late spring frost (Gemmell et al., 1996; Setiawan et al., 2016) or reduce apparency for herbivores (Castagneyrol et al., 2013), but may also reduce light transmission and therefore negatively impact growth rates (Gemmell et al., 1996).

While trees through their size are more easily individually observable than non-woody plants (Scherer-Lorenzen et al., 2007), their slow growth makes experiments run long and more

easily confoundable through changing abiotic conditions and stand dynamics throughout the years (Baeten et al., 2013). Their slow growth also makes harvesting less practical and desirable, which is particularly problematic for root characteristics (Meinen et al., 2009) and differences in allocation of biomass to different parts of the tree (Domisch et al., 2015). To look at these characteristics in greater detail, we harvested four-year old oak saplings which had grown for three years within two experimental tree diversity plantations of the FORBIO experiment in Belgium (Verheyen et al., 2013). We investigated the influence of neighbourhood tree species composition on multiple characteristics of oak saplings linked to growth. Specifically, we looked at above- and belowground coarse and fine dry biomass (and their ratio), specific leaf area, total leaf area and leaf nutrient contents of carbon (C) and nitrogen (N). We defined tree species composition both as species richness and species identity, i.e. the absence or presence of certain tree species. Additionally, to refine our understanding of which mechanisms were at play, we linked these growth characteristics to two important factors influencing oak sapling survival and growth: powdery mildew infection severity and degree of shading.

## 2. Materials and methods

### 2.1. Field sites

Our study took place in two of the three sites of the FORBIO project in Belgium. FORBIO (FORest BIODiversity and Ecosystem Functioning) is a network of three relatively large (ca. 9 ha) experimental forest sites, 'designed specifically to test the effects of tree species diversity on forest ecosystem functioning' (Verheyen et al., 2013). We worked within the sites in Zedelgem and Gedinne, both of which were planted in winter-early spring of 2009–2010. One to three year old saplings of five different tree species were planted with a planting distance of 1.5 m × 1.5 m in 40 plots of typically 42 m × 42 m (Fig. 1). Each plot had a species composition of one up to four different species and consisted of 81 planted monoculture groups of 3 by 3 trees (4 by 3 at two of the four plot edges) or 784 trees total. Groups were distributed randomly for the three- and four species mixtures, but evenly for the two species mixtures. All five monocultures and four-species mixtures were represented; five randomly selected compositions were chosen for the two- and three species richness level. All 20 compositions were replicated once for the total of 40 plots. The tree species used differed between sites due to their different edaphic conditions and because species important in local silviculture were preferred, to make the experiment more representative (Verheyen et al., 2013). In Zedelgem, pedunculate oak (*Quercus robur*), European beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), small-leaved lime (*Tilia cordata*) and silver birch (*Betula pendula*) were planted; in Gedinne, European beech, sessile oak (*Quercus petraea*), sycamore maple (*Acer pseudoplatanus*), hybrid larch (*Larix × eurolepis*) and Douglas fir (*Pseudotsuga menziesii*) were planted.

The abiotically more favorable site of Zedelgem is located on a former agricultural field and has a sandy to loamy sandy soil. It is located not far from the North Sea and has a very mild, temperate climate. The less favorable site of Gedinne lies at greater elevation and consists of two separate subsites, called Gribelle and Gouverneurs, separated by about 4 km and each containing all different species compositions. Both subsites were planted on former Norway spruce (*Picea abies*) forest after clearcut. Their soils are more organic, with the soil in Gribelle more exposed and with a higher stone content. Monthly rainfall data during the course of our study can be found in (Dillen et al., 2016). More info on the FORBIO sites can be found in Verheyen et al. (2013).

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