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Influence of growth dominance and individual tree growth efficiency on *Pinus taeda* stand growth. A contribution to the debate about why stands productivity declines

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ABSTRACT

A well recognized pattern during even-aged stands development is the growth decline after reaching a peak. We studied the effect of changes in stand structure, characterized by growth dominance, upon stand growth, stand growth efficiency and tree growth efficiency in thinned and unthinned plots of *Pinus taeda*. According to the stated hypothesis (Binkley, 2004), stand growth decline would be related to a decrease in growth efficiency of smaller trees due to the increase of growth dominance. Growth dominance in unthinned plots continuously increased with age, although it was very low compared to other genus, particularly *Eucalyptus*. In thinned plots, growth dominance was even lower and no consistent trend through time was observed. In general large trees were more efficient than small trees in unthinned and thinned plots, however, growth efficiency of both, small and large trees, showed the same pattern with age. Nevertheless, in both treatments, the difference between growth efficiency of smallest and largest trees increased with developing growth dominance because the increasing difference in tree size with age. At stand level lower growth dominance levels did not result in higher stand growth efficiency. Based on the low growth dominance levels, we cannot conclude that increasing growth dominance during stand development can be responsible for its growth decline. Growth dominance appears not to be the cause but the consequence of growth efficiency differentiation between small and large trees of a stand.

1. Introduction

The growth of forest plantations and even-aged forests changes with forest age, reaching a peak relatively soon in stand development followed by a substantial decline. This pattern nearly always occurs and has been the subject of research for decades (e.g. Yoda et al., 1965; Kira and Shidei, 1967; Gower et al., 1996; Ryan et al., 1997; Smith and Long, 2001; Ryan et al., 2004); nevertheless, the causes of this decline still remain unclear. The available evidence (Ryan and Waring, 1992; Ryan et al., 2004; Drake et al., 2011) does not support the classic stem-respiration hypotheses (Yoda et al., 1965; Kira and Shidei, 1967). According to Ryan et al. (2004) and Drake et al. (2011) growth decline is mainly caused by a decline in gross primary productivity (GPP). This general decline in GPP may be related to stomatal closure promoted by tree height (Yoder et al., 1994) or more complex branching patterns, other limits to photosynthesis (Barnard and Ryan, 2003), decline in leaf area index (Ryan et al., 1997), change in stand structure (Binkley, 2004), limits to the plasticity of allocation, or changes in leaf demography to an older average population (Ryan et al., 2004). In this study, we focused on the potential effects of changes in stand structure.

Binkley et al. (2002) suggested that changes in stand structure contribute to the decline in stand growth by increasing differences in resource use efficiency (RUE, defined as wood production per unit of resource use) between dominant and nondominant trees. In agreement with this idea, Binkley (2004) proposed that the decline in stand growth near canopy closure is driven by increasing dominance of site resources by larger trees and to declining efficiency of resource use by smaller ones. Thus, growth decline is related to the establishment of growth dominance and declining resource use efficiency of smaller trees, leading to an overall

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decline in stand level resource use efficiency (Binkley, 2004). According to these ideas, stands gradually go through four phases of growth dominance – from an early phase of null growth dominance through an increasing growth dominance phase and to a phase of "reverse growth dominance" – during their development (Binkley et al., 2002, 2006; Binkley, 2004).

The growth dominance pattern has been supported by several studies in stands of *Eucalyptus saligna* (Binkley et al., 2003; Doi et al., 2010), *Facaltaria moluccana* (Binkley et al., 2003), native forest co-dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea sitchensis* and *Alnus rubra* (Binkley, 2004), *Pinus elliottii* and *Pinus taeda* (Martin and Jokela, 2004) and *Pinus resinosa* (Bradford et al., 2010). However, the magnitude and pattern of growth dominance have been different between species (Binkley et al., 2006; Fernández and Gyenge, 2009; Fernández et al., 2011). In addition, once growth dominance has been established in *Eucalyptus* spp. stands, larger trees were more efficient in the use of light, water and nitrogen than smaller trees, and also had higher growth efficiency (the ratio between stem growth and leaf area; Waring, 1983) (Binkley et al., 2002). These differences did not exist in young stands (open canopy) of *Eucalyptus* spp. (Binkley et al., 2002). Contrarily, differences in water use efficiency (WUE) between different size-trees have been observed in *Pinus ponderosa* stands; nonetheless, growth dominance was null or very low in those stands (Fernández and Gyenge, 2009). Naidu et al. (1998) also found that dominant trees of *P. taeda* have higher growth efficiency than suppressed trees. However, in the study they did not include measurements of growth dominance.

Growth dominance in managed stands may be different from unmanaged stands as described by Binkley (2004) and Binkley et al. (2006). In thinned stands, resource acquisition and utilization are strongly influenced by increased levels of resource availability and higher levels of resource acquisition through an increase in leaf area of residual trees (Long et al., 2004). Because thinning treatments typically remove weaker competitors, the size and resource use inequalities that may appear during stand development as a result of intraspecific competition (Weiner and Thomas, 1986) may be less pronounced in thinned stands. This should result, as observed in *P. resinosa* stands (Bradford et al., 2010), in lower growth dominance in thinned than unthinned stands. At our knowledge, no other study has documented thinning impact on growth dominance patterns of forest plantations.

The aim of this study was to evaluate the relationship between growth dominance and stand growth in *P. taeda* plantations throughout stand development, and the contribution of tree and stand growth efficiency to stand growth and growth dominance. The effect of thinning on these relationships was also analyzed. Although previous studies have found evidence for the growth dominance hypothesis (Binkley, 2004), none have tested the full hypothesis. The effect of thinning on the relationship stand growth – growth dominance – growth efficiency has not been evaluated either. This information may be valuable to understand and to predict forest growth patterns, as well as to develop management strategies leading to delay stand growth decline.

Based on growth dominance hypothesis (Binkley, 2004) and assuming the growth efficiency as a *proxy* of resource use efficiency we stated four predictions:

1. Before maximum stand growth, there is no growth dominance (sensu Binkley, 2004) or it is very low. After maximum stand growth, growth dominance begins to increase and becomes higher as stand develops.
2. Before maximum stand growth, when growth dominance is null or very low, all trees of a stand have the same growth efficiency. Increasing growth dominance leads to a decrease in growth efficiency of smaller trees and therefore, stand growth efficiency. The largest trees maintain similar growth efficiency levels than they had before maximum stand growth.
3. Because thinning from below removes the smallest trees (weaker competitors), it decreases growth dominance level. In consequence, growth efficiency of thinned stands is higher than unthinned stands.
4. The difference in individual growth efficiency between dominant and suppressed trees increases as growth dominance increases.

2. Materials and methods

To test the hypothesis is necessary to evaluate growth dominance and growth efficiency of the stand and of different-size trees along stand development and to compare these variables with stand growth pattern.

2.1. Study site and experimental design

For the purpose of this research we examined 21 years of growth records from a thinning experiment in loblolly pine located at 25° 58′ 41.41″ S and 4° 22′ 44.76″ W (Misiones, Argentina). The experiment is part of a net of thinning experiments for different species of Montecarlo INTA Experimental Station (National Institute for Agricultural Technology of Argentina). The experiment was installed in 1992 in a stand planted in 1987 (5 years old) with an initial density of 1736 trees per hectare (initial spacing 2.4×2.4 m). We analyzed data corresponding to the unthinned plots and to a thinning treatment (thinned from below): thinning every 6 years leaving a post-thinning residual basal area equivalent to the 66% of the basal area in the unthinned plot at the same age. These two situations are expected to represent different growth dominance levels. The experiment had a randomized block design with three replicates of each thinning treatment (864 m^2 each plot without border). In each block two unthinned plots were established.

2.2. Measured and estimated variables

We combined diameter and height measurements with allometric equations to estimate stem and leaf biomass for every tree at each age (Parresol, 1999). Diameter at breast height (*dbh*: outside bark diameter at 1.3 m above ground) of all trees and total height (h) of a subsample of trees were measured at ages 5, 7, 9, 11, 13, 15, 17 and 21 years (close to the rotation age in the study region) on each plot. The subsampling of height was made considering the *dbh* distribution of each plot (Clutter et al., 1983; Prodan et al., 1997). Data from the height subsample was used to fit the Curtis model (Curtis, 1967) in order to estimate tree height of unmeasured trees. Stem and leaf biomass were estimated based on equations developed by Fassola et al. (INTA Montecarlo, unpublished data) with loblolly pines of the same (and other) stands. These equations were developed with dummy variables, that is, considering the influence of different management systems (including thinning). For the control treatment (unthinned) we used the equations corresponding to the unmanaged system and for the thinning treatment we used the equations corresponding to the traditional management system. For both plot and trees, stem biomass growth was estimated as the difference in stem wood biomass between successive measurement periods. Stand-level growth was estimated as gross growth of the initial volume (Beers, 1962; Marquis and Beers, 1969).

Growth and biomass were used to estimate growth dominance (G_D) and growth efficiency (G_E). Growth dominance was calculated following Binkley (2004) and Binkley et al. (2006). Briefly, trees