Identity rather than richness drives local neighbourhood species composition effects on oak sapling growth in a young forest

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ABSTRACT

In light of global biodiversity loss, the influence of species composition on ecosystem functioning has attracted increasing attention. However, questions remain whether neighbourhood species richness or identity is more important and what mechanisms drive these composition effects. We investigated the role of local species richness and identity on oak sapling growth in young forest stands, and attempted to link growth with two commonly expected mechanisms: oak powdery mildew (PM), a host-specific leaf pathogen, and degree of shading. Furthermore, we studied how such effects might interact with reduced rainfall.

We established a reduced rainfall gradient on oak (Quercus) saplings planted within two sites of a young tree diversity experiment (FORBIO). We found no effect of species richness on growth, whereas presence of particular species had a significant impact. In one site, we found an identity effect on growth through negative effects of oak (Q. robur) presence, which was linked to increased PM infection severity. Such link was less clear in the other site, where the impact of PM and oak (Q. petraea) presence was lower and there was no relation between the two. Other identity effects were related to levels of shading, which were themselves influenced by fast early growth rates of the neighbouring trees. We found no consistent effects of reduced rainfall on growth. Host-mediated effects through oak PM and functional size-mediated effects through shading were the most important composition effects in our young forest experiment, with no support for species richness effects through local environmental conditions or natural enemies.

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1. Introduction

In the last two decades, more and more research was undertaken into effects of species diversity and species composition on ecosystem functioning (Cardinale et al., 2012; Hooper et al., 2005; Tilman et al., 2001, 2014). After initial experiments with synthetic species assemblages in grasslands (Hector et al., 1999; Weigelt et al., 2010), the scope was broadened to include many other types of ecosystems, including forests (Scherer-Lorenzen et al., 2007; Zhang et al., 2012; Vilà et al., 2013). The original impetus to investigate these effects of biodiversity was the strong ongoing decline of biodiversity on a global scale, linked to the widespread environmental changes of the Anthropocene (Hooper et al., 2012). However, some researchers have cast doubt on the link between biodiversity loss at a local scale, as studied in the mentioned experiments, and the observed biodiversity loss at a regional or global scale (Sax and Gaines, 2003; Vellend et al., 2013). Nevertheless, in systems such as grasslands or forests, species composition can often be influenced or even controlled by the manager. Hence studies covering the impact of local scale biodiversity on ecosystem functioning will have implications for the management of these ecosystems (Tilman et al., 2006; Pretzsch and Schütze, 2009; Gamfeldt et al., 2013).

Studies into composition effects in forests can take multiple approaches (Nadowski et al., 2010). This includes looking at existing inventory data (Gamfeldt et al., 2013; Paquette and Messier, 2011; Vilà et al., 2007), gathering data from different compositions in extant forest (Baeten et al., 2013; Firn et al., 2007) and establishing new plantations designed with compositional comparisons in mind (Verheyen et al., 2015). New plantations have the advantage of a well-controlled composition gradient, with fewer (unknown) confounding variables such as differences in site history (Leuschner et al., 2009; Scherer-Lorenzen et al., 2005). However,
the slow growth of trees makes the representativeness to mature forest of such experiments poor in the short term, as tree interaction mechanisms, such as root competition, will have much less of an impact initially than they are expected to have in mature forest (Domisch et al., 2015; Meinen et al., 2009).

While some mechanisms such as root competition do not play a big role yet, it is known that young trees are much more susceptible to certain pests and diseases because they have less reserves to fall back on in severe years or to support defense mechanisms (Barton and Hanley, 2013). For instance, the oak powdery mildew fungus (PM, predominantly Erysiphe alphitoides) is not considered a severe problem for mature trees, but can cause substantial mortality and growth reduction in young saplings (Maçais and Desprez-Loustau, 2012). Hence, composition-based mechanisms related to mitigating the impact of pests or pathogens are expected to play a more important role in younger stands.

Examples of these mechanisms are the dilution of resources favored or required by these pests as the density of nonsusceptible species increases and an enriched top-down control by natural enemies, who may benefit from greater structural diversity or diet mixing in more species diverse neighbourhoods (Jactel and Brockerhoff, 2007; Sobek et al., 2009). In the case of oak PM, which is a specialist biotrophic leaf parasite of various Quercus species, an increased density of nonsusceptible trees may decrease the spore load for the susceptible ones. This may be particularly so for oak PM, as the most virulent species of this fungus, E. alphitoides, tends to hibernate in sexual form outside the host, which necessitates the fungus to infect its hosts anew with ascospores every year (Peau et al., 2012). The fungus also spreads on a leaf-by-leaf basis during a growing season by continuously producing asexual spores as fast as possible from newly infected leaves (Maçais et al., 2009).

Hence, reducing the availability of suitable host trees at the local scale would reduce the initial spore load and therefore reduce the probability of infection as well as the proportion of initially infected leaves, whereas oak leaves are only susceptible to PM in the first two weeks of their life (Edwards and Ayres, 1982). Changes in neighbourhood composition may also influence natural predators of PM, such as mycophagous ladybugs by offering them alternate food sources such as pollen or powdery mildew fungi of other plant species that may be available earlier in the growing season (Sutherland and Parrella, 2009).

Another composition mechanism is the Janzen-Connell effect (Bagchi et al., 2010), where proximity to the mother tree increases the pressure of pests and pathogens on offspring. The presence or density of conspecifics in the local neighbourhood can be expected to have a strong impact, facilitating host-specific pest dispersal as well as increasing patch attractivity (Jactel et al., 2005). Similar effects of species identity could also be associated with other, allospecific tree species with certain high impact functional traits such as nitrogen fixation (Forrester et al., 2006). Such impacts of species identity in the local neighbourhood have been found in multiple studies (Firn et al., 2007; Hantsch et al., 2013; Nadowski et al., 2010; Setiawan et al., 2014), related to traits such as susceptibility to specialist pathogens (Hantsch et al., 2013) or tree size and its relationship to microclimate and apparent for insects (Castagneryl et al., 2013; Hantsch et al., 2014). Tree size is obviously related to shading, which may have negative consequences for growth, but it also influences microclimate, possibly reducing the likelihood of spore-dispersing pathogens to find a host (Bock et al., 2010).

More recently, researchers have been looking into how positive effects of neighbourhood composition are influenced by other ecosystem characteristics, such as the resource stress the species present are suffering from Jucker et al. (2015), Paquette and Messier (2011), Steudel et al. (2012) and Toigo et al. (2015). They considered that such diversity effects might be stronger or more important under more stressful circumstances, for instance because this opens up more opportunities for (and therefore more expected instances of) facilitation between species (Bertness and Callaway, 1994). Evidence supporting this so-called Stress Gradient Hypothesis (SGH) was found in multiple forest studies, finding stronger composition effects under less favorable site conditions (Eränänen and Kozlov, 2008; Jucker et al., 2015; Paquette and Messier, 2011; Toigo et al., 2015). If such a relationship were to be quite generic, it could have serious implications for conservation ecology and production ecosystems as these are associated with a trend of biodiversity loss or a low imposed species diversity respectively. Both are also expected to be subjected to increasing stress and disturbance events through the various mechanisms of Global Change, including climate change, invasive (pathogenic) species and changes in land use (Rockström et al., 2009). The realized diversity of both natural and synthetic ecosystems could therefore prove to be more important than currently perceived.

Here, we attempted to elucidate the relationship between local neighbourhood composition, growth and reduced rainfall in two young forest stands, which were each incorporated with a balanced tree species diversity gradient (Verheyen et al., 2013). Potted oak saplings were planted within the plantation and subjected to a reduced rainfall gradient. We hypothesized that local neighbourhood tree species richness would have a positive effect on tree growth or that the presence of certain tree species in the local neighbourhood influenced growth as an identity effect, in particular if this species was the same as the focal species (oak), due to the Janzen-Connell effect. To assess the mechanisms by which either such relationship might come to be, we compared both indices of neighbourhood composition to the severity of powdery mildew and to the degree of shading the focal tree was subjected to, as we expected these to be the most likely to operate on our potted oak saplings. We expected a negative effect of reduced rainfall on growth and stronger positive effects of neighbourhood composition along the reduced rainfall gradient.

2. Materials and methods

2.1. Sites

Our experiment was set up within two sites of the FORBIO project, Zedelgem and Gedinne. FORBIO (FORest BIODiversity and Ecosystem Functioning) is a network of three relatively large (ca. 9 ha) experimental forest sites in Belgium, ‘designed specifically to test the effects of tree species diversity on forest ecosystem functioning’ (Verheyen et al., 2013). In each site, young saplings of five different tree species were planted in compositions that ranged from monocultures to up to four different species mixed together. Due to differences in juvenile growth, the trees were always planted in groups of 3 by 3, sometimes 4 by 3. This would make it possible to sustain mixtures for a longer time, by reducing strong competitive interspecific interactions. All monocultures and four-species mixtures were represented, as well as 5 randomly selected compositions for the other two species richness levels (Table A.1). These 20 compositions were replicated once for a total of 40 plots. Planting distance was 1.5 m × 1.5 m and typical plot size was 42 m × 42 m. 13 plots in Gedinne were only 42 m × 37.5 m (Fig. 1). Each site also had a few extra plots containing different provenances of Quercus (Zedelgem) or Fagus (Gedinne). These were not included in this experiment, which was limited to plots 1–41 in each site, omitting plot 38.

The site of Zedelgem was planted in late 2009 and early 2010 on former agricultural field with a sandy to loamy sandy soil. The five species used here are pedunculate oak (Quercus robur), European beech (Fagus sylvatica), Scots pine (Pinus sylvestris), small-leaved...
lime (*Tilia cordata*) and silver birch (*Betula pendula*). The site of Gedinne was divided into two parts, about 4 km from each other and all composition levels were present in each site. The part called Gribelle has a stony soil and is more exposed than Gouverneurs, which has a shallow soil. Both were planted on Norway spruce (*Picea abies*) clearcuts in early spring 2010. The species used here are European beech, sessile oak (*Quercus petraea*), sycamore maple (*Acer pseudoplatanus*), hybrid larch (*Larix × eurolepis*) and Douglas fir (*Pseudotsuga menziesii*). Monthly rainfall data for 2013–2014, based on weather station proxies (KMI, Belgium), can be found for the oak growing season months in Table A.2. The summer of 2013 was rather dry, in particular in August, whereas the summer of 2014 was much wetter than normal. 2015 fell somewhere in between, with July being a bit drier than average but not as severe as August 2013. More info on the FORBIO sites can be found in Verheyen et al. (2013).

### 2.2. Experimental setup

In late April and early May 2013, one-year old saplings of oak were planted in pots between the trees of the FORBIO site. The same oak species was used as present in the site, but not the same provenance as some plots in Zedelgem contained multiple *Q. robur* provenances. Three such phytometers were planted in 20 l black pots and placed together between four of the older, larger trees (1–3 m higher) in each of the 40 plots (Fig. 1). These black pots had drainage holes in the bottom and were placed in the ground to reduce solar heat absorption and ensure that the soil level was more or less equal in and outside of the pots. The four neighbouring FORBIO trees were always representative of the whole plot’s composition. We set up our phytometers as far from the plot edge as possible (i.e. close to the center), but in practice this was not always the case for mixtures of 3 or 4 species (cfr. Figs. A.1 and A.2). In those plots, the crossings were the surrounding composition matched were limited and often already claimed as permanent sampling plots for long term study of the sites. Soil from the sites themselves was used, collected from an unused patch in Zedelgem and from two separate patches for the two blocks in Gedinne for logistic reasons. No potting soil was used as a difference in nutrient status might influence the attractivity of the phytometers to herbivore pests (White, 1984).

Late May (Zedelgem) and late June (Gedinne) in the same year, a reduced rainfall treatment was installed on these phytometers. Small PVC gutters with a diameter of 3.2 cm were placed above the pot surface but below the tree canopy in two of the three phytometers of every plot. One and two pairs of gutters were used as can be seen in Fig. 2. The theoretical interception rates based on pot surface covered are 18 and 35%, mimicking average summer precipitation reduction expectations for the region according to climate model predictions (Willems et al., 2009). The interception treatments were defined as the control (0% interception), the medium treatment (18%) and the severe treatment (35%). In 5 of the 40
plots, collectors were installed at the gutter ends (Fig. 2) to obtain estimates of the rainfall removal. The pots were kept free of major understorey influence by frequent weeding and the collectors were measured and emptied regularly. A full precipitation assessment of the growing season was not possible, as the four-gutter collectors could overflow after one major rain event (max. 33 mm per collector). The rainfall reduction treatment was removed at the end of each growing season (late October, early November) and reinstated in early May, because winter precipitation reductions per climate change are unexpected for this region (Willems et al., 2009).

In July and August of 2015, volumetric soil moisture content was measured in all pots using a ML3 ThetaProbe (Delta-T Devices). For each pot, two measurements were made at the pot surface (0–6 cm) and two at a depth of 14–20 cm, using a small PVC tube to gather soil from this depth and subsequently inserting the ThetaProbe’s sensor pins into the entubed soil to perform the measurement. This depth measurement was not possible in the Gribelle part of the Gedinne site due to the high number of rocks in the soil. A third measurement at the surface was made instead. The standard conversion parameters for a mineral soil type were in the soil. A third measurement at the surface was made instead. The standard conversion parameters for a mineral soil type were used in the further analysis.

A monitoring for leaf damage symptoms was undertaken in July, August, October 2013; July, September 2014 and August 2015 in Zedelgem as well as in July and August 2013, 2014 and August 2015 in Gedinne. First order shoots, i.e. shoots on the main stem or, in unclear cases, all main stems, were scored for different leaf damage symptoms using four % classes: 0–5%, 5–30%, 30–60% and 60–100% of leaf area affected. Different symptoms were scored separately. To correct for increasingly differing sizes of the first order shoots, from October 2013 onwards relative leaf area weights were estimated for each shoot. To determine these weights, we assumed an average-sized single oak leaf from the lower canopy to have a leaf area of 1 and subsequently approximated the total leaf area of each first order shoot in multiplications of such an oak leaf unit (e.g. a single shoot might have a total leaf area of approximately 12 average-sized leaves). We used a typical lower canopy leaf as our single unit, because leaves growing alone from the main stem were mostly only found there. These weights were later used to calculate a weighted average symptom score at the whole tree level.

Other than oak powdery mildew (PM), the following leaf damage symptoms were also assessed: chewing, skeletonization, mining and brown discoloration. Leaf galls were counted at the shoot level; no gall species differentiation was made, but a grand majority were Cynips divisa. This differentiation was based on results from previous surveys on the FORBIO trees (Setiawan et al., 2014) and a pilot survey on the phytometers. During this pilot survey, the presence of these symptoms on the older FORBIO trees was also ascertained. Symptoms were only assessed during dry weather conditions, as PM hyphae become less visible when a leaf is wet. Monitoring of all symptoms was continued for all measuring moments, but PM was the most important symptom by far. Leaf chewing overall only minimally reduced leaf area and was impossible to quantify accurately when it was significant, as this typically surmounted to whole leaf or shoot loss. Leaf mining was rare, while skeletonization was limited mostly to the end of the growing season only, when its impact on growth was expected to be minimal. Brown discoloration was more abundant, but could be linked to various different, not very easily differentiable causes, including late spring frost, drought stress, PM-induced mortality and early onset of autumn. Galls were only found in less than 20% of our trees. Hence, we opted to only take the PM data into account for further analysis. Data of all symptoms can be found in the Supplemented data files for this paper.

In July and August of 2015, the degree of shading for each phytometer was estimated using a spherical densiometer (Baudry et al., 2014). A% value for East, South and West was determined separately above each sapling. Collinearity between these values was high, so an average was calculated for each phytometer and used in the further analysis.
2.4. Calculations

Class scores of leaf damage symptoms were scaled up to phytometer level by averaging the class mid values (0, 17.5, 45 and 80%), using the relative shoot size scores as weights if available. For the lowest 0–5% class, 0 was used instead of the class mid as this class was supposed to correct for the difficulty in determining very small or beginning infestations. Hence, using the class mid would distort the meaning of the 0 value in this case. The galls count data were not averaged but summed.

The diameters were transformed into (circular) basal area (mm²) and its relative increment (BAIr) calculated for the 2013, 2014 and 2015 growing seasons as well as across all three seasons. Relative height increment (HIr) was determined similarly, though only from winter 2013–2014 onwards:

$$\text{BAIr} = \frac{B_{A2} - B_{A1}}{B_{A1}}, \quad \text{HIr} = \frac{H_{2} - H_{1}}{H_{1}}$$

One phytometer with the severe reduced rainfall treatment in a beech monoculture was dead in Gedinne by the 2014 growing seasons (cause unknown). Six phytometers were dead in Zedelgem by 2014, mostly because of attack by macro-herbivores (hare, rabbit, possibly wild boar). Three of these were in the same plot, a 4–species mixture without birch. The other three were in an oak monoculture (medium rainfall reduction treatment), an oak-beech mixture (medium) and a 4–species mixture without lime (severe). All of these were omitted from all analyses. Three incorrect measurements (two diameter, one height) in Zedelgem were also omitted from the growth models.

2.5. Statistical analysis

All statistical analyses were performed using R (R Core Team, 2015). Mixed models were run using the package lme4 (Bates et al., 2015), with lmerTest extension (Kuznetsova et al., 2015) to determine Satterthwaite approximated p-values.

The soil moisture content (SMC) data were compared to the reduced rainfall treatment using a linear mixed model with intercept. In Zedelgem, weather conditions preceding the measurements in block 2 were much drier than those in block 1. In Gedinne, the stone density of the soil in block 1 made measurements at a depth of 14–20 cm impossible. The model was therefore run separately for the two sites and for the two replication blocks at a depth of 14–20 cm impossible. The model was therefore run separately for the two sites and for the two replication blocks at a depth of 14–20 cm impossible. Due to the 3 × 3 group-planted FORBIO design, this also corresponds to the tree composition of the 36 FORBIO trees closest to the phytometer plot. All models were linear mixed models with plot as random factor and including an intercept.

First, the relationship between the annual or total relative increments and neighbour composition was tested. The model also incorporated the reduced rainfall treatment and its interaction with composition, to test for the Stress Gradient Hypothesis. The indices of composition, richness and identity, could not be tested together in the same model, as richness would always be a linear combination of all identity effects.

$$\text{BAIr}, \quad \text{HIr} = \frac{5}{C_{0}} + \frac{5}{C_{1}} + \frac{5}{C_{2}} + \frac{5}{C_{3}}$$

Second, similar models tested the relationship between neighbour composition and the two potential driving mechanisms: PM infection severity and the level of shading (SH). PM levels of the different measuring moments were included separately, as PM infections can occur throughout the growing season while the Lammas shoots develop.

$$\text{PM or SH} = \frac{5}{C_{0}} + \frac{5}{C_{1}} + \frac{5}{C_{2}} + \frac{5}{C_{3}}$$

Finally, we linked the driving mechanisms directly relative to relative increment. The mechanism variables were individually centered around their mean and rescaled from percentages to fractions, both to facilitate interpretation of their effect sizes.

$$\text{BAIr}, \quad \text{HIr} = \frac{5}{C_{0}} + \frac{5}{C_{1}} + \frac{5}{C_{2}} + \frac{5}{C_{3}}$$

3. Results

3.1. Treatment validation

A combined dataset of all ratios of reduced rainfall treatment collectors compared to the in-plot control collector yielded 67 values for the pots with one pair of gutters and 61 for those with two pairs. Average interception rates were estimated in confidence intervals of 12.95 ± 0.9% and 26.13 ± 1.6%, respectively, which correspond relatively well with the theoretical interception rates of 18% and 35%. These values were all determined for Zedelgem, as there was not enough good data for a similar assessment in Gedinne due to frequent collector failure. However, as the same
design was used in both sites, we assume the Zedelgem values to be fairly representative.

The results of the soil moisture content models can be found in Table A.3. A barchart differentiating the most important predictors can be found in Fig. 3. The difference in soil moisture content was 2–3%; always significant between the control and the most severe reduced rainfall treatment, but the medium treatment did not always differ from the severe or control treatment. Measurements at 14–20 cm depth in Zedelgem showed larger differences than those at the surface, although this interaction was not significant. The level of shading had little impact on soil moisture content (Table A.3).

In our composition model results, there were little to no effects of the reduced rainfall treatment in Zedelgem or Gedinne. Our collector data supported that precipitation was removed as expected and we did see an effect of the treatment on soil moisture content (SMC). However, the effect on SMC was only minor and did not consistently follow our interception gradient. Therefore, we also ran all models without the reduced rainfall treatment or its interactions to facilitate interpretation of our other two hypotheses. The results of these simplified models can be found in Tables 1–3. The original results, including the reduced rainfall effects, can be found in Tables A.4–A.7.

### 3.2. Model results

Neither BAI or HI were influenced by species richness in either of the two sites (Table 1). In contrast, particularly in Zedelgem, there were strong effects of identity. From 2014 on the presence of oak had in Zedelgem an increasingly negative significant impact on BAI, as well as on HI, in the 2015 growing season. A less strong, but still overall negative impact of oak was found in Gedinne, but this was only significant in the 2014 growing season (Fig. 4). Other identity effects were less strong or consistent, though the presence of beech and lime did seem to be generally beneficial in Zedelgem, while the presence of larch improved HI in Gedinne.

Species richness did have a negative impact on PM symptoms in Gedinne in August 2013 and 2015, while the trend was negative at other times as well (Table 2). Graphic exploration and running the model with species richness as a factor variable revealed that this

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**Table 1**

<table>
<thead>
<tr>
<th>Species richness</th>
<th>Species identity</th>
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<tr>
<td></td>
<td>Zedelgem</td>
</tr>
</tbody>
</table>

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Fig. 3. Soil moisture contents and their confidence intervals separated between block and measurement depth for the sites of (a) Zedelgem and (b) Gedinne. Black bars indicate the control, light grey bars the most severe reduced rainfall treatment. There were no measurements at 14–20 cm in block 1 of Gedinne (‘Gribelle’) due to the high stone content. Significant differences according to the models is indicated using the digits a and b. Note that the model was not run separately for different depths of measurement and that the interaction between depth and level of rainfall reduction was never significant (Table A.3). Hence, the graphical interpretation of the confidence intervals may differ from the mixed model results.

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### Table 1

Table with the species richness and identity model results for basal area and height increment in Zedelgem and Gedinne. 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. B is the blocking factor. 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. Square root (sqrt) transformations to compensate for residual heterogeneity are indicated, with an " indicating that the response variable was first pre-transformed by adding a constant to have a minimum of 0. These minima can be found in the rightmost column.
was caused by a strong difference between monocultures and the three other richness levels. Increasing richness also had a strong negative influence on the level of shading in Zedelgem, but did not seem to influence PM levels. Identity effects increasing the infectivity of PM were found for oak and to a lesser extent lime in Zedelgem, and for none of the five species in Gedinne. Mitigating effects were found for pine and to a lesser extent beech in Zedelgem, and weakly for larch and beech in Gedinne. Strikingly, maple in Gedinne had a mitigating effect in 2013 and 2015, while its effect was (not-significantly) positive in 2014. Unexpectedly, oak in Gedinne had barely any impact on PM levels, with the small effect sizes even being mostly negative. Levels of shading in Zedelgem differed markedly between the two extremes of either birch and pine or beech and lime. Oak fell somewhere in between. In Gedinne, larch caused most shading by far, while maple was associated with the least – most likely related to its high mortality in the site with 20% of the local neighbourhood maples deceased.

Negative effects of PM on BAIr were found in both sites (Table 3). Correlation within years as measured with VIF’s was high in Gedinne, but not in Zedelgem. Because of this, the August data for Gedinne were dropped from the models. Negative effects were strongest in Zedelgem in July 2014, which seemed to dominate all other PM responses despite the poor level of multicollinearity and also had a negative impact on the following year both in terms of BAIr and HIr. PM effects were less strong in Gedinne and did not have an effect on growth in 2015. Shading had a negative impact on BAIr in Zedelgem, contrasting with a positive impact on both BAIr and HIr in Gedinne.

4. Discussion

In our experiment, effects of identity were much more important than those of species richness, which did not seem to have an influence on growth at all in either site. While other studies have found positive effects of increased species richness on basal area (Piotto, 2008) and height increment (Haase et al., 2015) of young trees, these effects were generally small and mostly a difference between monoculture and mixture, not a gradient effect. However, such a binary effect on growth was not seen in our experiment either (data not shown). In our design, increasing species richness did not correspond to increased dilution of hosts for specialist herbivores and pathogens, as the probability of a specific species being present increased along the richness gradient, while species density was constant across all richness levels. Hence, we would not expect a species richness effect through host dilution,

Table 2

<table>
<thead>
<tr>
<th>Species richness</th>
<th>Species identity</th>
<th>Zedelgem</th>
<th>Gedinne</th>
</tr>
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<tbody>
<tr>
<td>tf SR B C</td>
<td>tf Oak Beech Lime Birch Pine B C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jul 13 sqrt -0.09** 1.09** 1.64**</td>
<td>sqrt 0.45 -0.49 0.54 -0.29 -0.69* 1.07** 1.66***</td>
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<td></td>
</tr>
<tr>
<td>Aug 13 sqrt 0.00 0.44 2.90***</td>
<td>sqrt 0.15 -0.35 0.73** 0.24 -0.55* 0.45* 2.91***</td>
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<tr>
<td>Oct 13 sqrt 0.07 0.06 3.81***</td>
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<tr>
<td>Jul 14 sqrt 0.01 -0.07 4.36***</td>
<td>sqrt 1.59*** -0.36 -0.39 -0.18 -0.58 -0.09 4.36***</td>
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<td></td>
</tr>
<tr>
<td>Sep 14 sqrt 0.10 1.36** 3.06***</td>
<td>sqrt 0.65 -0.42 0.46 0.33 -0.59 1.36** 3.09***</td>
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<td></td>
</tr>
<tr>
<td>Shade 9.2** 4.71 37.52***</td>
<td>4.33 -6.04 -7.23 31.10*** 20.11*** 6.01 38.12***</td>
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<td></td>
</tr>
</tbody>
</table>

Fig. 4. Relative increment of basal area (BA) and height (H) in (a) Zedelgem and (b) Gedinne from 2013 to 2015 and across the three years. Bars in dark are phytometers without oak in the local neighbourhood, whereas grey bars represent phytometers with oak. Confidence intervals at 95% are indicated. Significant differences according to the models is indicated using the digits a and b.

Table 3

<table>
<thead>
<tr>
<th>Species richness</th>
<th>Species identity</th>
<th>Maple</th>
<th>Larch</th>
<th>Douglas</th>
</tr>
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<tr>
<td>tf SR B C</td>
<td>tf sqrt 0.39 -0.36 -0.42 0.11 -0.58 0.50 4.96***</td>
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</tr>
<tr>
<td>Jul 13 sqrt -3.06* 3.56 38.21***</td>
<td>sqrt -0.10 -0.33 -0.57* -0.17 -0.02 0.30 6.07***</td>
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<tr>
<td>Aug 13 sqrt -0.04 -1.00* 4.47***</td>
<td>sqrt -0.44 -0.29 0.60 -0.46 0.42 -1.00* 4.46***</td>
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<tr>
<td>Jul 14 sqrt -0.17 -0.93* 5.56***</td>
<td>sqrt 0.13 -0.50 0.41 -0.92* 0.03 -0.92* 5.53***</td>
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<tr>
<td>Aug 15 sqrt -0.54* -0.09 4.30***</td>
<td>sqrt -0.26 -1.08* -0.73* -0.34 -0.29 -0.08 4.29***</td>
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<tr>
<td>Shade 0.30 0.71 3.92*</td>
<td>0.56 -0.59 -1.85*** 2.67*** 0.64 0.71 3.92***</td>
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whereas such host-density mediated effects have been found elsewhere (Hantsch et al., 2013; Peacock et al., 2001). This suggests that, at least in young forests, the influence of neighbourhood tree species richness lies more with resource dilution for specialist herbivores and pathogens, rather than effects of altered local environment (Hantsch et al., 2014) or by increased support for natural enemies (Jactel et al., 2005).

Support for a negative identity effect of the presence of oak on growth was found in both sites, but the strongest effect by far was in Zedelgem. While mortality was too low to assess a Janzen-Connell effect sensu stricto, growth reductions were substantial, with BA1 from 2013 to 2015 being 54% lower and HI 61% from Zedelgem (Table 1). This effect only became apparent from the high levels seen in July in Zedelgem. This is not surprising, as initial oak PM sexual spore production is known to peak about a month after bud burst (Feau et al., 2012) and oak leaves are prone to host dilution, but they could link it to identity effects of certain species and implied the lowest probability of encountering a specific species. A possible explanation could be that the monotonous environment as a result of a low functional diversity generates a stable physical environment that facilitates infections. A previous study found only a weak effect of functional diversity which even promoted herbivory instead (Haase et al., 2015), but this was attributed to associational susceptibility where the herbivores could benefit from a more diverse diet. This would not be the case for oak PM, a specialist parasite. A study covering oak PM on Q. petraea found a mitigating effect of tree species richness on PM infections that was not related to host dilution, but they could link it to identity effects of certain non-host tree species (Hantsch et al., 2014). In their experiment, an increasing proportion of coniferous species decreased fungal infestation, while Fraxinus excelsior, which suffered severely from ash dieback, had the opposite effect. Diseased trees with poorly developed crowns might have had a reduced ability to conceal their neighbours from infectious spores, analogous to an increased apparency for herbivores (Castagneryol et al., 2013). However, this contrasts with the mitigating effect of maple on PM infection in our experiment, as the species also suffered from poor vitality and even mortality (Van de Peer et al., 2016). Further supporting the theory that environmental conditions, rather than effective dispersal, were limiting to oak PM in this site is the absence of a link between oak presence and oak PM infection levels. A link to natural enemies seems unlikely too, as almost no signs of PM grazing were found and mycophagous ladybirds (Sutherland and Parrella, 2009) were only very rarely spotted within this site.

The presence of beech and lime in Zedelgem had positive effects on growth, though it is not immediately clear why. While lime had a positive effect on BA1 and HI, beech had no influence on HI. In contrast with the effect of oak, both species did not have an impact in 2014. Beech and lime were associated with lower levels of
shading than the other three species, in particular pine and birch (Table 3). Hence, an effect of diminished light competition might be at work here, in particular as we do not find these identity effects in 2014. That year, growth was suboptimal due to late spring frost and subsequent severe oak PM infections. These drivers would have been limiting rather than competition for resources. Both a facilitative nursing effect and a mechanism through pathogen mediation seem less supported by our data, as we would expect drought to be more severe under more open canopies and we found contrasting results for the impact of beech and lime presence on oak PM levels (Table 2).

The presence of larch in Gedinne was positively related to height increment in 2015. Larch was the most shade-casting species, but greater levels of shading are not known to influence juvenile height growth in Quercus (Jensen et al., 2012; Niinemets, 1998). Nevertheless, greater levels of shading were also associated with greater HI, in 2015 in Gedinne. Possibly a protective microclimate effect by large, nursing larches is an explanation, though we do not see this relationship to hold for BAI.

Data from the soil moisture content measurements and the lack of strong, consistent effects in our models suggests that our reduced rainfall treatment had little effect on the drought stress of our phytometers, even in very dry months such as August 2013. Interception rates as measured by the collectors fit our expectations, with the lower values found explainable by evaporation from the gutters and possibly even the dug-in collectors themselves. The soil moisture content values were generally 2–3% lower in the most severe treatment as compared to the control, and this effect generally increased at the depth of 14–20 cm as suggested by the effect size of the interaction between measurement depth and interception treatment (Table A2). Hence, there was also less water inside the treated pots than in the controls, but possibly not sufficient to become limiting even during dry spells. In addition, oak is considered to be quite tolerant of drought and not at great risk concerning expected climatic changes in summer precipitation (Campioli et al., 2012). However, such risks are typically evaluated in terms of mortality, not growth. Drought stress has been found to reduce growth for oak, even if compensatory leaf flushes follow the dry spell (Kuster et al., 2011; Scharnweber et al., 2011; Speijl et al., 2012).

5. Conclusion

In this study, we found a negative identity effect on growth of oak presence in the local neighbourhood of a young forest, which can be seen as a Janzen-Connell effect working primarily through the host-specific pathogen powdery mildew. This effect was seen in both our experimental sites but differed considerably in its strength, which might be explained by contrasting abiotic conditions or by the lower susceptibility to PM of Q. petraea. Other identity effects could be related to different levels of shading as a result of different juvenile growth rates of the tree species in the local neighbourhood. We found no effect of species richness influencing growth, but we did find higher PM levels in monocultures regardless of whether the neighbour species was the same species as our phytometers. We found no effects of reduced rainfall but this might change if a treatment with a stronger impact on soil moisture conditions is applied. We did find contrasting effects of shading on growth between the sites of Zedelgem and Gedinne, which might be related to their differences in edaphic and microclimatic conditions. More research is needed to disentangle the influence of environmental conditions such as shading or rainfall on growth and oak PM infections, in particular concerning the impact of tree species that show poor vitality (such as F. excelsior due to ash dieback) and may therefore cast less shade or have lower apparency.

The implications of our findings may not hold for other species than Quercus or for older stands, in particular given the strong impact of the specialist PM fungus. However, even if the contemporary impact of PM infections decreases with tree age, it might still be interesting to study the effect of young sapling infections on vitality and size in older trees. If severe PM infections are expected in a plantation, (temporarily) mixing the oak stand with other tree species at an individual level can be recommended to mitigate the spread of spores and reduce the odds of initial infection, as well as opting for Q. petraea over Q. robur.

Acknowledgments

MD was supported in this research by an FWO and an Ubbo Emmius grant. We would like to thank Luc Willems, Kris Ceunen and Filip Ceunen for their help with setting up the experiment and performing the fieldwork, as well as Evy Ampoorter for help with the statistical analysis.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.09.004.

References


