Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation

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ABSTRACT

It is acknowledged that trees behave remarkably plastic in response to environmental conditions. Even so, knowledge of how tree architecture in pure and mixed stands compare is largely underexplored. Such information is relevant from a fundamental ecological and an applied silvicultural perspective, given the increased attention for mixed species silviculture and the close linkages between tree architecture and high-quality timber production. The main objective of this work was to test the effects of competition, diversity and species identity of neighboring trees on the architecture of five important European tree species (*Quercus robur, Betula pendula, Fagus sylvatica, Pinus sylvestris* and *Tilia cordata)* in a temperate plantation before and during canopy closure.

Data were collected in FORBIO-Zedelgem, a five-year old tree diversity experiment in Belgium. For 396 trees we measured architectural properties including branchiness, tree height-to-diameter (HD) ratio, branch diameter and branch insertion angle, and we investigated how these properties were shaped in different competitive neighborhoods using mixed regression models.

Species showed contrasting architectural responses to neighborhood competition, in line with species life-history strategies. In more competitive environments, trees of *Q. robur* (slow growing and light-demanding) increased HD ratio and branch insertion angle to optimize light foraging in the upper canopy; trees of *B. pendula* (fast growing and light-demanding) increased HD ratio and decreased branching following the branch autonomy principle; trees of *F. sylvatica* (slow growing and shade tolerant) increased branching to improve light uptake under shading and finally, trees of *P. sylvestris* (fast growing and light-demanding) and *T. cordata* (slow growing and shade tolerant) were not shaped in response to competition. Diversity and identity of species in a trees' neighborhood did not contribute to the architectural plasticity, although competitive differences between pure and mixed stands underpinned such effects for *B. pendula,* with lower branching in the highly competitive monocultures.

We conclude that competition between trees, but not diversity, influences the architecture of young plantation trees before and during canopy closure in mixtures. To guide tree architectural development towards high-quality timber, management may have to pay considerable attention to competitive processes already in the juvenile forest stages.

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1. Introduction

The growing interest in mixed species silviculture is motivated by awareness that forest functioning is under threat at low diversity levels (Balvanera et al., 2006; Nadrowski et al., 2010; Carnol et al., 2014). Understanding mixed forest dynamics is crucial in this context, particularly with regard to the complex interspecific inter-

actions that may occur (Forrester, 2014). Tree-tree competition - hereafter referred to as competition- is an interaction between trees in a common growing space, with the purpose of individual trees to maximize capturing of limited resources (i.e. water, light and nutrients) by their growth and development and this at the expense of other trees' resource availability (Craine and Dybzinski, 2013). Competition is thus an ecosystem process that largely shapes environmental conditions and that triggers architectural and physiological plasticity, which is the continuous acclimation of a tree's structure and functioning to the dynamic environment (Longuetaud et al., 2013). Such plasticity expresses the capacity of, and the need for, species to optimize fitness and

furthermore, it is an important aspect in the feedback system between tree functioning, tree structure and the environment (Schröter et al., 2012; Pretzsch, 2014). Among all different types of plasticity, aboveground architectural plasticity is acknowledged as a proper process to study forest dynamics when tree growth and development is mainly driven by competition for light (Thorpe et al., 2010).

Previous studies focused on light-mediated crown plasticity by simple measures of crown size and shape (Schröter et al., 2012; Longuetaud et al., 2013). They concluded that crown development differs across individuals due to genotypic variation, with strong species-specific trends that relates with species strategies to tolerate or avoid shading. Furthermore, some studies showed that crown plasticity tends to stimulate light complementarity and overyielding in mixed forests and is therefore a key component to understand the relationships between biodiversity and ecosystem functioning (Dieler and Pretzsch, 2013; Pretzsch, 2014).

Crown plasticity is the result of complex mechanisms operating at lower levels of organization, i.e., the dynamic development of twigs and branches (Niinemets, 2010; Lang et al., 2012). Architectural plasticity at the level of branches has rarely been elucidated so far, in particularly not for young forest trees. Nevertheless, such study would give detailed information on light acquisition strategies and biomass allocation to optimize tree functioning in contrasting competitive environments (Lintunen and Kaitaniemi, 2010; Lang et al., 2012). So far, only few predictive models for conifer (Mäkinen and Hein, 2006; Hein et al., 2007; Kantola et al., 2007; Duchateau et al., 2015) and broadleaved species (Hein, 2008; Kint et al., 2010) relate branch development to environmental factors (such as nutrient status, water availability and climate) and management (such as species choice and stand density control).

Nevertheless, tree architecture has been a topic of interest for a long time (Heikinheino, 1953; Curry and Endersby, 1965; Persson, 1976), as it determines the growth and the stem quality of trees, two key factors for the provisioning service of forests (Duchateau et al., 2015). Prevailing silvicultural strategies focus on stand density control to guide tree architectural development (Kint et al., 2010). Generally, these strategies aim at the early shedding and occlusion of lower branches, the development of strait stems and desirable height-to-diameter ratio's (HD) to ensure physical stability (Kantola et al., 2007). As most studies were executed in monoculture stands, they did not specifically address the influence of species mixing (but see Bayer et al., 2013; Rozenbergar and Diaci, 2014). Such knowledge is relevant from an economical point of view, given the increasing interest in optimizing financial returns from species diverse plantations through high-quality timber production (Pretzsch and Rais, 2016).

In this study we investigated tree architecture within a framework that is novel in two ways. First, an experimental set-up on mixed forest functioning allows studying architectural plasticity in the context of tree species mixing. Monocultures and mixtures were planted in synthetic communities, at the same time, at constant density and on a homogeneous site to exclude confounding environmental factors. Second, our study addresses the underexplored young forest stage before and during canopy closure. As young trees are expected to be sensitive and respond quickly to competition, it is most interesting to investigate inter-tree interactions in this stage.

We measured the architecture of 396 trees from five temperate species (*Betula pendula* Roth., *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill. and *Pinus sylvestris* L.) in a young experimental plantation. With this data we wanted to test following hypotheses: (i) light-mediated competition triggers architectural plasticity at the tree level (number of branches and stem diameter-to-height ratio) and at the branch level (branch diameter and insertion angle); (ii) plastic responses differ among species and can be explained with species autecology; and (iii) architectural plasticity is influenced by the diversity and identity of neighboring trees, in particular concerning competitive differences between inter- *vs.* intra-specific neighbors and light-demanding *vs.* shade-tolerant neighbors.

2. Material and methods

2.1. Experimental design

Data were collected at FORBIO-Zedelgem (FORest BIOdiversity and Ecosystem Functioning; www.treedivbelgium.ugent.be and Verheyen et al., 2013), a five year old tree diversity experiment in Belgium, western Europe. The experiment (51°9′N 3°7′E) was established in 2010 in a region with a mild Atlantic climate (mean annual precipitation: 850 mm; mean annual temperature: 10.9 °C, altitude 11–16 m above sea level; data from Royal Meteorological Institute of Belgium, 1981–2010). The 9.5 ha site borders the Vloethemveld forest in the north and west and managed pasture land in the south and east. The parent material consist of relatively dry sandy soil with minimum water table depth of 90–120 cm (Podzol) to moderately wet loamy sand soil with minimum water table depth of 40–60 cm (Gleysol). Before plantation establishment, the site was in intensive agricultural use. Soil analyses conducted prior to plantation establishment revealed a pH-KCl of 5.07, a total P concentration of 1132 mg kg^{-1} and a C/N ratio of 13.41.

The site was planted with five well-adapted tree species from local provenances, seeded in commercial nurseries and planted as two or three year old saplings (Verheyen et al., 2013). The species pool consists of one conifer, *P. sylvestris,* and four broadleaved species, *B. pendula*, *F. sylvatica*, *Q. robur* and *T. cordata.* They are common species in west European forests and functionally, they are strongly dissimilar to each other concerning morphological and physiological traits (Appendix A). Most relevant differences for the competition in this study are shade tolerance (ST) according to the index of Niinemets and Valladares (2006) and average height growth rates (HGR) according to data from the FORBIO experiment (2010−2012): *P. sylvestris* (ST = 1.67, HGR = 57 cm year^{-1}), *B. pendula* (ST = 1.54, HGR = 85 cm year^{-1}), *F. sylvatica* (ST = 4.56, HGR = 34 cm year^{-1}), *Q. robur* (ST = 2.45, HGR = 28 cm year^{-1}) and *T. cordata* (ST = 4.18, HGR = 38 cm/year).

The design of this experiment is comparable with other synthetic community studies of the global TreeDivNet network (www.treedivnet.ugent.be and Verheyen et al., 2015), where gradients of tree species richness have been established under relatively homogeneous site conditions. More specific for FORBIO-Zedelgem, 20 different species compositions, including monocultures and mixtures of two, three and four species were planted in plots and replicated in two blocs. Frequencies of occurrence are similar across the species, both within and across species richness levels. With two additional monocultures of oak, the site contains 42 plots of 42 m × 42 m. In these plots, 32 810 saplings were planted in a regular grid (1.5 m × 1.5 m) with monospecific patches of 3 × 3 individuals (Fig. 1). Four permanent monitoring zones (PMZ) in the central area of each plot were marked to monitor ecosystem functioning over the long run. The PMZs consist of 16 trees each and reflect the species composition of the associated plot (Fig. 1).

The site was fenced to prevent browsing damage by hare, rabbit and wild boar. Sapling mortality occurred at rates of 12%, 4% and 2% in the first three years after planting respectively and replanting was done during wintertime using saplings of two years old (Van de Peer et al., 2016). Furthermore, sapling mortality was on average not related with species diversity and also not affected by environmental heterogeneity. Data on tree architecture revealed an