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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., 2015; 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., 2017) 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).

Fig. 1. Lay-out of the experimental setup in the two FORBIO sites. Bottom: Situation of all plots in both FORBIO sites, color-coded with their species richness. Top Right: An example of a four-species plot, where each numbered cell represents a tree and each color represents a different species. Three oak saplings were planted between four such trees, in one of the black rectangles where the plot composition matches, as can be seen in the top left. There were only three saplings per plot so only one of those rectangles was used.

2.2. Experimental setup

To study the effects of different compositions on oak saplings specifically, one-year old saplings were planted between the FORBIO trees in April–May 2013. We used the same oak species as was present in the site (i.e. *Q. robur* in Zedelgem, *Q. petraea* in Gedinne). Three such saplings were planted together between four of the FORBIO trees in all 40 plots, for a total of 120 saplings per site (Fig. 1). Plots 38 and 42 were not used in either site, and neither were plots 43 and 44 in Gedinne. The saplings were planted in black pots of 20 L to make it possible to subject them to a gradient of rainfall reduction. The pots had holes in the bottom to prevent waterlogging and were dug in so as to minimize solar heating and equalize the soil levels in and outside the pot. Soil from the (sub)sites themselves was used, collected from unplanted patches. A treatment reducing rainfall was added in May–June of 2013 and, after being removed each winter, installed again around the same time in the subsequent two years. Small PVC gutters were placed above the pot surface but below the sapling's crown to intercept precipitation. A control and one to two pairs of gutters were used as can be seen in Fig. 1. In a previous analysis of growth data, this rainfall reduction treatment was found to have no impact on growth rates or powdery mildew infections and only minor impact on soil moisture conditions (Dillen et al., 2016). Therefore the rainfall reduction gradient was only included in this analysis as a covariate.

2.3. Measurements of powdery mildew and shading

Monitoring for powdery mildew was performed in Zedelgem in July, August and October of 2013 and July and September of 2014. There was virtually no powdery mildew in Zedelgem during the

2015 growing season. In Gedinne, mildew monitoring was performed in July and August of 2013 and 2014 as well as in August 2015. Estimates of leaf area affected by the fungus were made for each first order shoots using four classes: 0–5%, 6–30%, 31–60% and 61–100%. From October 2013 onwards, these first order shoot units were also given relative weights estimated to reflect their size as part of the crown to reflect the rapidly increasing size asymmetry between shoots. Shoot scores were subsequently scaled up to the sapling level by calculating a (weighted) average using the shoot size weights if available and the class mids for each class except that 0 was used for the lowest class. Other symptoms of leaf damage, such as mining and galls, were also evaluated, but found to be far less important than powdery mildew. Shading was measured once using a spherical densiometer (Baudry et al., 2014) in July and August of 2015. A value in% was obtained right above the crown of each sapling for light from the East, South and West, but collinearity was high so that the average of those three values was used in subsequent analysis. More info on this monitoring protocol can be found in (Dillen et al., 2016).

2.4. Measurements of growth characteristics

From September to November 2015, all 240 saplings planted in the experiment were removed from the sites. In Zedelgem, six saplings were dead and had been at least since 2014. Three were in one plot, a four-species mixture without birch. The others were in a monoculture of oak, a mixture of oak and beech and a four-species mixture without lime. These were all omitted from further analysis. One dead sapling was noted in Gedinne in a monoculture of beech and also omitted.

In September, all leaves were harvested from all saplings. To determine Specific Leaf Area (SLA, leaf area/leaf dry weight), a

selection of ten leaves per sapling representative for the whole sample was scanned fresh using a copying machine. The selected leaves were then dried and weighed individually (0.001 g precision). The remaining leaves were also dried at 70 °C and weighed together to determine a total crown leaf weight per sapling (excluding the selected leaves). Before weighing, leaf galls were removed from all leaves. The total crown leaf weight samples were then grinded to prepare them for chemical analysis. Total C and N concentrations were then measured by high-temperature combustion at 1150 °C using an elemental analyzer (Vario MACRO cube CNS, Elementar, Hanau, Germany).

The surface area of the scanned leaves was determined digitally using a batch macro in ImageJ (Rasband, 2016), first thresholding the scans to binary images then using the built-in *Analyze Particles* function with minimal size (1000) and circularity (0.1) restrictions to count the number of pixels per leaf. These were subsequently converted to mm² using the resolution of 300 DPI. The SLA was now obtained from the leaf surface area and dry weight data, assuming the same hierarchy for each ten values. The Total Leaf Area (TLA) was determined by multiplying the average SLA of the ten selected leaves with the total crown leaf weight.

Between September and November 2015, the woody biomass of all saplings was collected and dried at 70 °C until constant weight. Roots were removed from the soil but not washed before drying. After drying, aboveground biomass with diameter < and ≥ 3 mm was weighed separately per sapling. The cut-off point between above- and belowground was defined as the soil line marked on the stem. Belowground biomass was cleaned of soil, stones and herbaceous roots manually, before separately weighing it for roots < and ≥ 2 mm.

2.5. Statistical analysis

Our statistical analysis was performed in R (R Core Team, 2015). To evaluate the shoot weight approach used during the powdery mildew monitoring to estimate relative crown size, we compared the determined TLA to the sum of all weights as estimated in August 2015 in both sites. We also made allometric relationships between diameter in September 2015 (as measured by Dillen et al. (2016)) and belowground, aboveground and total dry biomass for both sites. To derive these relationships, we made a linear regression between the natural logarithm of the diameter and the different types of dry biomass. Results for both validations can be found in the Appendix A.

For the analysis of the influence of species composition on growth characteristics, we used linear mixed models from the *lme4* package (Bates et al., 2015) with *lmerTest* extension (Kuznetsova et al., 2015) to determine Satterthwaite approximated p-values. We ran models separately for data from the two sites, due to the difference in oak species, the neighbourhood tree species compositions and abiotic conditions. Composition in the local neighbourhood was defined as the four surrounding FORBIO trees, which also corresponded to the composition of the 36 closest FORBIO trees. For each site, the following three models were used

$$Y = SR$$

$$Y = \sum_{i=1}^5 SP_i$$

$$Y = SH + \sum_{i=1}^n PM_i$$

SR is a continuous variable for species richness (1–4), **SP_i** is a two-level fixed factor describing the absence or presence of species **i**, **SH**

Table 1

List of all growth characteristics (Y) used in the models.

Symbol	Description	Unit
Rf	Fine belowground dry biomass (<2 mm)	mg
Rc	Coarse belowground dry biomass (≥2 mm)	mg
Wf	Fine aboveground dry biomass (<3 mm)	mg
Wc	Coarse aboveground dry biomass (≥3 mm)	mg
TBM	Total dry biomass	mg
R/W	Below-/aboveground dry biomass ratio	
SLA	Average Specific Leaf Area	mm ² /mg
TLA	Total Leaf Area	cm ²
Leaf N	Leaf N concentration by weight	%
Leaf C	Leaf C concentration by weight	%
Leaf C/N	Leaf C to N ratio	

is the degree of shading (between 0 and 1) and **PM_i** constitutes all different powdery mildew scores (between 0 and 1). The list of variables for **Y** can be found in Table 1. All models included an intercept and plot as a random factor. They also included a fixed factor for the rainfall reduction gradient (RR) with the no reduction control treatment as the base level (represented as 0) and the other two as 1 and 2 with increasing reduction of rainfall. Another two-level fixed factor was included for the replication of the different species composition treatments (plots 1–20, 21–41), which also corresponded to the two subsites in Gedinne. We applied log transformations if residual heterogeneity was noted. Species richness and species identity were modeled separately as the former is always a linear combination of all the latter. Multicollinearity in the last model was evaluated with Variance Inflation Factors (VIF), using a modified function of the package *rms* (<https://github.com/aufrank/R-hacks/blob/master/mer-utils.R>).

3. Results

General results for all growth characteristics and scores of powdery mildew (PM) and shading can be found in Table 2. As expected, total biomass (TBM) was lower in the abiotically less favorable site of Gedinne. Biomass was disproportionately lower aboveground than belowground in this site, as reflected in a below-/aboveground dry biomass ratio (R/W ratio) that was twice as high as in Zedelgem. Leaf C varied little, so that the leaf C/N ratio

Table 2

Mean values and standard deviations for the growth characteristics measured, the different PM scores and the degree of shading. Note that the units used here may differ from those used in the statistical models. Descriptions of the symbols can be found in Table 1.

	Zedelgem		Gedinne	
	Mean	SD	Mean	SD
Rf (g)	9.47	4.83	6.88	3.20
Rc (g)	31.57	23.23	25.76	14.36
Wf (g)	8.43	5.22	4.58	2.28
Wc (g)	30.40	21.29	12.41	9.83
TBM (g)	79.87	51.49	49.63	27.04
R/W	1.14	0.35	2.14	0.75
SLA (mm ² /mg)	17.88	2.94	14.44	2.77
TLA (dm ²)	24.16	15.23	13.47	8.76
Leaf N (%)	2.48	0.28	2.06	0.37
Leaf C/N	20.15	2.18	25.27	4.84
Leaf C (%)	49.39	0.67	50.29	0.96
PM Jul 13 (%)	6.82	8.27	28.03	18.18
PM Aug 13 (%)	11.74	9.52	35.88	16.20
PM Jul 14 (%)	22.61	16.80	12.16	13.08
PM Aug 15 (%)	2.08	6.13	10.87	13.6
Shade (%)	62.84	25.75	39.24	27.47

Table 3

Results of the three models in Zedelgem. Symbol descriptions can be found in Table 1. Significant or semi-significant parameter estimates are shown in bold, with °, *, ** and *** indicating a significance of <0.1, <0.05, <0.01 and <0.001 respectively. The intercept C was virtually always significant and was included in the table to allow interpreting the order of magnitude of the different parameter effect sizes. It was more or less identical in value for the species richness and identity models, as were the estimates of the reduced rainfall treatment (RR), with 1 and 2 indicating increased reduction of rainfall. Hence, they are only listed for the Species Richness model, with virtually identical values for the Species Identity model. The fixed factor for the replication of the different composition treatments is not shown. Log transformations were performed on all response variables to compensate for residual heterogeneity. PM scores that are not listed were omitted from analysis due to high VIF's. PM scores for 2015 were never included as a grand majority of trees was PM-free that year.

	Species Richness				Species Identity					PM and shading						
	C	SR	RR1	RR2	Oak	Beech	Pine	Lime	Birch	C	Jul13	Aug13	Jul14	Shading	RR1	RR2
Rf (mg)	8.91 ***	−0.03	0.24 **	0.14	−0.37 **	0.22	0.13	0.09	−0.20	9.35 ***	−0.12	−0.65	−0.91 ***	−0.39 °	0.21 *	0.13
Rc (mg)	10.15 ***	−0.06	0.25 *	0.14	−0.46 **	0.31 *	0.01	0.26 °	−0.36 *	11.14 ***	0.04	−0.42	−1.61 ***	−1.10 ***	0.15	0.09
Wf (mg)	8.57 ***	0.03	0.15	0.20 °	−0.59 **	0.24	0.36 *	0.19	−0.01	9.02 ***	1.38 °	−0.27	−1.34 ***	−0.11	0.10	0.16
Wc (mg)	9.98 ***	0.01	0.27 *	0.16	−0.52 **	0.29 °	0.20	0.25	−0.14	10.70 ***	0.40	−0.50	−1.41 ***	−0.51 °	0.21 °	0.13
TBM (mg)	11.02 ***	−0.02	0.24 *	0.15	−0.48 **	0.28 °	0.13	0.22	−0.22	11.74 ***	0.36	−0.53	−1.34 ***	−0.63 **	0.18 °	0.11
R/W	0.19 °	−0.06 *	0.00	−0.02	0.09	0.02	−0.19 **	−0.01	−0.21 **	0.31 *	−0.36	−0.26	0.13	−0.44 ***	−0.01	−0.01
SLA (mm ² /mg)	2.77 ***	0.04 *	−0.03	0.00	−0.04	−0.02	0.15 ***	−0.05	0.14 ***	2.65 ***	−0.09	−0.14	−0.07	0.40 ***	0.00	0.01
TLA (cm ²)	7.24 ***	0.08	0.20°	0.15	−0.62 ***	0.34 *	0.40 *	0.21	0.08	7.94 ***	0.80	−0.39	−1.75 ***	−0.10	0.15	0.11
Leaf N (%)	0.89 ***	0.01	0.00	−0.02	0.04	−0.01	0.01	−0.03	0.05 *	0.82 ***	0.24 °	−0.18	0.07	0.12 **	0.01	−0.01
Leaf C/N	3.02 ***	−0.01	0.00	0.02	−0.04	0.01	−0.02	0.03	−0.05 *	3.09 ***	−0.23 °	0.19 °	−0.07	−0.14 **	−0.01	0.01
Leaf C (%)	3.90 ***	0.00	0.00	0.00	0.00	0.00	−0.01 *	0.00	0.00	3.91 ***	0.00	0.00	0.00	−0.01 °	0.00	0.00

Table 4

Results of the three models in Gedinne. Symbol descriptions can be found in Table 1. Significant or semi-significant parameter estimates are shown in bold, with °, *, ** and *** indicating a significance of <0.1, <0.05, <0.01 and <0.001 respectively. The intercept C was virtually always significant and was included in the table to allow interpreting the order of magnitude of the different parameter effect sizes. It was more or less identical in value for the species richness and identity models, as were the estimates of the reduced rainfall treatment (RR), with 1 and 2 indicating increased reduction of rainfall. Hence, they are only listed for the Species Richness model, with virtually identical values for the Species Identity model. The fixed factor for the replication of the different composition treatments is not shown. Log transformations were performed on all response variables to compensate for residual heterogeneity. PM scores that are not listed were omitted from analysis due to high VIF's.

	Species Richness				Species Identity					PM and shading						
	C	SR	RR1	RR2	Oak	Beech	Douglas	Maple	Larch	C	Jul13	Jul14	Aug15	Shading	RR1	RR2
Rf (mg)	8.67 ***	0.01	−0.07	0.06	−0.12	0.23 *	0.09	−0.08	−0.06	9.22 ***	−0.66 **	−1.02 **	−0.18	−0.36 *	−0.11	−0.01
Rc (mg)	9.86 ***	0.03	−0.22 °	−0.03	−0.01	0.18	0.11	−0.01	−0.13	10.65 ***	−0.70 *	−1.53 ***	−0.48	−0.55 *	−0.28 *	−0.14
Wf (mg)	8.15 ***	−0.02	−0.17 °	0.00	−0.05	−0.04	0.08	−0.16	0.06	8.38 ***	−0.76 **	−0.48	0.07	−0.03	−0.20°	−0.05
Wc (mg)	9.02 ***	−0.05	−0.20	0.07	−0.06	−0.07	0.11	−0.24	0.03	9.38 ***	−0.69 **	−1.25 **	0.05	−0.07	−0.26°	−0.01
TBM (mg)	10.54 ***	0.00	−0.20 °	0.00	−0.05	0.10	0.10	−0.09	−0.06	11.14 ***	−0.69 **	−1.30 **	−0.27	−0.35 °	−0.25 *	−0.09
R/W	0.74 ***	0.06 °	0.00	−0.05	0.02	0.25 ***	0.00	0.19 **	−0.15 *	1.17 ***	0.01	−0.44 °	−0.47 °	−0.44 ***	−0.01	−0.09
SLA (mm ² /mg)	2.69 ***	−0.02	0.04	−0.02	−0.03	−0.10 *	−0.02	−0.07 °	0.10 *	2.53 ***	0.02	−0.04	0.31 **	0.29 **	0.03	0.00
TLA (cm ²)	6.83 ***	0.02	−0.15	−0.06	0.06	0.01	0.13	−0.23	0.11	7.38 ***	−0.83 **	−1.49 **	0.09	0.12	−0.22 °	−0.14
Leaf N (%)	0.72 ***	−0.01	0.00	0.02	0.04	−0.06	0.02	−0.11 *	0.08 °	0.62 ***	0.06	−0.03	0.33 *	0.13 °	−0.01	0.04
Leaf C/N	3.19 ***	0.01	0.00	0.00	−0.04	0.07	−0.02	0.11 *	−0.08 °	3.30 ***	−0.08	0.03	−0.33 *	−0.16 *	0.01	−0.04
Leaf C (%)	3.91 ***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	−0.01	3.93 ***	−0.02 °	0.00	0.00	−0.02 *	0.00	0.00

was very strongly correlated to leaf N ($r = -0.98$ in Zedelgem and -0.96 in Gedinne). Values for shading were a fair bit lower in Gedinne (39%) than in Zedelgem (63%), while PM scores were generally lower in Zedelgem (with the notable exception of July 2014).

Results for the three models per site can be found in Tables 3 and 4. All variables were log transformed. Species richness had virtually no effects, only correlating with R/W ratio and SLA in Zedelgem. Conversely, species identities had strong impact in this site, on biomass variables as well as TLA. The presence of oak, and to a lesser extent birch, had a negative impact on biomass characteristics, whereas the other three species and in particular beech showed positive effects. Negative effects of oak presence were slightly stronger on aboveground than belowground biomass (41 and 37% reductions in coarse BM respectively), but the difference was not significant given the small, insignificant effect on the R/W ratio. The presence of pine much like beech positively influenced aboveground biomass, in particular fine BM and TLA, but also had similar effects as birch on R/W ratio

and SLA. In contrast, identity effects in the site of Gedinne were much weaker, finding only effects for R/W ratio, SLA and leaf N characteristics.

Collinearity for the PM scores in the third model was large ($VIF > 2$) in both sites and hence variables with the highest VIF were omitted. The impact of the most severe PM infections of July 2014 in Zedelgem is dominant on all biomass traits and TLA (Fig. 2). Shade also had a notable negative effect, increasing average SLA and leaf N as well, but not affecting TLA or fine aboveground BM. The average infection with PM in July 2014 is associated with 29% less total biomass at the end of 2015 compared to an uninfected sapling. The average degree of shading results in 36% less biomass compared to no shade. In Gedinne, the negative impact of PM on biomass was visible in both 2013 and 2014 (Fig. 2), but not 2015. PM in 2015 did have an effect on the leaf traits of SLA and leaf N. Negative effects of shading on BM were less pronounced in this site, with total BM reductions of 13%, 13% and 17% for shading and PM in July 2013 and July 2014 respectively (Fig. 2).

Fig. 2. Scores for total sapling biomass in function of powdery mildew affected leaf area and degree of shading in both sites. The lines shown are model predictions based on the full model results in Table 2, assuming all other continuous parameters to be equal to their mean.

4. Discussion

Neighbourhood species richness had no effect on any of our measurements, as was previously found in the same sites for relative growth data (Dillen et al., 2016) as well as growth of the older FORBIO trees (Setiawan et al., 2017). Little to no effect of tree species richness on growth and biomass was previously noted by other authors as well, with composition effects more strongly associated with the functional identity of those tree species present (Nadrowski et al., 2010; Ratcliffe et al., 2015; Sobek et al., 2009; Tobner et al., 2016). In our experiment, the identity of the neighbourhood species had quite pronounced effects in the site of Zedelgem, but not in Gedinne. Negative effects of the presence of oak on all aspects of dry biomass and total leaf area in Zedelgem might be explained by the equally strong effects of powdery mildew. The oak-specific pathogenic fungus was found to cause substantial infections at least once in each site during the course of the experiment, most notably in July 2014 in Zedelgem after late spring frost. Dantec et al. (2015) suggested that there exists a genetic trade-off between early and late flushing in oaks, where early

flushing increases the odds of avoiding PM infection on the first leaf flush, but increases the risk of losing these leaves entirely to late spring frost. Such a loss of leaves results in utter dependency of the tree's photosynthetic capacity on the later leaf flushes, which tend to be infected more severely (Pap et al., 2012). Hence, saplings which are not severely infected in one year, may be infected more under the different abiotic conditions of other years. The poor correlation between the PM scores of 2013 and 2014 in Zedelgem would support that, but no strong conclusions can be made from only two years of data (2015 being almost fully PM-free). This trade-off between years would reinforce the importance of composition mechanisms such as resource dilution, as it would be less likely for an optimal genotype in respect of PM susceptibility to perform best across all years in the longer term.

In Zedelgem, the positive identity effect of beech and to a slightly lesser extent of small-leaved lime on all aspects of biomass might be partially explained by the low degree of shading cast by these species at this age (Dillen et al., 2016), while shading had a pronounced negative effect on biomass in this site. However, shading had a disproportionate impact on root biomass, which is not

seen in the species identity effects of lime and beech, while the most shade-casting species, silver birch, did have stronger negative effects on belowground biomass. The influence of shading on leaf traits, increasing SLA and reducing leaf C/N (Jensen et al., 2012; Niinemets, 1998; van Hees, 1997), could be found for birch, but was also not mirrored for the identity effects of beech and lime. This suggests another mechanism of facilitation besides shading may be at work here, although complementarity for resources at the root level is unlikely as all oak saplings were planted in pots.

The other shade-casting species in Zedelgem, Scots pine, had similar effects as birch on SLA and R/W ratio, but not leaf C/N or BM. While this may partially be due to a diminished association of presence with shading in this site compared to birch – 20 and 31% increase, respectively (Dillen et al., 2016) – the positive effects on fine aboveground BM and TLA are remarkable. Despite the large difference in degree of shading, pine was on average of similar height as the other three species present (ca. 2 m in 2014), whereas birch was almost twice as tall and very close to crown closure (Setiawan et al., 2017, Appendix A). Hence, the shade cast by birches from much higher was inescapable for the rarely taller than 1 m oak saplings, whereas pines cast their shade from much lower and grew more horizontally, keeping the incentive for stem growth and crown development stronger. This does not explain the discrepancy between a greater SLA yet no lower leaf C/N; however, this may be due to the greater sensitivity to changing light conditions of SLA than leaf N in *Q. robur* (Niinemets, 1998).

Species identity effects were much less prominent in the site of Gedinne. The characteristics related to shading (R/W ratio, SLA and leaf C/N) were associated with the most shade-casting species hybrid larch in this site, as well as inversely with sycamore maple and beech, which suffered from high mortality and slow juvenile growth rate, respectively (Setiawan et al., 2017; Van de Peer et al., 2016). Yet there were no strong associations with BM characteristics or TLA, not even of oak despite the negative effects of PM both in 2013 and 2014 on all aspects of BM and leaf area. A likely explanation is lower susceptibility of *Q. petraea* to PM than *Q. robur* (Dillen et al., 2016; Marçais and Desprez-Loustau, 2012). This is supported by the lower impact of PM on BM in July 2013 in Gedinne than in July 2014 in Zedelgem, despite the average affected area in Gedinne being over 50% greater. We cannot disentangle this hypothesis from the different abiotic conditions between both sites, however, as illustrated by the much less negative impact of shading on BM and total dry BM per sapling being over 60% greater in Zedelgem than in Gedinne. This might be indicative of some sort of stress gradient influence as in Jucker et al. (2015), although with less composition effects in the less abiotically favorable site, but any conclusion at this point would be preliminary due to the small sample size of only two sites differing in multiple ways not only related to plant stress (Verheyen et al., 2013). The higher R/W ratio might reflect incentive for stronger root development, such as water or nutrient shortages, or less incentive for shoot development due to the lower degree of shading and its lower impact on biomass.

The occurrence of PM in Gedinne in 2015 reveals a strong impact of the disease on leaf characteristics, increasing SLA and reducing leaf C/N. Previous research found opposite response of leaf C/N, with leaf C increasing and leaf N decreasing with increasingly severe infection, and no response of SLA (Hajji et al., 2009; Tack et al., 2012). However, their results also show that leaf N was elevated in infected leaves when compared to uninfected ones. This difference dwarves the trend among infected leaves, which was strongest for severe infections of more than 25% of leaf area affected, compared to the 11% in our data. Another study did not look at differences in leaf area, but found higher leaf dry BM in

infected leaves, which does not support our results for SLA either (Pap et al., 2014).

5. Conclusion

In this study, we looked at the influence of neighbourhood tree species composition, defined as either species richness or absence/presence of certain species, on various growth characteristics of oak saplings. We also linked these characteristics to scores of leaf area infected by powdery mildew and the degree of shading. We found no effects of species richness in neither site, yet strong effects of species presence or absence in the abiotically more favorable site of Zedelgem. These effects could be linked to the strong negative impact on biomass of powdery mildew and shading, which were both associated differently with the five species. Effects of shading differed between above- and belowground biomass and varied depending on which shade-casting species was present. Higher biomass values in the presence of slower growing and therefore – while young – less shade-casting species like European beech and small-leaved lime could not be fully linked to this absence of shading. The abiotically less favorable site of Gedinne showed little effects of species composition on oak saplings and less negative impact of shading or powdery mildew. This can be explained by poorer susceptibility of *Q. petraea* to oak PM than *Q. robur* or by a smaller impact of the disease under harsher abiotic conditions.

Our results suggest that, while increased tree species richness showed little impact on dry biomass production or other growth characteristics per se, admixing certain species in the local neighbourhood can have a considerable negative or positive impact. Mixing of species on individual basis can be recommended in particular if high impact specialist pathogens such as oak powdery mildew are to be expected. *Q. petraea* may also be a preferable species to *Q. robur* in high risk circumstances. Even though we found little effect of species richness *sensu stricto*, our study did not look into impacts on other ecosystem functions or on longer time scales. The substantial impact of disease in our experiment strengthens the argument for mixing species as risk mitigation against future calamities, in particular in the light of globalization and its associated greater risk of invasive pests and pathogens.

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Appendix A

Results of the crown size estimate validation can be found in Fig. A1. Adjusted R^2 was 0.78 for Zedelgem and 0.69 for Gedinne, with residual variance increasing with greater crown size. Results for the allometric relationships can be found on Fig. A2. Adjusted R^2 values for Zedelgem were 0.82, 0.83 and 0.72 for TBM, W and R biomass respectively. For Gedinne, they were 0.74, 0.80 and 0.62. Variance was notably higher for Gedinne belowground biomass.

Fig. A1. Linear regression between Total Leaf Area as determined after harvest in September 2015 and estimated crown size as estimated by the sum of shoot weights used during monitoring for PM. Adjusted R^2 was 0.78 for Zedelgem and 0.69 for Gedinne.

Fig. A2. Allometric relationships between diameter and dry biomass, respectively total (TBM), aboveground (W) and belowground (R), in 2016. Adjusted R^2 values for Zedelgem were 0.82, 0.83 and 0.72 respectively. For Gedinne, they were 0.74, 0.80 and 0.62 respectively.

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