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Tree diversity effect on dominant height in temperate forest

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ABSTRACT

For forest ecosystems, studies dealing with diversity-productivity relationships are often based on diameter increment observations. Studying how height growth is affected by species interactions can provide new insights on this issue. We studied the mixture effect on dominant height growth in order to answer two questions. Do species interactions in mixed forest modify the dominant height growth of species? Does the diversity effect on diameter found in previous studies correspond to actual overyielding, or rather to an effect on allocation of growth between diameter and height?

We used the French National Forest Inventory (NFI) data to model the mixture effect on dominant height. We included biophysical factors in the models to compare the dominant height of mixed and monospecific stands, all other parameters being equal. We studied five target species – *Quercus petraea* (Matt.) Liebl., *Fagus sylvatica* L., *Picea abies* (L.) Karst., *Abies alba* Mill., and *Pinus sylvestris* L. – in association with sixteen other species.

Mixture effects on dominant height were weak, though often significant. They were either positive or negative according to species association. We showed that mixture effect on dominant height corresponds to a leveling process between species: the taller one limits its growth while the smaller one's growth increases. Furthermore, most of the time, mixture effects on dominant height are in the same direction as those found on diameter, though with a lower magnitude. Our results confirm that tree diversity results in overyielding rather than in a different allocation of volume between the parts of the tree.

1. Introduction

The diversity-productivity relationship has long been investigated for herbaceous plant species (Hector and Hooper, 2002), but has only more recently been studied for forests. Recent studies have shown the positive effects of tree species diversity on forest productivity (overyielding), even if results have not been systematic (Río and Sterba, 2009; Morin et al., 2011; Paquette and Messier, 2011; Zhang et al., 2012; Condés et al., 2013). However, most of the studies conducted from retrospective measurements give results for basal area increment only (Toïgo et al., 2015). Furthermore, the studies providing results in terms of volume often use allometric equations that do not include a diversity effect. It is therefore important to evaluate whether the diversity effect corresponds to a different allocation of produced matter towards height or diameter, or if the effects on height and on diameter are in the same direction, thus indicating real over- or underyielding.

The height growth of the trees in a stand is driven by competition for resources and is strongly affected by competition for light (Jucker et al., 2014; Morin, 2015). Competition for light is the main mechanism that shapes the structure and the composition of forests even if belowground resources also play an important role (Coomes and Grubb, 2000). Interspecific competition for light in mixed forests can modify tree height growth. For instance, a shade intolerant species has to overtop a more shade tolerant species in order to have enough light to grow and survive (Forrester, 2014). Studying how dominant height growth – which is one of the most important features to characterize forest stands (Assmann, 1970) – is affected by species interactions can give new insights on the mechanisms involved in the diversity-productivity relationship for forest ecosystems.

In forest studies, several ways have been used to explore the diversity-productivity relationship: plantations, field-based, semi-experimental (by selecting triplets of mixed species stands and pure corresponding stands), modelling. The analyses need to account for many factors such as ageing effects or management, and there is a lack of long-term experiments designed to evaluate the diversity-productivity relationship in many species associations, and in many dendrometrical or site conditions. However,

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the National Forest Inventories (NFI) have upgraded their programs with more measurements of biophysical factors, thus providing researchers with an opportunity to include environmental factors in forest studies (Bontemps and Bouriaud, 2014). This has three major interests. First, including these factors in the analyses is crucial to compare mixed and monospecific forests all other things being equal. Second, by identifying the environmental factors altering the diversity-productivity relationship, we can come to a better understanding of how mixed forest function (Forrester et al., 2013; Pretzsch et al., 2013, 2015; Toïgo et al., 2015). Finally, including biophysical factors help to take a step towards the definition of general patterns in the results.

Herein, we hope to answer the two following questions: (1) Do species interactions in mixed forest stands modify dominant height growth? (2) Is the overyielding found on basal area compensated for by a decrease in dominant height or not? We conducted our analyses based on NFI data in order to cover a wide range of species mixtures and environmental conditions and to provide generalized results.

2. Materials and methods

2.1. General principle

The general principle applied in this study is similar to the one previously used to estimate mixture effect on radial growth (Vallet and Perot, 2011; Toïgo et al., 2015). We first developed a dominant height-growth model for a target species in pure stand, including environmental variables. Including these environmental variables is mandatory to make it possible to adapt the model to all the site conditions in mixed stands. This growth model was then applied to the target species in the mixed stands to assess its expected dominant height as if it had grown in pure stands. The differences between this expected dominant height and the observed dominant height is an estimate of the mixture effect. This approach enabled us to compare pure and mixed stands, all other parameters being equal.

2.2. Study location and target species

The plots in this study are located throughout France. The French climate is mainly temperate, with an oceanic influence from the West (Atlantic Ocean) and a continental influence from the East. In the South-East, the climate is Mediterranean. These climatic variations across the country make it possible to study the effects of abiotic factors on forest growth.

We chose to focus on widespread species - in order to ensure sufficient data for robust analyses, and on species with contrasting characteristics - to increase generality in our results. The five species selected were sessile oak (*Quercus petraea* (Matt.) Liebl.), common beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and Scots pine (*Pinus sylvestris* L.). We did not restrict the species associated with these target species in mixed stands.

2.3. NFI plot characterization

We used data from the French National Forest Inventory (NFI, http://inventaire-forestier.ign.fr/) from 2008 to 2012. The French NFI is composed of temporary plots distributed throughout the country on a systematic 1 km-by-1 km grid. The plots are made up of four concentric circles with radii of 6, 9, 15 and 25 m. A general stand description is carried out on the largest disk. Dendrometric measurements are collected on the 6, 9 and 15 m disks for trees with diameters above 7.5 cm, 22.5 cm, and 37.5 cm respectively. Dendrometric measurements include circumference, total height, and radial increment in the last 5 years (taken from a core).

Two trees per plot are cored to the pith for age measurement. They are chosen from the six largest trees on the plot. If a single species accounts for at least 75% of the canopy cover of these six largest trees, both sample trees are randomly chosen within this species. If not, one tree is randomly chosen from each of the two dominant species.

Soil characteristics are described for each plot (a pit is dug at the plot center). A floristic inventory completes the data, enabling bio-indication of soil variables such as pH, carbon-to-nitrogen ratio (Gégout et al., 2005) and Ellenberg values (1992). Finally, we used the plots coordinates to obtain monthly climatic variables (temperature, precipitation) from the Meteo France Aurelhy model, calibrated for the 1961–1990 period (Bénichou and le Breton, 1987). Evapotranspiration, soil water deficit and water balance were derived from these data following Piedallu et al.'s method (2013).

2.4. Plot selection

To implement our method, two datasets were necessary for each target species: one for pure stands to calibrate the models, and one for mixed stands to assess the mixture effect. To obtain the two datasets, we applied the following criteria to the NFI data. The plots were all high forest with only one cover layer (excluding, for example, coppice-with-standards regimes). The plots were all even-aged: additionally to selecting plots with only one cover layer, we also selected plots where ages did not differ by more than 25% from the youngest of the trees cored for age measurement.

Table 1
Summary of datasets for dendrometrical and environmental descriptions. Mean values are given by species for pure and mixed stands (2.5% and 97.5% quantiles in parenthesis).

	Number of plots		Age (Yr)		Height (m)		Mean annual temperature (°C)		Annual precipitation (mm)		Elevation (m)	
	Pure	Mixed	Pure	Mixed	Pure	Mixed	Pure	Mixed	Pure	Mixed	Pure	Mixed
Sessile oak	494	468	94 (19–190)	102 (26–177)	22.2 (7.9–34.8)	23.6 (10.4–33.0)	10.3 (8.9–11.9)	9.8 (8.8–11.2)	796 (615–1197)	886 (624–1328)	227 (62–604)	274 (63–560)
Common beech	439	572	108 (23–200)	99 (24–176)	23.6 (8.6–36.6)	24.9 (10.5–36.1)	9.1 (6.1–11.4)	9.0 (6.6–10.5)	1142 (684–1865)	1074 (691–1877)	627 (58–1484)	452 (85–1193)
Scots pine	516	156	65 (19–144)	72 (24–151)	14.5 (5.5–25.3)	18.6 (6.8–31.9)	8.9 (5.8–11.6)	9.5 (6.7–11.9)	925 (645–1347)	911 (630–1400)	765 (88–1559)	513 (85–1316)
Silver fir	263	173	86 (30–177)	88 (29–173)	24.8 (8.8–36.3)	25.5 (12.2–38.1)	8.2 (6.0–10.8)	7.9 (5.7–9.4)	1203 (794–1900)	1368 (852–2003)	828 (292–1492)	818 (370–1349)
Norway spruce	450	190	51 (18–136)	78 (27–159)	22.2 (7.6–34.4)	26.0 (11.6–38.3)	8.0 (4.9–10.3)	7.8 (4.9–9.7)	1266 (777–1918)	1341 (836–1992)	774 (157–1488)	831 (285–1396)