Forest Ecology and Management 390 (2017) 36–46

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Coexistence, association and competitive ability of *Quercus petraea* and *Quercus robur* seedlings in naturally regenerated mixed stands

Catherine Collet *, Ruben Manso, Ignacio Barbeito

LERFoB, AgroParisTech, INRA, F-54000 Nancy, France

ARTICLE INFO

Article history:
Received 16 June 2016
Received in revised form 28 November 2016
Accepted 20 January 2017

Keywords:
Natural regeneration
Species coexistence
Spatial pattern
Pair correlation function
Competition
Growth model

ABSTRACT

In most mixed-species forestry systems, regeneration is a critical step for individual tree survival and species coexistence. Species coexistence is driven by the fine-scale spatial patterns and competitive abilities of species. In naturally regenerated mixed oak (*Quercus petraea* and *Quercus robur*: QP and QR, respectively) stands, species coexistence was assessed by analysing the spatial distribution of both species and their growth responses to intra- and interspecific competition.

Four sites located in North Eastern France with an established (1.4–2.8-m-high) mixed QP and QR regeneration were selected for the study. In a first step, individual seedling location was recorded along line transects to analyse the spatial distribution of the two species. Univariate pair correlation functions were used to test for spatial aggregation for each species and bivariate pair correlation functions were used to test for spatial associations between the two species. In a second step, seedlings were measured in small plots to analyse their response to local competition. Mixed linear models were used to estimate the combined effects of density, mixture, seedling size and seedling status on seedling growth.

QP and QR were both highly aggregated in monospecific patches, and the two species were strongly segregated at a decametric scale. Transition zones between monospecific patches were reduced to a few meters. For both species, mixture had no effect on seedling growth. In all sites, the two species showed very similar diameter and height growth rates in response to density, mixture, seedling size and seedling status, and similar intra- and interspecific competitive abilities.

Highly patchy patterns of QP and QR regeneration strongly reduce interactions between the two species and, in transition zones between monospecific patches where the two species are mixed, no species is expected to outcompete its companion species. For each species, long-term persistence at the stand scale is determined by intraspecific competition rather than by interspecific competition. At this developmental stage, the QP-QR mixture appears to be very stable and no specific silvicultural treatment is required to maintain the mixture.

1. Introduction

In mixed-species forests, regeneration is a critical step since it can act as a bottleneck for the successful establishment of each tree species (Peet and Christensen, 1987; Nakashizuka, 2001). Seed production, dispersal and germination, seedling establishment, growth and recruitment are successive steps of the regeneration process that may act as a filter against the different tree species potentially available on the site (Clark et al., 1999). The regeneration process may lead to species loss: species present in the adult stand may disappear during the regeneration stage and may eventually not contribute to the future stand (Rother et al., 2013).

Species loss during the regeneration stage is mainly driven by biotic interactions and, more particularly, by resource competition with other tree seedlings, adult trees or neighbouring vegetation (Messaoud and Houle, 2006; Olson and Wagner, 2011). Resource competition among tree seedlings is considered as a major determinant of seedling survival and growth and, consequently, of species coexistence during the regeneration stage (Nelson and Wagner, 2014). Two alternative mechanisms related to competition among seedlings may lead to tree species coexistence at the stand scale during the regeneration stage:

1. Seedlings from different species may be spatially segregated and not interfere (Raventos et al., 2010). In such conditions, competition occurs only among conspecific seedlings and does not lead to any species loss. During the regeneration stage, spatial segregation between tree species frequently occurs at the

* Corresponding author.
E-mail address: catherine.collet@inra.fr (C. Collet).

http://dx.doi.org/10.1016/j.foreco.2017.01.021
0378-1127/© 2017 Published by Elsevier B.V.

stand scale (Wang et al., 2010). It may result from small-scale spatial heterogeneity in environmental factors (such as light availability), seed dispersal ability, or from interactions with other plant species (Grubb, 1977; Traissac and Pascal, 2014). Additionally, silvicultural operations to control the development of the regeneration may also lead to species spatial segregation in managed forests. Because of the small size of tree seedlings, segregation at very small scales (below 1 m) may be effective to prevent competition among tree species at the seedling stage. If the species are segregated at such small scales, they will eventually compete at later stages when the trees become larger and their zones of influence increase.

2. Seedlings from different species may be mixed and strongly compete for below-ground or above-ground resources, but they may coexist as long as intraspecific competition is more intense than or equal to interspecific competition (Chesson, 2000; Wilson, 2011). Coexistence will be unstable if intra- and interspecific competition are equal for both species (Wilson, 2011) and will be stable if intraspecific competition is higher than interspecific competition (Collet et al., 2014). During the regeneration stage, large differences in competitive abilities among species, mainly determined by differences in seedling height and in height growth rates, have been observed (D'Amato and Puettmann, 2004; van Couwenberghe et al., 2013). If large differences in seedling height growth occur among tree species in mixed regeneration patches, they may lead to rapid differentiation in stature among species and eventually to the exclusion of slow-growing species (Vickers et al., 2014).

Assessing potential species coexistence during the regeneration stage makes it necessary to quantify species spatial segregation within the stand. In regeneration patches where species are mixed and actually interfere with each other, it is also necessary to estimate the competitive abilities of the two species. In this study, we assessed species coexistence in naturally regenerated mixed *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. (QP and QR) stands.

QP and QR are two major broadleaved species of Western and Central Europe, with high economic and ecological value (Thomas et al., 2002; Annighöfer et al., 2015). Their ecological niches largely overlap and they often grow in mixture at the stand scale (Chybicki and Burczyk, 2010), although differences in their ecological requirements exist. QR has higher resource requirements (light, water, nutrients) and is more sensitive to drought and more tolerant to waterlogging than QP (Epron et al., 1992; Friedrichs et al., 2009). Present management recommendations are to favour QP and QR mixtures over pure stands in order to increase the adaptive potential of the stands to future climatic conditions (Thomas et al., 2002).

Oak regeneration has been intensively studied in Europe, from its reproduction characteristics to ecological requirements for seedlings. Oak seeds are dispersed at very short distances and most seedlings grow almost beneath the mother tree (Chybicki and Burczyk, 2010). The seed dispersal pattern may lead to spatial segregation between QP and QR seedlings at a scale corresponding to the size of adult tree crowns in mixed oak stands. QP and QR are masting species (Crawley and Long, 1995) and, during mast years, regeneration is prolific and seedlings strongly compete for available resources. In the first years, QP and QR seedlings differ in their height growth rates and in their growth responses to environmental factors such as drought, waterlogging and light availability (Vivin et al., 1993; Wagner, 1996; Parelle et al., 2006; Arend et al., 2011). This may potentially lead to different relative competitive abilities of QP and QR when growing in mixture, which may change along environmental gradients. Guibert and Généré (2000) and Généré and Le Bouler (1996) conducted a series of experiments where QP and QR were grown in pure or in mixed plots, without strong limitations in light, waterlogging or water supply. They showed that QR was favoured by mixture and QR outcompeted QP in all mixtures.

Maintaining existing mixed oak stands to comply with current policies aimed at increasing forest diversity requires good knowledge of the dynamics of oak mixtures at all developmental stages. Most studies that have analysed the dynamics of young QP and QR trees, either naturally regenerated or planted, have focused on pure stands. The few studies that analysed oak mixtures used artificial mixtures established in nursery or plantation experiments, and their results cannot be extrapolated to natural regeneration since natural mixed regenerations differ from mixed plantations in many ways (higher seedling density, irregular spatial distribution of species and individual seedlings, seedling populations supposedly adapted to the local environmental conditions). Very few data are actually presently available to assess the dynamics of mixed oak regeneration and to derive practical recommendations for maintaining species mixtures during the regeneration stage.

Species coexistence in naturally regenerating mixed QP-QR stands was assessed by analysing (i) the spatial patterns of QP and QR seedlings, and (ii) their growth responses to intra- and interspecific competition. The following hypotheses were tested: (1) for each oak species, the seedlings are spatially aggregated at metric to decametric scales; (2) the two species are spatially segregated at the same spatial scales; (3) QR seedlings have higher height growth rates than QP seedlings; and (4) compared to pure conditions, mixture enhances QR seedling growth and reduces QP seedling growth.

2. M&M

2.1. Study sites

Four sites were selected in North Eastern France: Bride, Etevaux, Tart-le-Haut and Vaudémont (hereafter referred to as B, E, T and V; Table 1). Sites were located at the core of QP and QR distribution in Europe (EUFORGEN, 2009b,a). At all sites, stands were former coppice with standards dominated by oak and contained the two oak species. In such stands, regeneration is carried out through successive cuttings: the primary cutting removes sub-canopy trees and all tree species other than oak, and secondary cuttings begin just after a masting event. The number of secondary cuttings and their rhythm depend on the quality of the regeneration. Ideally, the duration of the entire regeneration should not exceed 10 years (Sardin, 2008).

In B, E and T, the remaining overstory had been completely removed before the beginning of the study. In site V, the final cut had not been performed when the study started, and some residual seed trees had been left. Canopy openness, estimated using a densiometer (Baudry et al., 2014), ranged between 30 and 60%, above the threshold that would limit oak seedling growth (van Couwenberghe et al., 2013).

These stands were selected because: (1) the previous stand was dominated by QP and QR; (2) both QP and QR were present in the regeneration; (3) other tree species known to be competitive towards oak were either absent (*Fagus sylvatica* L., *Fraxinus excelsior* L.) or present at low density (*Carpinus betulus* L.); and (4) no tending operation had yet been performed on oak regeneration.

Two-meter-wide parallel silvicultural strips had been previously opened and maintained through regular vegetation crushing (every year or every other year). Tree seedlings occurred only in the 4-m-wide bands between strips (Fig. 1) (Sardin, 2008). A few cleaning operations (mainly removal of *Carpinus betulus* seedlings