

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



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ABSTRACT

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.

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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; Spiecker, 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

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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 (Castagnyrol 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 (Castagnyrol 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 (Castagnyrol 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).

Tree species diversity experiments (cf. the network TreeDivNet, see www.treedivnet.ugent.be) are a promising approach to study the effects of tree species diversity and composition on the ecosystem functioning, e.g., the regulation of pests and diseases. We focus on the FORBIO experiment in Belgium (see Verheyen et al., 2013), established in 2010. To investigate the relation between tree species diversity and pest and disease regulation, we assessed three different damage symptoms related with the crown condition of ca. 5500 trees, i.e., branch and shoot damage, defoliation, and crown discoloration. We assessed branch and shoot damage since it reflects how much of a tree's shoot system is no longer productive. The three hypotheses tested in this study were: (1) the damage degree shows significant interspecific variation and different damage symptoms predominate for different species; (2) the damage degree will be lower for trees growing in a more species-diverse neighbourhood due to associational resistance; (3) the damage degree of a tree is affected by the species identity of the trees in its local neighbourhood. The results of our study may help in selecting optimal mixtures to reduce damage caused by pests and diseases in new plantations.

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 Gouverneurs (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 pseudoplatanus* 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

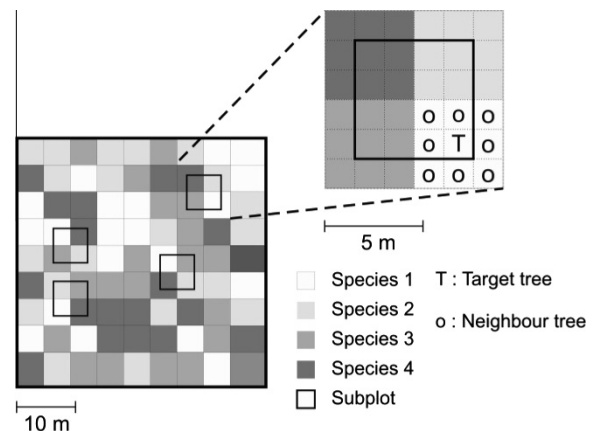


Fig. 1. The four subplots (6 m × 6 m) in a mixed plot (42 m × 42 m) with four tree species. Each shade of grey represents a different tree species. All the trees in the subplots (target trees) were assessed, i.e., 16 trees per subplot, and the species of the 8 surrounding (neighbour) trees for all target trees in each subplot were recorded. The detailed subplot on the right shows the neighbour trees for one of the 16 target trees in the subplot.

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