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Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir

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ABSTRACT

Context: Growth partitioning among trees in forest stands is pivotal to silviculture, making it crucial to understand its control by factors such as stand development, stand density, or thinning. Since growth partitioning primarily depends on the partitioning of environmental resources among individuals, climatic change further calls for extending this framework to explicit climatic factors. Recent debate on adapting management to such changes also requires larger density gradients to be encompassed. *Methods:* We primarily aimed to investigate the effects of stand density and climatic factors on growth partitioning, in even-aged stands of sessile oak and Douglas-fir, two species currently managed under contrasted silvicultural regimes. We used two original permanent plot networks designed to explore effects of large density gradients, from open-grown to self-thinning situations. Growth partitioning was assessed on basal area growth, using both the growth dominance index, and the within-stand size-growth relationship. Their dependence on stand density, age, thinning, and climatic predictors was modeled statistically. A one-at-a-time sensitivity analysis of these models was performed to evaluate the magnitude of the effect of each predictor on growth partitioning. Simulations of the effect of extreme climatic conditions on stand growth, and on dominant, intermediate and close-to-suppressed trees growth were also performed. *Results:* For both species, stand density was found to strongly increase growth partitioning toward the biggest trees. Stand growth in sessile oak was reduced by high summer soil water deficit, with a particularly severe growth reduction for suppressed trees, suggesting asymmetric belowground competition for water in this species. In Douglas-fir, a stand growth reduction was found for high summer temperatures, with an increase in growth dominance that suggested a higher temperature-driven stress for suppressed trees. In addition, age slightly increased/decreased growth dominance in sessile oak/Douglas-fir, respectively. *Conclusions:* Growth dominance and size-growth relationships offered complementary insight into growth partitioning. Stand density appears to be the major driver of growth partitioning. Climatic factors were also shown to significantly affect growth partitioning, with species differences, in addition to stand density and ageing. These results suggest to maintain stands at medium density levels to reduce rotation length and minimize risk of exposure to extreme climatic events.

1. Introduction

Growth partitioning among trees in forest stands is a central concern to silviculture, and conditions forest stand development and forest structure. Growth partitioning may be actively controlled through stand density, thinning intensity and rotation age as dimensions of silviculture (Long et al., 2004). As stand develops and canopy closes, competition among trees becomes more intense, especially for small trees, which results in larger trees accounting for a disproportionately larger fraction of stand growth (Binkley, 2004; Binkley et al., 2006; Bradford et al., 2010). Later in stand development, the resource use efficiency of larger trees decreases, thus reducing the proportion of stand growth they represent (Binkley et al., 2004). Stand management effects on growth partitioning have stimulated much research (Dhôte, 1994; Deleuze et al., 2004), which are now integrated into simulators of forest dynamics (Pretzsch and Biber, 2010; Le Moguédec and Dhôte, 2012). These research are however mainly restricted to traditional (medium to high) density ranges.

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While many studies have focused on the effect of competition control (for example by thinning) on growth partitioning, fewer studies explicitly address the effect of a change in resource availability if trees were released from competition on growth partitioning. These studies are nevertheless crucial as growth partitioning results from resource partitioning among individual trees, including light, water or nutrient resources (Schwinning and Weiner, 1998). As the upper stratum of the forest intercepts most radiations (Pacala et al., 1996), light partitioning is inherently in favor of the tallest trees in the stand. Belowground competition for nutrient results in a more evenly distributed resource repartition (Casper and Jackson, 1997; Schwinning and Weiner, 1998), but little is known on the water partitioning process (Schwinning and Weiner, 1998; Craine and Dybzinski, 2013).

Adapting forest management to climatic change is of growing concern (Allen et al., 2010). It requires assessing the concomitant impact of climatic factors and stand structure on stand dynamics and growth partitioning. Some studies have attempted to explicit the role of site fertility in growth partitioning (Hein and Dhôte, 2006; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010; Coomes et al., 2011). Site fertility however remains implicit as regards to environmental factors (Skovsgaard and Vanclay, 2008) and more analytic approaches are now largely implemented (Bontemps and Bouriaud, 2014). Other investigations have highlighted the specific role of water availability in growth partitioning but show contradictory results (Dhôte, 1994; Wichmann, 2001; Pretzsch and Dieler, 2011; Castagneri et al., 2012; Zang et al., 2012). Therefore, a substantial effort remains to be done for integrative approaches including factors reflecting forest structure (age, density), management (thinning intensity) and the abiotic environment (with a special focus on water availability).

The context of adapting management to climate change has further fostered debate about reducing tree density and stand leaf area in order to reduce stand water consumption (Martin-Benito et al., 2010; Sohn et al., 2013; Gebhardt et al., 2014), with however possible long-term drawbacks due to hydraulic architecture acclimation and higher individual leaf area in low density treatments, likely to increase drought vulnerability (McDowell et al., 2006; D'Amato et al., 2013). In this context, there is renewed need to properly assess the effect of stand density on growth partitioning, on much wider ranges than traditionally considered on permanent plot trials in North-America and Europe (Dhôte and Herve, 2000; Pretzsch, 2005; Zhang and Oliver, 2006). Ideally, the widest view on the issue would require considering open-grown to self-thinning tree communities.

We based our analysis on a network of silvicultural experiments (Bédénaux et al., 2001), that includes different species, sampled over their production area, and encompasses large density gradients from open-grown to self-thinning stands. We restricted the analysis to *Quercus petraea Liebl.* (sessile oak), the second largest broadleaved growing stock in France with 281 Mm^3 (IFN, 2013) and a high commercial interest, and *Pseudotsuga menziezii* (Douglas-fir), constituting the first Douglas-fir resource in Europe (Schmid et al., 2014) and outside its region of origin with 107 Mm^3 of growing stock in France (IFN, 2013). Sessile oak growth is known to have a low response to climatic conditions; yet, its main climatic driver is summer water stress (Lebourgeois et al., 2004; Friedrichs et al., 2009; Merian et al., 2011). Sessile oak growth has further been identified as sensitive to climatic change (Dolezal et al., 2010). Douglas-fir is thought to be more resistant to drought than other vulnerable coniferous species (Lévesque et al., 2013), yet it requires higher levels of precipitation than sessile oak (Angelier, 2007; Waring et al., 2008; Carnwath et al., 2012) and it is also considered as sensitive to climate change (Sergent et al., 2012).

In the present study, we aimed to explore the effects of stand structure and management (age, relative density and thinning intensity) and climate (precipitation, soil water content, vapor pressure deficit and air temperature) factors on growth partitioning, and to integrate these factors in models in order to weight their respective contributions. Growth partitioning was analyzed through both the stand-scale growth dominance index (Binkley et al., 2006), and the tree-scale size-growth relationship between diameter and basal area growth over a tree population (Dhôte, 1994). Growth consequences of drought for trees belonging to differing social statuses were also investigated.

The hypotheses tested were: (i) stand growth is more concentrated in the biggest trees in high-density stands than in low-density stands. (ii) Summer drought is expected to reduce tree growth and the magnitude of the growth reduction depends on tree social status, modifying growth dominance within the stand under drought conditions. In addition, we paid a specific attention at behavioral differences between the two species under study as regards drought effects.

2. Material

2.1. Study area and sampling design

We focused on sessile oak and Douglas-fir in their production area in France. Our data originate from two long-term experimental networks belonging to the "coopérative de données des peuplements forestiers" (Bédénaux et al., 2001), specifically designed to explore the effect of large density gradients, from open grown tree to self thinning stands situations, on forest dynamics of even-aged stands. The network area covers the plains of Northern France for sessile oak and mid elevation mountainous areas for Douglas-fir (Fig. 1). As is common practice for even-aged forestry in France, stands have been naturally regenerated in the oak network (Huffel, 1927; Jarret, 2004) and planted in the Douglas-fir network (Oswald and Pardé, 1984). Each network includes trials,

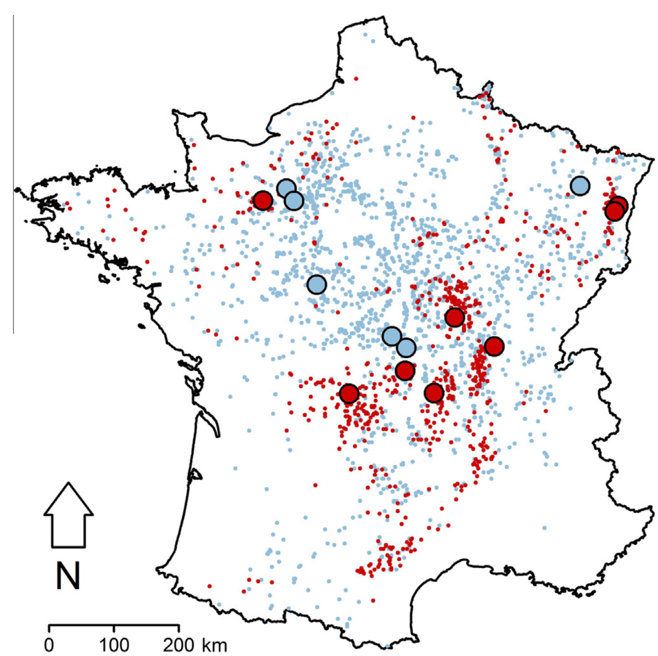

Fig. 1. Geographical location of the experimental sites in Northern France. Large circles indicate sessile oak (light blue) and Douglas-fir (dark red) sites, while small points represent the distribution of pure stands of sessile oak and Douglas-fir according to NFI data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)