The effects of local neighbourhood diversity on pest and disease damage of trees in a young experimental forest

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A B S T R A C T

Pests and diseases causing defoliation and crown discolouration are important risks threatening the vitality of forests, especially in the early stages of forest development. Mixing different tree species in a forest stand has been described as a possible solution to tackle this problem through the mechanism of associational resistance. However, most research up till now has focused on mature forests. We assessed three different damage symptoms related with tree crown condition, i.e., branch and shoot damage, defoliation, and crown discolouration, for nine common tree species at two sites of a recently established tree species diversity experiment in Belgium. The assessment was done in two subsequent years. A tree’s damage degree was influenced by the site characteristics and the timing of the assessment, and the species identity of the target tree was more important than the effect of local neighbourhood diversity per se in explaining a tree’s damage degree. Our results only partially support the hypothesis that trees in more diverse young plantations show less crown damage. Nevertheless, some particular mixtures resulted in reduced damage degrees.

1. Introduction

The crown condition of forest trees is commonly used as an indicator of forest health and vitality, e.g., by the European monitoring network ICP Forests (http://icp-forests.net). Two main crown condition criteria that are commonly assessed are (1) the loss of foliage area or defoliation and (2) crown discolouration. Defoliation and discolouration reduce a tree’s photosynthetic capacity (Führer, 1998); discolouration may lead to higher herbivore damage due to the increase in soluble nitrogen in the leaf tissues, which attracts invertebrate herbivores (White, 1984). Insects are the most common pests causing defoliation in European forests (Becher et al., 2014). Discolouration can be caused by several environmental stresses, e.g., drought or nutrient deficiency, and diseases, e.g., fungi or viruses (Hopkins and Hüner, 2009; Taiz and Zeiger, 2010). Pests and diseases naturally occur in the forest ecosystem (Ostry and Laflamme, 2009) and may serve as one of the key factors shaping the dynamics and diversity of forested landscapes, next to anthropogenic influences, abiotic factors, and large herbivores (Holdenrieder et al., 2004). Diseases may cause tree mortality, which will lead to the formation of canopy gaps in mature forests. Small-scale succession in these canopy gaps helps to maintain tree species and age diversity in the forest (Castello et al., 1995). Yet, for forest management, the damage caused by insect activities or diseases is considered a threat if it reaches a certain threshold, i.e., affecting 25% of single trees (Eichhorn et al., 2010).

The risk for pest and disease damage is related to the probability of occurrence and the behaviour of populations of damaging agents (Hambäck et al., 2014; Hambäck and Beckerman, 2003; Jactel et al., 2009), which is in turn influenced by the forest stand composition and management. Indeed, the occurrence of most pests and pathogens largely depends on stand density, the presence of host trees, the abundance of non-host trees, and other stand characteristics, such as stand composition and age structure (Barbosa et al., 2009; Hambäck et al., 2014; Hambäck and Beckerman, 2003; Vehviläinen et al., 2007). Mixed stands consisting of site-adapted species may be more resistant to pests and diseases compared to monocultures (Jactel et al., 2005; Speicherd, 2003). Indeed, a focal tree’s vulnerability to predation or parasitism can be altered by the identity, diversity, and abundance of its neighbouring species (Underwood et al., 2014). This phenomenon, also called associational resistance (Tahvanainen and Root, 1972), can be explained by the resource concentration theory (Root, 1973), i.e., the resources are more concentrated in...
monocultures and thus more easily found by pathogenic fungi or insect herbivores. Yet, the results of studies on the relation between tree species diversity and crown damage are not consistent and depend on the environmental conditions (Koricheva et al., 2006; Vehviläinen et al., 2007). In mixed stands, populations of specialized herbivores may be reduced, but generalist herbivores (Koricheva et al., 2006) and heteroecious fungal pathogens (Jactel et al., 2009) can be positively affected. Tree species diversity seems to have less effect than tree species composition. For instance, herbivore damage was less when mixed forests were comprised of taxonomically or phylogenetically more distant tree species or when the host tree species were surrounded by a higher proportion of non-host tree species (Castagneyrol et al., 2014; Jactel and Brockerhoff, 2007). The associational resistance in a certain neighbourhood may also change through time, e.g., between seasons, from year to year, or as the trees get older (Montagnini et al., 1995; Vehviläinen et al., 2007). However, most studies on the effect of tree species diversity on the resistance of trees to pests and diseases have been done in mature forests (Castagneyrol et al., 2014; Haas et al., 2011; Jactel and Brockerhoff, 2007; Koricheva et al., 2006; Vehviläinen et al., 2007, 2006). Only few studies have focused on the young stages of forest development (Castagneyrol et al., 2012; Hantsch et al., 2013; Sobek et al., 2009). Yet, the young stages of forest development, especially the particularly vulnerable regeneration stage, are important in determining the character of the trees and the stand in the later stages of forest development (Barton and Hanley, 2013).

2. Materials and methods

2.1. Study sites

Our study was conducted at two plantations of the Belgian FORBIO experiment, which were planted in spring 2010. The Gedinne site consist of two subsites, 2 km apart, i.e., Gribelle (49°60′N 4°59′E) and Gouveneurs (49°59′N 4°59′E); the second study site lies in the municipality of Zedelgem (51°9′N 3°7′E). The two sites differ in altitude, soil type, climate, and former land use (see Verheyen et al., 2013). The soil of both sites reflects the land-use history. The soil of the Gedinne site, a former spruce forest, has a lower pH, a lower total phosphorus content, and a higher C/N ratio compared with the Zedelgem site, which was formerly used for agriculture. Gedinne has a higher annual precipitation (1021 mm) and a lower mean annual temperature (6.9 °C) than Zedelgem (855 mm, 10.5 °C; 1981–2010 KMI).

The design of the FORBIO plantations follows a classical synthetic community approach, using a fixed species pool of five tree species in each plantation. Monocultures and mixtures of two up to four tree species were planted on an environmentally homogeneous site: all five monocultures, all five possible four-species combinations and a random selection of five two- and three-species combination. All combinations were replicated twice. Each site thus comprises 40 plots of 42 m × 42 m, 5 plots for each of the four diversity levels (1, 2, 3, and 4 species) and one replication. An extensive soil survey prior to the planting enabled attributing treatments and replicates to the experimental plots in such a way that there is no covariation between any of the soil variables and the presence/absence of a tree species or the diversity treatments, a major strength of the FORBIO experiment compared to the other tree diversity experiments worldwide (Verheyen et al., 2013). Five site-adapted, functionally dissimilar species were planted per site. The overall species pool consists of broadleaved as well as coniferous tree species that are particularly relevant for forestry in Western Europe. The species differ in, e.g., root characteristics, phenology, and shade tolerance. In Gedinne, the planted species are Acer pseudoplatanum L., Fagus sylvatica L., Quercus petraea (Mattuschka) Liebl., Larix x eurolepis Henry, and Pseudotsuga menziesii (Mirb.) Franco. In Zedelgem, Betula pendula Roth, Fagus sylvatica L., Quercus robur L., Tilia cordata Mill., and Pinus sylvestris L. were planted. Two of the species, i.e., F. sylvatica and Quercus (Q. petraea in Gedinne, Q. robur in Zedelgem), do occur at both sites. For more information about the design of the experiment, we refer to Verheyen et al. (2013).

2.2. Data collection

The FORBIO plots were planted in a chequerboard design with homogeneous cells of 3 × 3 trees and with planting distances of 1.5 m × 1.5 m (ca. 4400 trees/ha). We established four subplots of 4 × 4 trees in the central area of every plot. In mixed plots, we made sure that the selected subplots contained the most diverse combination of tree species (Fig. 1). We did the damage assessment for all the trees of each subplot (N = 64 trees/plot). In total, we assessed 2816 trees in Gedinne and 2688 trees in Zedelgem.

Damage symptoms or a tree’s condition due to damaging agents were assessed in three categories, i.e., (1) branch and shoot damage, (2) defoliation, and (3) crown discoloration. The assessment was a modification of the ICP crown condition assessment
The branch and shoot damage of a tree was quantified as the percentage foliage damage in the assessed tree crown as compared to a reference tree, i.e., a healthy tree in the vicinity. The percentage foliage damage was calculated as the multiplication of two estimates, i.e., the incidence and the intensity of the damage, with incidence the percentage of leaves that shows herbivore damage and intensity the percentage of the leaf area of these damaged leaves that is affected. Defoliation was assessed only on broadleaved tree species. Crown discoloration was quantified as the estimated percentage of the crown that showed a colour different from the usual leaf colour of the species, caused by environmental stress or pathogens, e.g., necrosis due to fungi.

The main causes of defoliation we encountered were insect herbivores, i.e., leaf chewers, leaf miners, and skeletonizers. These three groups of herbivores can be categorized as ectophagous species (leaf chewers), i.e., species consuming plant material by browsing, and endophagous species (leaf miners, skeletonizers), i.e., species disintegrating plant material from within. These insect herbivores mostly emerge following the bud burst of the trees. The leaf damage will accumulate until the second bud burst in early summer or until leaf fall in autumn. Therefore, we performed our assessments when the leaves were fully developed, i.e., in early summer (July–August 2013) and early autumn (October 2012) for the same target trees.

2.3. Data analysis

Tree identity and neighbourhood diversity were two important factors expected to influence a tree’s damage symptoms. Tree identity was defined as the species identity of the assessed tree. The design of FORBIO is based on a range of plot-scale diversity levels, but the actual diversity of a tree’s local neighbourhood (the eight surrounding trees, see Fig. 1) is expected to have a more direct effect (Barbosa et al., 2009; Uriarte et al., 2004). The local neighbourhood diversity was expressed as the exponent of the Shannon diversity index, i.e., giving the effective number of species weighted by abundance (Jost, 2006), calculated using the proportional abundances of the species identities of the eight trees surrounding the target tree. The analyses were done separately for the two sampling periods, i.e., early autumn 2012 and early summer 2013, and the two sites, i.e., Gedinne and Zedelgem.

All analyses were done in R version 3.0.3 (R Core Team, 2013); graphs were made with the R package ggplot2 (Wickham, 2009). First, we graphically checked for spatial autocorrelation in the damage data (Borcard et al., 2011). Second, correlations between the degrees of damage in the three damage categories and correlations between the degree of damage in each damage category and the total cover of the understory vegetation (data from Verheyen et al., 2013) were calculated using Pearson correlation. Third, we tested the effects of tree species identity and local neighbourhood diversity for each damage category in a generalized least squares model using the gls function in the nlme package (Pinheiro et al., 2014). The damage percentages of each damage category were used as the response variables; tree species identity, local neighbourhood diversity, and their interaction were used as the explanatory variables. In order to normalize the data, all damage values were logit-transformed (Warton and Hui, 2011). To account for the spatial autocorrelation in the data, we included a spatial correlation structure (i.e., spherical, linear, ratio, gaussian, or exponential) in the model and evaluated the best fit with AIC values and variograms (Zuur et al., 2009).

Last, we tested the effects of the abundance of the different tree species in the local neighbourhood on the damage degree of the target trees for the different damage symptoms. We again used gls with spatial autocorrelation, but we now used the abundances (% of stems) of each tree species in the local neighbourhood of the target tree as explanatory variables. We then used the coefficients of the fitted models to (1) calculate the expected mean damage, with 95% confidence interval, of a target tree surrounded by a monoculture of the target tree species and (2) predict the mean damage of the target tree if 50% of the local neighbourhood would consist of another tree species, i.e., for each tree species, we tested the effect of mixing the species with each of the other tree species planted at the site.

2. Results

The number of dead trees was generally low, but higher in Gedinne than in Zedelgem (Table 1). Similarly, the number of surviving trees with at least one damage symptom or with more damage than the 25% threshold was higher in Gedinne than in Zedelgem. Overall, damage symptoms were more frequent in early autumn 2012 than in early summer 2013, except for branch & shoot damage (Zedelgem) and defoliation (both sites). For instance, F. sylvatica showed lower damage percentages in 2013 than in 2012 (Fig. 2). Note the spatial clustering of damage for F. sylvatica in Fig. 2, a clustering that was also found for the other damage symptoms and species. Based on the AIC values and variograms, an exponential autocorrelation structure provided the best model fit for the data. The most frequently occurring damage symptoms were crown discoloration (Gedinne, both years; Zedelgem, 2012) and defoliation (Zedelgem, 2013). The species showing the highest mean crown discoloration in Gedinne were Q. petraea (mean damage value with standard deviation: 61.4 ± 28.1%) in 2012 and P. menziesii (29.9 ± 18.8%) in 2013. In Zedelgem, the species with the highest mean damage were F. sylvatica (50.2 ± 28.5%) and T. cordata (48.7 ± 26.8%) for crown discoloration in 2012; and T. cordata (30.8 ± 26.4%) for defoliation in 2013.

In Gedinne, we saw significant differences in damage between the two subsites, i.e., Gribelle and Gouverneurs, in 2013. Branch and shoot damage (Kruskal–Wallis: p < 0.001) and crown discoloration (p < 0.001) were larger in Gribelle; defoliation (p < 0.001) was larger in Gouverneurs. For Fagus and Quercus, the two species present in Gedinne and Zedelgem, branch and shoot damage (Kruskal–Wallis: p < 0.001) and crown discoloration (p < 0.001) were higher in Gedinne, while defoliation was higher in Zedelgem (p < 0.001). Damage caused by leaf chewsers (ectophagous species) was found in all the broadleaved tree species, while damage caused by leaf miners and skeletonizers (endophagous species) was only found in Q. petraea and Q. robur.

Branch and shoot damage was positively correlated with crown discoloration (r = 0.14, p < 0.001, N = 10136) and negatively with defoliation (r = −0.08, p < 0.001, N = 10136). Crown discoloration and defoliation showed no correlation (r = 0.01, p = 0.58, N = 10136). In Gedinne, the correlation between branch and shoot damage and understory cover was low (r = 0.10, p < 0.001, N = 4949); there was no significant correlation between understory cover and defoliation (r = 0.01, p = 0.44, N = 4949) or crown discoloration (r = 0.01, p = 0.46, N = 4949). In Zedelgem, the correlations between understory cover and the damage categories were also low: branch and shoot damage (r = 0.03, p < 0.001, N = 5187), crown discoloration (r = 0.04, p = 0.001, N = 5187), and defoliation (r = −0.08, p = 0.02, N = 5187).

The damage degrees of all damage symptoms differed significantly between the target tree species (Table 2). The diversity of the local neighbourhood was significant only for the branch and shoot damage in Gedinne in 2013, i.e., lower damage percentages in more diverse local neighbourhoods, and for the defoliation in Zedelgem in 2012, i.e., more defoliation in more diverse
The linear models used to test the effects of tree species identity (Identity), local neighbourhood diversity (Diversity), and their interaction on the percentage damage for the three damage symptoms, in the two study sites and the two years.

Target trees growing in monocultures showed lower branch and shoot damage in early summer 2013 than in early autumn 2012, except for *P. menziesii* in Gedinne (Fig. 3) and *B. pendula* in Zedelgem (Fig. 4). The defoliation was also lower in 2013 in Gedinne, except for *A. pseudoplatanus* (Fig. 3). In Zedelgem, the defoliation was always higher in 2013 than in 2012, except for *B. pendula* (Fig. 4). The crown discolouration was also lower in the early summer (2013) compared with the early autumn (2012) survey, except for *P. menziesii* in Gedinne (Fig. 3) and *Q. robur* in Zedelgem (Fig. 4).

The estimated changes in mean damage percentage with the addition of a second tree species in the local neighbourhood were different for every target tree species. We did not see any consistent pattern of increase or decrease in damage with the addition of a second species to the local neighbourhood, not even when mixing a broadleaved with a coniferous tree species. However, we saw indications of reduction in damage for some of the target tree species when certain tree species were added to the local neighbourhood, i.e., for (1) *P. menziesii* if *Q. petraea* was added; (2) *B. pendula* if *P. sylvestris* was added; (3) *Q. robur* if *B. pendula* was added (Figs. 3 and 4).

### 3. Discussion

In our study, the tree species identity of the target trees was more important than the tree species diversity of the local neighbourhood in influencing a tree’s damage degree. Different tree species showed different damage patterns, i.e., differences in damage frequency, mean damage percentage, and the damage symptom. For example, in Gedinne in 2012, crown discolouration was frequent in *Q. petraea* (438 trees) and *L. eurolepis* (459 trees), but the mean damage percentage was higher in *Q. petraea* (64.3 ± 25.2%) than in *L. eurolepis* (33.9 ± 20.0%). Similar identity effects have also been found in experiments in temperate grasslands (Scherber et al., 2006), boreal forests (Koricheva et al., 2006), and young temperate forest (Hantsch et al., 2013; Sobek et al., 2009). The negative correlation between branch and shoot damage, i.e., the percentage of the crown that was dead, and defo-

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**Table 1**
The number of trees (percentage between brackets) out of the 2816 and 2688 trees assessed in Gedinne and Zedelgem that show a certain damage symptom.

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<tr>
<td>Shoot &amp; branch damage</td>
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<td>&lt;.0001</td>
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**Table 2**
The linear models used to test the effects of tree species identity (Identity), local neighbourhood diversity (Diversity), and their interaction on the percentage damage for the three damage symptoms, in the two study sites and the two years. *P* values smaller than 0.05 are indicated in bold.

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Fig. 3. The expected mean damage (in percentage) for a tree growing in a local neighbourhood consisting of its own species (monoculture) or in a local neighbourhood in which trees of a second species represent 50% of the neighbours (+50%) for the Gedinne site. The expected mean damage percentages were estimated with gls models relating the damage degree of the sampled trees to the abundances of the different tree species in their local neighbourhood (see Section 2.3). The order of the tree species in the graphs is linked to their phylogenetic relatedness (see Appendix A). The mean damage percentages of the monocultures are given with the 95% confidence interval and are also represented by the dashed lines. Filled dots indicate species of which the abundance in the local neighbourhood significantly affects the damage of the target tree and empty dots indicate that the presence of the second tree species does not significantly affect the target tree’s damage level, compared to the damage level in the monoculture. Note that the X axes are scaled differently for the different species and damage symptoms.
Fig. 4. The expected mean damage (in percentage) for a tree growing in a local neighbourhood consisting of its own species (monoculture) or in a local neighbourhood in which trees of a second species represent 50% of the neighbours (+50%) for the Zedelgem site. The expected mean damage percentages were estimated with gls models relating the damage degree of the sampled trees to the abundances of the different tree species in their local neighbourhood (see Section 2.3). The order of the tree species in the graphs is linked to their phylogenetic relatedness (see Appendix A). The mean damage percentages of the monocultures are given with the 95% confidence interval and are also represented by the dashed lines. Filled dots indicate species of which the abundance in the local neighbourhood significantly affects the damage of the target tree and empty dots indicate that the presence of the second tree species does not affect the target tree’s damage level significantly, compared to the damage level in the monoculture. Note that the X axes are scaled differently for the different species and damage symptoms.
lation, i.e., the percentage of the living crown that was damaged, in our study reflects that an increased damage on branches and shoots reduces the amount of viable crown that can be affected by defoliators. Most defoliators, e.g., skeletonizers and leaf chewers, find their host trees based on chemical and visual cues. Trees with less foliage will be less preferential for these defoliators since there is less food available (Matthews and Matthews, 2010).

Although it is widely acknowledged that the identity and abundance of species in the local neighbourhood play a role in the regulation of pests on target trees (associational resistance), only branch and shoot damage (Gedinne, 2013) and defoliation (Zedelgem, 2012) were related to neighbourhood diversity in our study. In young plantations, such as the ones in our study, the understory vegetation may also influence the damage degree of the trees (Giffard et al., 2012). The herbaceous vegetation at the study sites was managed by annual mowing i.e., during the first three years in Zedelgem (2010–2012) and every year in Gedinne (2010–2014). In the years of our study, some of the young trees were as tall (see Appendix B) as the understory vegetation. In Gedinne, some ferns grew taller than 1.5 m. In such conditions, the effects of small neighbour trees might be negligible compared to the effect of the understory vegetation surrounding the target tree. This surrounding understory vegetation might hinder tree growth, but may also lower the probability of detection of the trees by invertebrate herbivores or even provide suitable habitat for natural enemies of the herbivores (Veres et al., 2013). Yet, in our study, we did not find any clear correlation between the observed damage degrees and the cover of the understory vegetation or the mean height of the tree species. In young plantations, the height of the understory vegetation might be as important as its cover. Unfortunately, however, we did not have data on the height of the understory vegetation in the years of sampling, nor on the height of the sampled trees in the second year of sampling.

Anyhow, even in our young plantation, we saw some indications that the presence of a second tree species in the local neighbourhood of a tree can affect its damage degree. For instance, the damage degree of Q. robur was higher in monocultures than in a two-species mixture with B. pendula. On average, B. pendula was taller than Q. robur (see Appendix B) and may thus shield Q. robur from its herbivores. We expect the mixture effects to become larger as the stand ages (Montagnini et al., 1995; Paul et al., 2011; Potvin and Dutilleul, 2009; Vehviläinen et al., 2007) or if more species are added to the mixture.

The magnitude of a local neighbourhood effect on damage caused by pests and diseases is regulated by factors such as the abundance of neighbour trees, the distance between neighbour and target trees, the season, the age or size difference between the target tree and the neighbour trees, and the phylogenetic relatedness between neighbour and target trees (Barbosa et al., 2009; Castagneyrol et al., 2014; Jacquet and Brockerhoff, 2007; Ness et al., 2011; Srivastava and Vellend, 2005; Vehviläinen et al., 2007). Differences in the sampling season and the phylogenetic relatedness between neighbour and target trees may be relevant in explaining the results of our study.

(1) In general, the damage was less in 2013 than in 2012, most probably due to the difference in timing of the assessment. In 2012, the assessment was done in early autumn, and tree species that generally do not have a second bud burst thus showed the damage that had accumulated during the entire growing season. In 2013, the assessment was done in early summer.

(2) Mixing conifers and broadleaved tree species, which are phylogenetically distinct, is considered a rule of thumb for reducing damage caused by pests and diseases (Castagneyrol et al., 2014). The more phylogenetically distant the tree species, the less likely they will share pests or diseases due to differences in traits that affect susceptibility to pests or diseases, e.g., leaf toughness, absence of certain secondary metabolites, or presence of trichomes. Mixtures of P. sylvestris and B. pendula, for instance, can promote associational resistance against European pine sawfly (Kaitaniemi et al., 2007). In our study, we only saw weak indications for a lower damage in mixtures compared to monocultures, e.g., for P. sylvestris with F. sylvatica. The tree species in FORBIO were selected to represent a broad range of trait values (Verheyen et al., 2013) and are phylogenetically distant (Appendix A), which may explain the strong tree species identity effect in our results.

Next to differences in season and phylogeny, the difference in former land use, and thus the nutrient concentrations in the soil between the sites may have also influenced the damage degrees. Trees growing in nutrient-rich soil have higher foliar nitrogen concentrations, which is preferred by invertebrate herbivores (Throop and Lerdau, 2004). For F. sylvatica and Q. petraea/robur, the two species that were present at both sites, we indeed saw more frequent and higher defoliation damage in Zedelgem, formerly used for agriculture, compared with Gedinne, formerly forested. The lower soil nutrient levels and the harsher climatic condition in Gedinne might be linked with the higher frequency and mean percentages of crown discolouration and branch and shoot damage at the site, compared with Zedelgem. Nutrient deficiencies disrupt plant metabolism and functioning, resulting in several symptoms: susceptibility to diseases, chlorosis, and necrosis of a part of the shoots or foliage (Taiz and Zeiger, 2010). At each of the two sites, we did also see clear spatial patterns in the damage levels of the sampled trees (see Fig. 2 for crown discolouration in F. sylvatica). The observed spatial autocorrelations in tree crown damage might have been generated by patterns in nutrient legacies of past land use or understory vegetation. Yet, more data are needed to explore these relationships.

To summarise, our results (1) demonstrate that a tree’s crown damage degree depends on its species identity and (2) only partially support the hypothesis that trees in more diverse forests show less crown damage. The effect of local neighbourhood diversity varied both spatially and temporally, and the impact of the presence of a certain tree species in the local neighbourhood on the crown condition of target trees was weak in this early stage of stand development. Yet, when planning stand composition in a forest management plan, it might be wise to gather information on specific pests or diseases infecting the target tree species and then select mixture species based on traits that are not preferred by the pests and diseases. The result of our study suggest that some two-species mixtures may reduce the damage degree of target trees: (1) P. menziesii growing together with Q. petraea, (2) B. pendula with P. sylvestris, or (3) Q. robur with B. pendula. Note, however, that the interrelations in the context of damage reduction might change over time and that other factors related to ecosystem services such as wood production, e.g., light competition between neighbouring trees, might not be maximized in the proposed mixtures.

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Appendix A

The dated phylogenetic tree (topology from DaPhnE; see Durka and Michalski, 2012) of the nine tree species planted at the Gedinne and Zedelgem sites of the FORBIO experiment (cf. Verheyen et al., 2013). The dark grey lines represent broadleaved species; the light grey lines represent coniferous species.

References


