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Increasing stand structural heterogeneity reduces productivity in Brazilian *Eucalyptus* monoclonal stands

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ABSTRACT

The effect of stand structural heterogeneity on production was examined in the northeastern region of Brazil using a set of spacing × genotype trials of *Eucalyptus* along a large gradient in site productivity. This experimental platform enabled an analysis of relationships between productivity and structural heterogeneity for entire rotations while controlling the confounding effects of species and genetic diversity. Stand heterogeneity was negatively correlated with productivity. A 10-unit increase in heterogeneity, quantified using Gini's coefficient, was associated with a loss of approximately 17 m^3 ha^{-1} to 23 m^3 ha^{-1} for the lowest planting density (667 trees ha^{-1}) and highest planting density (1667 trees ha^{-1}), respectively, by the end of a 7-year rotation. The most productive genotypes were generally the most homogeneous. While stand density increased productivity, it also increased structural heterogeneity. In general, the positive effect on productivity of increasing density was greater than the negative effect of heterogeneity, but we found that the contrary can also occur. The relationship between planting density and heterogeneity differed between genotypes, with some much less plastic than others. The results show that structural heterogeneity *per se*, in the absence of genetic diversity and species diversity, can have a strong negative effect on productivity, and an understanding of the mechanisms causing these contrasting patterns (with versus without genetic diversity) will be important when engineering forest reforestation projects and plantations for wood production, carbon sequestration and many ecosystem functions correlated with productivity.

1. Introduction

The global area of forests has declined by 36% or 16.5 million km^2 over the last 200 years (Meiyappan and Jain, 2012), resulting in large carbon (C) emissions, a lower capacity for C storage (van der Werf et al., 2009), and declines in biodiversity (Butchart et al., 2010). This problem is being partially addressed by increasing reforestation efforts and using plantations (FAO, 2010). For instance, even though the plantations' share of land comprised only 7% of the world's forested land, their share in the supply of roundwood, for example, was 30% in 2005 and is estimated to reach up to 80% by 2030 (Seppäla, 2007; Carle and Holmgren, 2008).

There has also been increasing interest in the establishment and use of mixed-species stands as opposed to monocultures due to their potential to provide higher levels of ecosystem services (Thompson et al., 2014). The potential of mixed-species stands is attributed, in part, to their greater structural heterogeneity compared with monocultures, such as the development of canopy or root stratification (Kelty, 1992; Forrester et al., 2006). Conversely, however, recent studies show that structural heterogeneity, in the absence of species and genetic diversity, can reduce productivity by up to 20% (Binkley et al., 2010; Stape et al., 2010; Ryan et al., 2010; Aspinwall et al., 2011; Luu et al., 2013). The reduction in stand-level productivity with increasing variability in tree sizes in monocultures is thought to result from contrasting responses by suppressed versus dominant trees (Binkley et al., 2010). That is, in more structurally heterogeneous stands, dominant trees are

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likely to have smaller neighbors than they would in less heterogeneous stands and they therefore grow faster because they capture more resources and use them more efficiently (Binkley et al., 2002, 2010, 2013; Campoe et al., 2013; Forrester et al., 2013). However, at the stand level, the faster growth of dominant trees is outweighed by the reduction in growth of the suppressed trees (Binkley et al., 2013; Campoe et al., 2013; Luu et al., 2013).

Clearly, the structural heterogeneity of monocultures, as well as mixtures, is a major factor influencing forest productivity and, therefore, probably also other ecosystem functions and services that are linked to productivity, including water use, carbon sequestration, nutrient cycles and the response and susceptibility of stands to droughts and other variations in climate.

The contrasting effect of structural heterogeneity, depending on the presence of genetic (or species) diversity, highlights the value of experiments using clonal monocultures. These allow species and genetic diversity to be reduced to zero in order to focus on the structural heterogeneity effects. Moreover, the importance of understanding the effect of structural heterogeneity on the productivity of monocultures is highlighted by the increasing contribution that monospecific plantations make to the global wood supply, and the related effects that these plantations have on other ecosystem functions. Some plantations, such as *Eucalyptus* in Brazil, are the most productive ecosystems in the world, capable of achieving current annual increments in excess of 70 m^3 ha^{-1} $year^{-1}$ or 35 Mg ha^{-1} $year^{-1}$ (Almeida et al., 2007; Stape et al., 2010). Due to their high productivity, plantations play an important role as carbon sinks in the face of climate change (Böttcher and Lindner, 2010). They have also reduced logging pressure on native forests in some regions (Gladstone and Thomas Ledig, 1990; Brockerhoff et al., 2008). Therefore, understanding the relationship between structural heterogeneity and productivity has both ecological and economic implications.

The reduction in stand-level productivity with increasing variability in tree sizes in monocultures is thought to result from contrasting responses by suppressed versus dominant trees (Binkley et al., 2010). That is, in more structurally heterogeneous stands, dominant trees are likely to have smaller neighbors than they would in less heterogeneous stands and they therefore grow faster because they capture more resources and use them more efficiently (Binkley et al., 2002, 2010, 2013; Campoe et al., 2013; Forrester et al., 2013). However, at the stand level, this increase in growth of dominant trees is outweighed by the reduction in growth and resource-use efficiency of the smaller trees (Binkley et al., 2013; Campoe et al., 2013; Luu et al., 2013).

Three factors that have a major influence on productivity, and potentially also on structural heterogeneity, are site quality, planting density and genotype. In this study, a regional assessment of the relationships between structural heterogeneity and productivity was done in tropical *Eucalyptus* plantations across northeastern Brazil.

The objective was to test the hypothesis that the heterogeneity reduces plot growth across genotypes, spacing, and site productivity. More specifically, this was divided into four main components: (1) Stand structural heterogeneity increases with age and with increasing planting density (because both increase the expression of dominance within a stand); (2) Increases in stand structural heterogeneity reduce productivity for a given site, planting spacing and age, and this is a general pattern across all the plantations examined; (3) Stand heterogeneity as well as the above mentioned relationships are influenced by genotype; (4) Increasing planting density increases productivity but also increases heterogeneity (which reduces productivity). This trade-off can be managed using genotypes that are less inclined to develop high structural heterogeneity.

2. Material and methods

We used six genotype × spacing experiments of *Eucalyptus* located in the state of Bahia in the northeast of Brazil, which were established with the main purpose of determining the best combination of genotype and spacing for each given region. These experiments were chosen because of the control of genotype and spacing. They were also selected because they maximize the variability in productivity and heterogeneity once they were established across sites with a wide range of site quality such that mean annual volume increment differed by more than 50 m^3 ha^{-1} $year^{-1}$ (20–71 m^3 ha^{-1} $year^{-1}$). A brief summary of the experiments' characterization is presented in Table 1.

Genotype G1 was used to compare site quality because it was the only genotype present in all experiments. Productivity values (MAI) in Table 1 were estimated as $V = \alpha(\beta - e^{(-\gamma Age)}) + \varepsilon$, fitted for each experiment, relating total plot volume (V; m^3 ha^{-1}) of Genotype G1 to age in years.

All experiments were implemented in a factorial (spacings × genotypes) scheme and a randomized block design with four blocks. Five spacings were compared in each experiment, corresponding to planting densities from 667 to 1667 trees ha^{-1}, namely: 4 × 3.75 m, 5 × 2.4 m, 4 × 3 m, 3 × 3 m and 3 × 2 m. The first number is the distance between tree rows and the second is the distance between trees within a row. The number of genotypes tested varied between experiments as shown in Table 1. The plots were composed of 50 trees in E6 and 72 trees in the other experiments, but only the innermost 25 and 36 trees, respectively, were analyzed.

To examine the relationship between production and stand structural heterogeneity, production was quantified as the over bark stem volume per hectare, hereafter named yield (m^3 ha^{-1}). Stand structural heterogeneity of each plot was quantified using the Gini coefficient (non-dimensional) calculated using the over bark stem volume of individual trees. Gini's coefficient was derived from the Lorenz curve in which the cumulative percentage of trees was plotted against the cumulative percentage of tree volume. Gini's coefficient was then calculated as one minus the ratio between the area under the Lorenz curve and the area under the perfect equality line (1:1 line). This coefficient is originally a proportion, ranging from 0 to 1, but we transformed it into percentage, by multiplying it by 100, which considerably reduced issues with non-convergence during the mixed effect fitting process (described below). The greater the value of Gini's coefficient, the more heterogeneous the plot. This index was calculated using the package "*ineq*" in R (Zeileis, 2014).

Table 1
Characterization of six genotype × spacing experiments of *Eucalyptus* in Bahia, northeastern Brazil. The experiments (Exp) were coded E1 to E6. Genotypes G2 and G6 are clones of *E. grandis*, and G1, G3, G4 and G5 are hybrids of *E. grandis* × *E. urophylla*. Age refers to the age of the last measurement (years). Precip, Tmed, Tmax and Tmin are, respectively, mean annual precipitation (mm) and monthly mean, maximum and minimum temperatures (°C) corresponding to the periods of 2005–2013 for E1 and E3; 2008–2013 for E5, E4 and E6; and 2007–2013 for E2. MAI is the mean annual increment (m^3 ha^{-1} $year^{-1}$) estimated at the age of 7 years for Genotype G1, the only genotype present in all experiments.

Exp	Age	Genotypes	MAI	Soil order	Precip	Tmed	Tmax	Tmin
E1	8	G1; G2; G3; G4	71.7	Ultisol	1498	23	28	20
E2	4	G1; G2	52.2	Ultisol	1459	23	28	20
E3	8	G1; G2; G3	50.3	Oxisol	1312	23	24	21
E4	7	G1; G2; G3; G4; G5	42.8	Oxisol	1075	22	27	20
E5	8	G1; G2	41.1	Ultisol	1392	24	28	21
E6	6	G1; G6	20.6	Oxisol	650	24	29	21