Forest Ecology and Management 382 (2016) 21–30

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Interactive effects of competition and water availability on above- and below-ground growth and functional traits of European beech at juvenile level

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ARTICLE INFO

*Article history:*
Received 18 July 2016
Received in revised form 21 September 2016
Accepted 22 September 2016

*Keywords:*
Mixed forest
*Fagus sylvatica*
Drought
Plant-plant interactions
Root development

ABSTRACT

European beech (*Fagus sylvatica*) is one of the most important commercial tree species in Europe. This species is known to suffer from strong intraspecific competition for above- and below-ground resources and recent studies suggest that mixing beech with other species enhances its growth. European Beech is also known to be very sensitive to drought and natural regeneration of this species is therefore threatened under expected climate change scenarios. Whether beech regeneration under future climate conditions could be favoured in mixed forests is still unknown. In the present study, we analysed how species interactions affect the response of beech seedlings to drought. We tested the followings hypotheses: (i) competitor presence and identity impact seedling performance, and (ii) water availability influences the strength and nature of the interactions. In a greenhouse pot experiment, beech seedlings were grown either alone or in the presence of one competitor seedling (beech, sessile oak, Scots pine). A drought treatment was applied to half of the pots and the other half was well-watered. After one growing season, the seedlings were harvested and above- and below-ground growth and functional traits were measured. Under well-watered conditions, functional traits and growth allocation favouring roots indicate that competition occurred mainly for soil resources. Specific fine root length as clearly altered by the presence of pine only, probably through allelopathy or soil acidification. Drought, however, had a strong impact on beech seedling performance whatever the treatment. Drought decreased the importance of negative interactions between seedlings and a positive interaction even occurred between beech and oak. Our results suggest that under the drier climatic conditions expected in the future, naturally regenerating European beech in mixtures with oak may be advantageous for beech seedling survival and growth. In contrast, favouring regeneration or developing plantations which include beech and pine seems less advantageous.



## 1. Introduction

The relationship between species diversity and plant community functions has been a hot topic in ecology for decades (Tilman et al., 2001; Hooper et al., 2005). Favouring highly diverse ecosystems has been deemed an interesting management strategy which could help to maintain high levels of ecosystem services in the context of climate change (Balvanera et al., 2006; Hector and Bagchi, 2007). However, existing studies on the relationships between species diversity and forest ecosystem functions have provided contrasting results. While some mixed forests were found to be more productive than monospecific ones (Zhang et al., 2012; Brassard et al., 2013), other studies found no, or even negative effects of species diversity (Chen and Klinka, 2003; Vila et al., 2003; Meinen et al., 2009). Similarly, the influence of species diversity on forest ecosystem resistance to drought was found to be positive (Pretzsch et al., 2013; Grossiord et al., 2014b; Gazol and Camarero, 2016), neutral (Grossiord et al., 2014b; Merlin et al., 2015) or negative (Grossiord et al., 2014a; Jucker et al., 2014). These discrepancies indicate that various parameters (e.g. species characteristics, local habitat) influence biodiversity/forest-ecosystem-function relationships: further research is therefore needed to disentangle these influences and to better understand the above- and below-ground processes leading to observed effects.

Plants are competing for space and resources such as light, nutrients and water. Competition between conspecific individuals or individuals from functionally redundant species is assumed to

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http://dx.doi.org/10.1016/j.foreco.2016.09.038
0378-1127/

be strong because of ecological niche overlap (Diaz and Cabido, 2001; Hooper et al., 2005). Such competition generally has a negative impact on plant performance, inducing lower growth and/or higher mortality in plant communities. In species-diverse communities, where individuals are interacting mainly with functionally non-redundant neighbours, competition is thought to be weaker than in pure or functionally redundant communities (Loreau and Hector, 2001). Niche differentiation among species and the emergence of facilitative processes (usually grouped together under the term "complementarity effect") should indeed positively impact community performance.

The role of environmental conditions in the relationship between species interactions and ecosystem functioning is still unclear and this hinders our ability to simulate the response of these ecosystems to environmental change. Drought episodes, whose frequency and severity are predicted to increase in the future in temperate areas (IPCC, 2013), severely affect plant survival and growth. How soil moisture impacts interactions among tree species is a crucial issue in mixed forests.

European beech (*Fagus sylvatica* L.) is the main broadleaved tree species in European forests; it is considered as a keystone species as it plays an important commercial and ecological role (Packham et al., 2012). In pure stands European beech is known to suffer from strong intraspecific competition and to be sensitive to pest and climate change hazards (Packham et al., 2012; Bosela et al., 2015). This species is very sensitive to drought and water limitation was proved to constrain its recruitment (Kunstler et al., 2007; Silva et al., 2012), thus being the most important limiting factor determining its geographical range (Packham et al., 2012). As higher growth rate and greater drought resistance of adult beech trees were found in mixtures (Condés and del Río, 2015; Pretzsch et al., 2013), it has been suggested that a strategy to promote beech regeneration in European forests could be to favour tree species diversity in order to alleviate intraspecific competition intensity. However we currently lack information about the combined effects of competition and water availability on beech performances at the juvenile stage.

In this study, we analysed how species interactions affect the response of beech juveniles to drought. Beech seedlings were grown in a semi-controlled experiment and submitted to competition from different neighbouring species under two differing soil water regimes. The competitor were either a conspecific, a sessile oak, or a scots pine as these three species present contrasting growth dynamics and functional characteristics. They are the most abundant species in European temperate forests and they can be found growing together in mixtures (Koeble and Seufert, 2001; Morneau et al., 2008). We characterized not only growth and leaf traits, but below-ground traits as well since root competition for resources has been found to be stronger than shoot competition (Wilson, 1988; Kiaer et al., 2013). We tested the following hypotheses: (1) both competitor presence and identity impact growth and functional traits of beech seedlings, and (2) the water regime alters the nature and the strength of the interactions between the competitors.

## 2. Materials and methods

### 2.1. Growth conditions

The experiment was established in mid-April 2015 in a greenhouse at INRA-Nancy (Champenoux, France; 48°45′10.40″N, 6°20′24.67″E) and ended mid-September of the same year. The average length of daylight during the experiment was 14.3 ± 1.1 h. The fraction of light intercepted by the greenhouse structure was 40%. Maximum daily photosynthetic active radiation varied between 400 and 950 μmol $m^{-2}$ $s^{-1}$ (cloudy versus sunny days). Temperature was maintained in the range of 19–26 °C thanks to air conditioning. Air humidity varied between 55 and 85% (day/night) and was not controlled.

Planting pots were grey PVC cylinders of 0.02 $m^3$ volume (height 80 cm, diameter 16 cm). They were covered with insulating reflective foil to prevent the soil from over-heating. The bottoms of the pots were pierced with several holes and contained 3 cm of gravel to prevent waterlogging. Pots were filled with a special substrate (70% fine sand, 30% flax compost mixed with 40 kg per $m^{-3}$ of clay, Terreau Flore Bleue, France). A preliminary experiment showed that this substrate provides optimum conditions for root growth and permits easy cleaning and minimized root loss at harvest. The substrate surface was covered with a thin layer of white gravel to limit evaporation and soil heating. The pots were fertilized in May and July (100 ml of TOP-Fert 2, NPK: 10/10/10 + minerals and trace elements, Plantin, France). Pests were prevented by biological control (*Hypoaspis*, *Swirskii*, *Chrysopa*, *Californicus* and *Kraussei* systems; Biobest, Belgium).

### 2.2. Experimental design

We analysed the effect of four different competition treatments in interaction with two water regimes on target beech seedlings. The beech seedlings were grown either alone (no competition, "B", 16 replicates), with one conspecific competitor (intraspecific competition, "BB", 30 replicates) or with one allospecific competitor (interspecific competition): either sessile oak (*Quercus Petraea* (Matt.) Liebl, "BO", 30 replicates) or Scots pine (*Pinus sylvestris* L., "BP", 30 replicates) (Fig. A.1). Beech and oak are both broadleaf deciduous species with a heart-like root system though beech is a late-successional and oak a mid-successional species. Scots pine is a pioneer evergreen conifer with a plate-like root system (Köstler et al., 1968; Bugmann, 1996; Curt and Prevosto, 2003). Mature trees of these three species have different rooting depths in natural conditions (Zapater et al., 2013; Merlin et al., 2015). Ecologically, beech is shade tolerant and drought sensitive while sessile oak and Scots pine are light demanding and drought resistant (Bugmann, 1996; Packham et al., 2012; Merlin et al., 2015). Potential shading from neighbours on the target beech seedlings was avoided by appropriate pot spacing and orientation.

Water treatments were applied five weeks after plantlets/acorns had been planted, once the seedlings were well-installed. Half of the pots in each of the four competition treatments were kept well-watered while the other half was subjected to drought. Soil water content was gravimetrically controlled and maintained within the range of 17–25% (corresponding to 55–80% of relative extractable water, REW) in the well-watered treatment, and within the range of 6–8% (corresponding to 20–25% REW) in the drought treatment (Fig. 1). Vertical profiles of soil water content were determined at harvest with a time-domain reflectometer (Pico 32, Trime, UK). In the well-watered pots, REW was around 70% from the top to −50 cm and up to 100% at the bottom of the pots. In droughted pots, REW was below 24% over the whole depth, with a minimum of 10% at 40–50 cm.

### 2.3. Plant material

One-year-old beech seedlings (28–45 cm in height) and two-year-old Scots pine seedlings (24–41 cm in height) in root-plug format were purchased from a commercial nursery (Robin Pépinières, Saint-Laurent-du-Cros, France). For sessile oak, acorns with a North-Eastern provenance (National Forests Office, Sècherie de la Joux, France) were germinated in pots in early April, since we expected oak to grow faster in greenhouse conditions.