ALVARO AUGUSTO VIEIRA SOARES

EFEITO DA HETEROGENEIDADE ESTRUTURAL NA PRODUTIVIDADE E NA DINÂMICA DO CRESCIMENTO DE POVOAMENTOS MONOCLONAIS DE EUCALIPTO

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EFEITO DA HETEROGENEIDADE ESTRUTURAL NA PRODUTIVIDADE E NA DINÂMICA DO CRESCIMENTO DE POVOAMENTOS MONOCLONAIS DE EUCALIPTO

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ciência Florestal, para obtenção do título de *Doctor Scientiae*.

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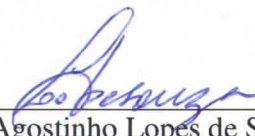
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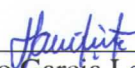
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Maria das Graças Ferreira Reis

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Daniel Brianezi

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Agostinho Lopes de Souza
(Coorientador)

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Helio Garcia Leite
(Orientador)

"Prefiro ter questões que não podem ser respondidas
a respostas que não podem ser questionadas."

Richard Feynam

"A frase mais empolgante de ouvir em ciência,
a que prenuncia novas descobertas, não é "Eureka",
mas sim "Isto é estranho...""

Isaac Asimov

"Se um homem, por mais sábio que seja,
se tem na conta de bastante sábio para poder desprezar os outros,
assemelha-se a um cego que leva uma lâmpada:
ilumina os outros, mas continua cego."

Buda

"Sei o que devo ser e ainda não sou,
mas rendo graças a Deus por estar trabalhando,
embora que lentamente, por dentro de mim próprio,
para chegar, um dia, a ser o que devo ser."

Chico Xavier

À HETEROGENEIDADE do mundo,
como força motriz de aprendizado e tolerância
entre as ciências e os povos...

DEDICO

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BIOGRAFIA

Alvaro Augusto Vieira Soares, filho de Elaís Aparecida Vieira Soares e Paulo César Costa Soares, nasceu no dia 21 de Julho de 1986 na cidade de Carmópolis de Minas, Minas Gerais. Viveu na cidade de Oliveira, Minas Gerais, até completar o ensino médio. Em 2005, mudou-se para Lavras para cursar Engenharia Florestal na Universidade Federal de Lavras-UFLA.

Durante seu curso de graduação, participou de diversos projetos acadêmicos como estagiário voluntário e bolsista de iniciação científica nas áreas de ecologia de florestas tropicais, inventário e manejo florestal, viveiros florestais e melhoramento florestal. Foi integrante do Núcleo de estudos em Silvicultura no qual ocupou os cargos de vice-presidente e presidente.

Nesta mesma instituição, cursou o mestrado em Engenharia Florestal na área de Silvicultura, desenvolvendo trabalhos na área de recuperação de áreas degradadas como recuperação de nascentes, recuperação de áreas mineradas na Amazônia, e recomposição de vegetação nas margens de reservatórios artificiais de hidrelétricas, sendo este o foco de sua dissertação. Concluiu o mestrado em 2012.

Concluído seu mestrado, trabalhou no Laboratório de Estudos e Projetos em Manejo Florestal-LEMAF da UFLA com quantificação de carbono no solo e compartimentos da biomassa de ecossistemas florestais de Minas Gerais e auxiliando em campanhas de campo para medição de experimentos de manejo sustentável de candeia.

Em agosto de 2012 mudou-se para Corvallis, Oregon, Estados Unidos, para cursar o doutorado em *Forest Ecosystems and Society* na *Oregon State Univerity*, sendo este interrompido em 2013.

Em agosto de 2013 começou o doutorado em Ciência Florestal na Universidade Federal de Viçosa-UFV na área de Manejo Florestal. Durante seu doutorado, desenvolveu trabalhos envolvendo modelagem de florestas plantadas de eucalipto, teca e araucária, estudos do crescimento e da produção, uso de redes neurais artificiais na modelagem florestal, entre outros, e auxiliou na ministração das disciplinas de Manejo Florestal e Métodos Estatísticos Aplicado à Ciência Florestal.

Passou o ano de 2015 desenvolvendo sua tese na *Albert-Ludwigs Universität Freiburg* (Uni-Freiburg), Freiburg, Alemanha, pelo programa de doutorado sanduíche da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior- CAPES.
Concluiu seu doutorado em fevereiro de 2017.

SUMÁRIO

RESUMO

SOARES, Alvaro Augusto Vieira Soares, D.Sc., Universidade Federal de Viçosa, fevereiro de 2017. **Efeito da heterogeneidade estrutural na produtividade e na dinâmica do crescimento de povoamentos monoclonais de eucalipto.** Orientador: Helio Garcia Leite. Coorientador: Agostinho Lopes de Souza.

A heterogeneidade estrutural, representada pela desigualdade do tamanho das árvores, é um atributo-chave nos povoamentos florestais. Por exemplo, algumas investigações em povoamentos mistos inequiâneos mostraram que a heterogeneidade estrutural pode ser positivamente correlacionada com a produtividade, enquanto em povoamentos puros equiâneos e especialmente em plantios monoclonais, o contrário tem sido freqüentemente encontrado. O objetivo desta tese, dividida em dois capítulos, foi contribuir para a compreensão de como a desigualdade do tamanho da árvore afeta a produtividade e a dinâmica de crescimento de povoamentos monoclonais de eucalipto. No primeiro capítulo, foram estudados o efeito da heterogeneidade estrutural na produção e o efeito do genótipo e espaçamento sobre a heterogeneidade. Utilizou-se um conjunto de ensaios de espaçamento × genótipo de *Eucalyptus* ao longo de um gradiente de produtividade. Foi verificada associação inversa entre a heterogeneidade estrutural e a produtividade dos povoamentos. A relação entre produtividade e heterogeneidade diferiu entre os genótipos, sendo mais produtivos aqueles que resultaram em povoamentos mais homogêneos. Dentro da faixa de densidades estudadas, o aumento da densidade resultou no aumento da produtividade e da heterogeneidade. Em geral, o efeito positivo do aumento da densidade sobre a produtividade foi maior do que o efeito negativo da heterogeneidade, embora tenha sido mostrado que o contrário pode ocorrer. No segundo capítulo, foram utilizados dados de experimentos de peso de desbaste para avaliar como a heterogeneidade estrutural e a dominância do crescimento se desenvolvem ao longo do tempo e como são afetados por diferentes pesos de desbaste. Os experimentos foram estabelecidos em três localidades com um gradiente de produtividade. Desbastes por baixo foram aplicados nas idades de 58 e 146 meses. Os pesos de desbaste testados foram de 20%, 35% e 50% de remoção da área basal, além de um tratamento adicional com 35% de remoção da área basal e desrama artificial feita aos 27 meses. A heterogeneidade estrutural e a dominância de crescimento foram imediatamente reduzidas pelo desbaste, resultando em povoamentos mais uniformes para maiores pesos de desbaste. A dominância do crescimento foi muito próxima de zero após cada desbaste. A heterogeneidade estrutural e a dominância do crescimento cresceram ao longo do tempo,

antes e após o primeiro desbaste, mas as taxas de aumento após o primeiro desbaste foram geralmente mais baixas do que antes do mesmo. Além disso, as taxas de aumento na heterogeneidade e dominância do crescimento foram inversamente relacionadas com o peso do desbaste. Após o segundo desbaste, a heterogeneidade estrutural tendeu a permanecer constante, enquanto a dominância do crescimento tendeu a diminuir, atingindo valores negativos. Por fim, os resultados e discussões apresentados reforçam que a compreensão dos mecanismos por trás do efeito da heterogeneidade estrutural dos povoamentos florestais contribui para o melhor entendimento dos processos que regem a dinâmica do crescimento florestal. No caso de plantios monoclonais, tanto a heterogeneidade estrutural como o efeito de dominância do crescimento constituem variáveis altamente influentes na dinâmica e partição do crescimento, com reflexo na eficiência e, consequentemente, na produtividade dos povoamentos. Logo, o uso de métricas dessas variáveis pode auxiliar no manejo para a obtenção de povoamentos mais produtivos e que usem os recursos de forma mais eficiente.

ABSTRACT

SOARES, Alvaro Augusto Vieira Soares, D.Sc., Universidade Federal de Viçosa, February, 2017. **Effect of stand structural heterogeneity on the productivity and on growth dynamics of *Eucalyptus* monoclonal stands**. Advisor: Helio Garcia Leite. Co-advisor: Agostinho Lopes de Souza.

Structural heterogeneity, as represented by tree size inequality, is a key attribute in forests stands. For example, some investigations in mixed stands have shown that the structural heterogeneity may be positively correlated with productivity, while in monospecific and especially in monoclonal stands, the opposite has often been found. The aim of this dissertation, divided in two chapters, was to contribute to the comprehension of how tree size inequality affects stand productivity and stand growth dynamics. In the first study, the effect of stand structural heterogeneity on production and the effect of genotype and spacing on heterogeneity were examined using a set of spacing × genotype trials along a large gradient in site productivity. As a result, stand heterogeneity was negatively associated with productivity. Within the range of densities hereby tested, the relationship between yield and heterogeneity differed between genotypes and the most productive genotypes were generally the most homogeneous. While stand density increased productivity, it also increased structural heterogeneity. The positive effect of increasing density on productivity was generally greater than the negative effect of heterogeneity, but it was shown that the contrary can also occur. In the second study, thinning-intensity experiments were used to assess how stand heterogeneity and growth dominance develop through time and across different thinning intensities in *Eucalyptus* stands. The experiments were established along a three-site gradient in productivity. The plots were thinned at ages 58 and 146 months. The thinning intensities tested were 20%, 35% and 50% of basal area removal and an additional treatment of 35% removal plus pruning at 27 months. Stand structural heterogeneity and growth dominance were immediately reduced by thinning from below. The more intense the thinning, the less heterogeneous the resulting stands. Growth dominance was very close to zero following each thinning event. Stand structural heterogeneity and growth dominance both increased before and after the first thinning but the rates of increase after the first thinning were generally lower than they were before the first thinning. Also, the rates of increase in heterogeneity and growth dominance were inversely related to thinning intensity. After the second thinning, structural heterogeneity tended to remain constant whereas growth dominance tended to decrease, reaching negative values. The results of the first study 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. Lastly, the results and discussions here presented reinforce the comprehension of the mechanisms behind the effect of the structural heterogeneity in forest stands contribute to a better understanding of the processes that governs the dynamics of forest growth. In the case of monoclonal stands, structural heterogeneity and growth dominance highly influence growth dynamics and partitioning, which reflects on growth efficiency and, consequently, on productivity. Therefore, taking these variables into account can furnish valuable information for managing forest towards more productive and resource-efficient stands.

1. INTRODUÇÃO GERAL

Ao longo das últimas décadas, avanços no manejo florestal intensivo permitiram um considerável aumento na produtividade de povoamentos de eucalipto no Brasil. Na década de 1970, quando se difundiam os plantios pelo Brasil, principalmente com os incentivos fiscais para reflorestamento, a média de crescimento dos povoamentos era de 15 m³ ha^{-1} ano^{-1}, em idade em torno do oito anos (QUEIROZ; BARRICHELO, 2007).

Atualmente tem-se a média de 36 m³ ha^{-1} ano^{-1} próximo aos seis anos de idade (IBÁ, 2016), podendo chegar a valores bem mais elevados em situações experimentais e específicas de sítio, solo, e manejo. Por exemplo, Stape et al. (2006) obtiveram o incremento médio anual aos seis anos de 62 m³ ha^{-1} ano^{-1} com tratamento suplementar intensivo de adubação e controle de formiga e matocompetição no estado de São Paulo. Estimativas de 48 m³ ha^{-1} ano^{-1} a 80 m³ ha^{-1} ano^{-1} foram obtidas em plantios comerciais no sul da Bahia (OLIVEIRA, 2007) e de 57 m³ ha^{-1} ano^{-1} a 103 m³ ha^{-1} ano^{-1} em experimentos de fertirrigação em Minas Gerais (LOURENÇO, 2009).

Este considerável salto de produtividade é fruto de esforços em pesquisa que embasaram importantes aprimoramentos silviculturais como a geração de clones mais produtivos e adaptados a determinadas características ambientais, produção de mudas de alta qualidade e a melhoria do sítio (STAPE et al., 2001; GONÇALVES et al., 2008; GONÇALVES et al., 2013). Neste último, destacam-se os aprimoramentos na fertilização, preparo do solo, otimização da densidade de plantas, combate a formigas, cupins e outras pragas, controle da matocompetição, entre outros. (STAPE et al., 2001, WILCKEN; RAETANO; FORTI, 2002; DU TOIT et al., 2010; SOUZA; ZANETTI; CALEGARIO, 2011, GONÇALVES et al., 2013).

Estas operações visam principalmente aumentar a disponibilidade de recursos como água, nutrientes e luz e diminuir fatores que podem restringir a disponibilidade e, ou, o uso dos mesmos. Ultimamente, investimentos em silvicultura de precisão, na qual o planejamento e a prescrição de tais tratamentos silviculturais são feitos específicos para escalas menores de área, auxiliados pelo uso de sistemas de informação geográfica, tem colaborado para a qualidade e adequabilidade dos tratamentos silviculturais e, consequentemente, para o aumento da produtividade dos povoamentos (XAVIER; SILVA, 2010, MACHADO, 2014; VALE et al., 2014; MAEDA et al., 2014).

Concomitante ao aumento da produtividade, os povoamentos, antes heterogêneos, com grandes diferenças na altura e diâmetro das árvores e mortalidade elevada, tornaram-se mais uniformes e com altas taxas de sobrevivência. Do ponto de vista operacional, a

uniformidade no tamanho das plantas já há tempo vem sendo apontada como uma caraterística vantajosa, que aumenta a eficiência da colheita e processamento da madeira (DAVIS, 1969 *apud* CARLISLE; TEICH, 1971), além de diminuir a taxa de mortalidade e o número de árvores suprimidas.

A heterogeneidade estrutural, como também pode ser chamada a heterogeneidade no tamanho das árvores, origina-se das diferentes taxas de crescimento em nível de árvore individual. Estas diferentes taxas estão relacionadas a três componentes: quantidade de recursos (água, nutrientes e luz) disponíveis, proporção destes recursos que as árvores são capazes de absorver e eficiência com a qual as árvores usam estes recursos para o crescimento (MONTEITH, 1977; BINKLEY, 2004). Qualquer fator que afete um destes três componentes será um promotor da heterogeneidade estrutural.

Na fase inicial de uma monocultura florestal, a heterogeneidade estrutural é afetada pelo tipo de propagação e a qualidade das mudas, pela heterogeneidade ambiental e pela qualidade das operações silviculturais. O tipo de propagação já determina se haverá diferença no uso de recursos. Se as plantas provêm de propagação seminal, a diversidade genética implica em uma potencial diferença, mesmo que pequena, no crescimento das plantas. Com a propagação vegetativa, as plantas são geneticamente idênticas e possuem, a princípio, o mesmo potencial de crescimento. No entanto, mesmo que propagadas vegetativamente, pode haver diferença na capacidade de crescimento inicial devido a qualidade das mudas, tal qual vigor e sanidade (XAVIER; SILVA, 2010), resultantes do processo de produção no viveiro e mesmo no transporte até a área do plantio.

A heterogeneidade ambiental é dada pela desuniformidade das características físico-químicas do solo, relevo e face de exposição. Manchas de solo mais ou menos férteis ou com camadas compactadas, pequenas áreas com má drenagem ou que acumulam muita água, terrenos ondulados, entre outros, podem favorecer o crescimento de algumas plantas, em detrimentos de plantas próximas, por aumentar ou restringir a quantidade de recursos disponível (SCHUME; JOST; HAGER, 2004; BOYDEN; BINKLEY, 2016; BOYDEN et al., 2012).

As operações silviculturais como plantio, preparo do solo, adubação, combate a formigas e cupins, controle da matocompetição, são prescritas com o intuito de aumentar a quantidade e a disponibilidade de recursos e reduzir os fatores que limitam do uso dos mesmos. Entretanto, quando efetuadas de forma inadequada, com implementos descalibrados e não obedecendo às prescrições, estas operações podem intensificar a heterogeneidade ambiental, promovendo uma maior desuniformidade no crescimento das plantas (RADTKE; WESTFALL; BURKHART, 2003).

À medida que as árvores crescem e suas copas e raízes se aproximam, dá-se início à competição por recursos. Após o fechamento do dossel, as plantas que, por consequência dos fatores supracitados, foram favorecidas e puderam crescer mais, desenvolvem, portanto, maior copa e maior volume de raízes, que farão com que elas sejam capazes de absorver mais radiação solar, nutrientes e água, e usá-los de forma mais eficiente (BINKLEY et al., 2002; BINKLEY et al., 2010b; CAMPOE et al., 2013; FORRESTER et al., 2013). Isto, por sua vez, permite que elas cresçam ainda mais em relação às plantas menores.

A competição passa a ser um fator de restrição ao crescimento das plantas menores, uma vez que as plantas maiores diminuem a disponibilidade de recursos para as plantas menores. Assim o povoamento se diferencia em várias classes de dominância (BINKLEY, 2004) cujo efeito dura por toda a rotação (DOI; BINKLEY; STAPE, 2010). Mesmo com o manejo intensivo, em plantios monoclonais com genótipos altamente produtivos e com prescrições silviculturais sítio-específicas, os povoamentos ainda podem portar considerável heterogeneidade no tamanho das plantas (LUU; BINKLEY; STAPE, 2013).

Só recentemente, com a intensificação das pesquisas em ecologia da produção e ecofisiologia de plantações florestais, a uniformidade estrutural dos povoamentos florestais (se e como ela afeta a produtividade) tem sido mais profundamente investigado. Em uma pesquisa direcionada a várias empresas florestais no Brasil, promovida pelo projeto *Brazil Eucalyptus Potential Productivity (BEPP)*, o efeito da uniformidade do tamanho das árvores na produção foi considerado um dos tópicos de maior relevância (BINKLEY; LACLAU; *et al.*, 2010)

Alguns trabalhos já mostraram que existe uma tendência de que povoamentos mais heterogêneos sejam menos produtivos que povoamentos mais uniformes. Stape et al. (2010) compararam talhões monoclonais heterogêneos, cujo plantio foi feito de forma escalonada (um terço das mudas plantadas inicialmente, outro terço plantado 40 dias depois e o terço final 80 dias após o plantio), com talhões mais uniformes, nos quais o plantio ocorreu em somente uma ocasião. Estes autores encontraram que as árvores dos tratamentos uniformes cresceram em média 13% mais que as árvores do tratamento heterogêneo.

Binkley et al. (2002) compararam o crescimento de talhões estabelecidos com mudas de origem seminal e clonal e evidenciaram que grande parte do maior crescimento dos plantios clonais pode ter resultado mais devido à maior uniformidade no tamanho das árvores do que da capacidade de crescimento dada pelo genótipo. Luu, Binkley e

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Stape (2013), estudando o efeito da competição com árvores vizinhas, uniformidade e do tamanho das árvores no crescimento das árvores em nível individual concluíram que tratamentos que promovam a uniformidade no tamanho das árvores podem resultar em um aumento de 5% a 15% na produção em nível de talhão.

Apesar de algumas evidências, há ainda muito a ser investigado não somente sobre o efeito da heterogeneidade estrutural na produtividade do talhão em si, mas também sobre como a heterogeneidade afeta a dinâmica do crescimento das árvores. O crescimento em nível de talhão emerge do crescimento das árvores individualmente. Este processo é fortemente afetado pelas complexas interações de competição, dominância e supressão que afetam a capacidade das plantas de usar os recursos do sítio. Desta forma, entender como a heterogeneidade se desenvolve, bem como sua relação com a dinâmica do crescimento das plantas é essencial para delinear e prescrever tratamentos que otimizem o crescimento.

Além disso, é necessário investigar os fatores promotores da heterogeneidade em plantios monoclonais, como eles interagem entre si, o quanto é possível manipulá-los para se obter maior produtividade e se é economicamente viável manipulá-los para tal. Estas investigações contribuirão não somente para o aprofundamento do entendimento sobre o crescimento de povoamentos florestais, como também abrem uma nova oportunidade para o aumento da produtividade.

O objetivo desta tese foi, portanto, contribuir com o melhor entendimento do efeito da heterogeneidade na produtividade e na dinâmica de povoamentos monoclonais de eucalipto. Dois capítulos são apresentados:

No primeiro capítulo, entitulado "*Increasing stand structural heterogeneity reduces productivity in brazilian Eucalyptus monoclonal stands*", estudou-se o efeito da heterogeneidade estrutural na produtividade. Para isso, foram utilizados dados de uma rede de experimentos de espaçamentos e clones conduzidos no sul da Bahia. Investigou-se também se duas importantes prescrições silviculturais, o espaçamento de plantio e o genótipo, têm efeito na heterogeneidade estrutural dos povoamentos.

No segundo capítulo, "*Development of stand structural heterogeneity and growth dominance in thinned Eucalyptus stands in Brazil*", objetivou-se estudar o desenvolvimento da heterogeneidade estrutural e do efeito de dominância do crescimento em povoamentos monoclonais de eucalipto com diferentes níveis de redução da competição via desbastes. Para este estudo, foram utilizados experimentos de pesos de desbastes no nordeste da Bahia.

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2. CAPÍTULO 1

INCREASING STAND STRUCTURAL HETEROGENEITY REDUCES PRODUCTIVITY IN BRAZILIAN *Eucalyptus* MONOCLONAL STANDS*

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 m³ ha^{-1} to 23 m³ 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.

Key words: Tree plantation; Stand structure; Stand uniformity; Gini's coefficient; Genotype; Planting spacing

2.1. 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 (Seppälä, 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 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).

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 m³ 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.

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.

2.2. 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 because 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.

Table 2.1. Characterization of six genotype × spacing experiments of *Eucapytus* 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 (m³ 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

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 by Equation 1 fitted for each experiment, relating total plot volume (V; m³ ha^{-1}) of genotype G1 to age in years.

$$V = \alpha\left(\beta - e^{(-\gamma Age)}\right) + \varepsilon \qquad\qquad \text{Equation 2.1}$$

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 (m³ 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).

Total tree height (ht) was measured with a Suunto clinometer with a precision of 0.5 m. Bole circumference at 1.3 m above soil surface was measured with a tape-measure with the precision of 0.5 cm, and converted to diameter (dbh). Both variables were measured approximately annually, starting at about the age of one year, but only data from the second year was used in this analysis. Individual tree over-bark stem volume (V) was estimated using Schumacher and Hall's model (equation 2), summed to compute total plot volume and converted to volume per hectare (Yield).

$$\ln(v) = \beta_0 + \beta_1 \ln(dbh) + \beta_2 \ln(ht) + \varepsilon \qquad \text{Equation 2.2}$$

The relationships between yield, Gini's coefficient, age, spacing and genotype were analyzed using generalized linear mixed effect models, following the 3-step model selection approach suggested by Zuur et al. (2009) and Pinheiro and Bates (2000). First, we decided the random structure in the presence of the full set of fixed effects (main effects and second-order interactions). When testing the random component, model fitting was performed via restricted maximum likelihood (REML). After selecting the random structure, we analyzed the fixed component. In this step, model parameterization was performed by maximum likelihood (ML). Spacing was entered as a categorical variable in the random component and as a continuous variable, "planting density" (trees ha⁻¹), when in the fixed component of the models. Two spacings had the same area per plant but different arrangements, 4 × 3 m and 5 × 2.4 m, therefore the latter, more rectangular spacing, was excluded to avoid potential confounding effects of rectangularity (DeBell and Harrington, 2002; Stape and Gonçalves, 2002). When necessary, the variance structure or autocorrelation were also modeled in this step. Inference was made after refitting the best models via REML.

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To test for an effect of spacing on stand structural heterogeneity, Gini's coefficient was modeled as a function of planting density, age and their interaction in the fixed component (Gini 1). We tried adding either only random intercepts or both random intercepts and slopes. When only random intercepts were used, experiment, block and genotype were initially added following the nested structure of genotype nested within block, nested within experiment. Random slopes were always related to age and whenever tested, spacing (always as categorical variable when in the random component) was also included in the random component as part of the nested structure (experiment/block/spacing/genotype). This allowed for each genotype inside the nested structure to have a different trajectory of heterogeneity development through time. This model was also used to check whether heterogeneity increases with time and whether different planting densities present different development of heterogeneity.

We rearranged the previous model to test for differences in stand uniformity due to genotypes and whether heterogeneity develops at different rates for each genotype. Genotype and age were included in the fixed structure while spacing was added to the random component that included either random intercepts or both random intercepts and slopes (Gini 2).

The effect of planting density, age and Gini on stem volume yield were examined by fitting yield as a function of these variables and their interactions (Yield 1) in the fixed component. The same random structure was used as in the Gini 1 model. The interaction with Gini's coefficient was used to test whether there was an increasing effect of heterogeneity as stands age ("Gini × Age" interaction) and whether the effect of heterogeneity increased with density ("Gini × planting density" interaction). To test whether heterogeneity impacts yield differently depending on the genotype, we shifted genotype to the fixed component and tree density was added in the random component, but as spacing (categorical variable) (Yield 2).

The assumptions of normality of residuals and homoscedasticity were graphically checked using scatterplots of the normalized residuals against the estimated values and for the continuous explanatory variables, using box plots of the normalized residuals against the categorical explanatory variables and normal probability plots (qq-plots) at all levels of nesting. The assumption of independence of the residuals regarding the time series was assessed by plotting variograms because the time span between measurements was not constant. The normal distribution of the coefficients of the random components were checked with qq-plots at all levels of nesting.

All analyzes were carried out using R (R Core Team, 2013). The partial F test and the log-likelihood test, both at 5% significance, were used, respectively, on the fixed and on the random components of the models. In the case of any non-nested models, comparisons were made with their Akaike's Information Criteria (AIC). Model fitting and tests were performed with the package "*nlme*" (Pinheiro et al., 2015).

2.3. RESULTS

For all experiments, disregarding treatments, Gini's coefficient had a mean of 20 and ranged from 4 to 51. In terms of the coefficient of variation of individual tree volume, this had a mean of 32% and a range from 8% to 84% with values concentrated between 10% and 45%. Figure 2.1 shows the frequency distributions of Gini's coefficient.

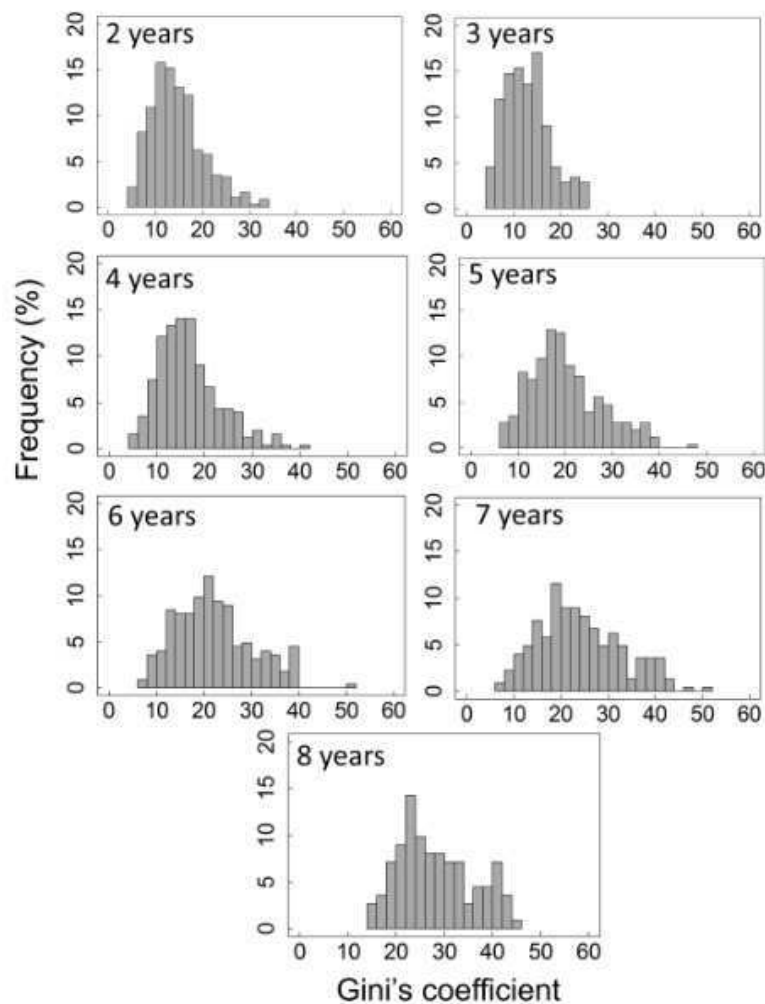**Figure 2.1.** Frequency distribution of Gini's coefficient in six genotype × spacing experiments of *Eucalyptus* in Northeastern Brazil throughout the rotation.

Block did not improve the fit of the models and was therefore removed from all of them. Assumptions were met for all of the models except by Yield 1. After the procedure of model selection, model Gini 1 contained age, planting density and their

interaction as fixed terms and random intercepts and slopes (in relation to age) for genotype nested within experiment. Significance of terms and goodness-of-fit statistics are presented in Table 2 (see Appendix A1 for the terms' estimated coefficients).

Table 2.2. Explanatory variables of the models for Gini's coefficient and stem volume yield and their p-values in the partial F-test at a 5% significance level. Main effects were tested as in sequential ANOVA and interactions as in marginal ANOVA. Gini = plot-wise Gini's coefficient for the over-bark stem volume of individual trees; age = age from planting in years; density = number of trees per hectare; R^2_{adj} = adjusted coefficient of determination; RMSE = root mean squared error in percentage; $r_{y\hat{y}}$ = Pearson's coefficient of correlation between estimates and observed values (all significant at a 5% level). * = statistics calculated at the lowest level of nesting.

Fixed component	Models			
	Gini 1	Gini 2	Yield 1	Yield 2
Age	<0.0001	<0.0001	<0.0001	<0.0001
Density	<0.0001	-	<0.0001	-
Genotype	-	0.0218	-	<0.0001
Gini	<0.0001	<0.0001	<0.0001	<0.0001
Age²	-	-	<0.0001	<0.0001
Density × Age	<0.0001	-	0.0098	-
Density × Gini	<0.0001	-	0.0428	-
Genotype × Age	-	<0.0001	-	<0.0001
Genotype × Gini	-	<0.0001	-	<0.0001
Age × Gini	<0.0001	<0.0001	<0.0001	<0.0001
R^2_{adj}*	0.82	0.81	0.93	0.98
RMSE (%)*	22.22	19.69	9.04	10.10
$r_{y\hat{y}}$*	0.86	0.89	0.99	0.99

Greater Gini's coefficient was associated with denser treatments and Gini also increased with age (coefficient = 0.13, p-value < 0.001, for "Age"). In addition, this increase in heterogeneity with age was even higher for denser treatments (coefficient = 0.002, p-value < 0.001, for the "Density × Age" interaction).

The final model relating Gini's coefficient to genotypes and age (Gini 2) consisted of genotype, age and their interaction in the fixed component allowing for random intercepts and slopes for genotype nested within spacing (as categorical variable) nested within experiment. According to this model, genotype had a significant effect on stand structural heterogeneity with a different rhythm of heterogeneity development with age

(p-value < 0.001 for the "Genotype × Gini" interaction, coefficients for each Genotype in Appendix A1).

The model Yield 1 contained a fixed component with age, age squared (to correct for curvature), planting density and Gini's coefficient and the interactions "density × age", "density × Gini" and "age × Gini". The random structure comprised of random intercepts and slopes for genotype nested within spacing nested within experiment. Several variance structures were tested to correct for heteroskedasticity across experiments.The best one was selected by comparing models using the log-likelihood test (at 5% significance level) or AIC for nested and non-nested models, respectively, aided by comparisons of plots of normalized residuals against estimates and against each of the explanatory variables.

The selected variance structure was implemented using the varIdent() function from the "*nlme*" package with "Experiment" as the grouping categorical variable, within which variance was allowed to vary (refer to Pinheiro and Bates, 2000 and Zuur et al., 2009) for computational methods and details). The model with the variance structure was statistically better than the one without it (AIC =14638.36 vs. 15021.36; log-likelihood ratio = 392.99 with p-value < 0.0001). After the addition of this variance structure, the diagnostic plots were rechecked.

An increase in stand heterogeneity was associated with a decrease in stem volume yield (Figure 2.2). The significant interaction between density and Gini resulted in a greater heterogeneity effects with increasing density (coefficient = -0.0006, p-value = 0.043).

The effect of heterogeneity on growth also increased with age (coefficient for "Gini × Age" interaction = -0.39, p-value < 0.0001), as shown by the steeper curves for lower levels of Gini in Figure 2.2. Notice that as density increases, so do the distances between the lines. This indicates that the negative effect of heterogeneity is stronger for denser stands and that this effect increases as the stands age (non-parallel curves).
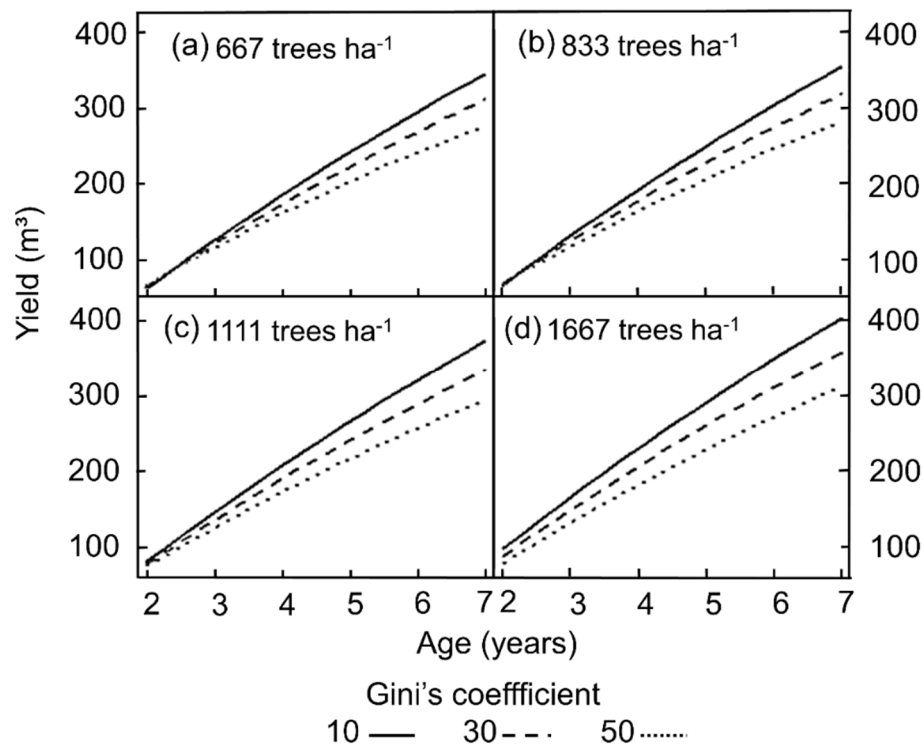
Figure 2.2. The effect of stand density and structural heterogeneity (represented by Gini's coefficient) on stem volume yield for an entire rotation in *Eucalyptus* plantations in northeastern Brazil.

The model Yield 2 showed a significant effect of genotype on yield with some genotypes presenting distinct growth rates (p-value for "Age × Genotype" interaction < 0.0001; coefficients shown in Appendix A1), increasing effect of heterogeneity on yield with age (coefficient for "Gini × Age" interaction = -0.44, p-value < 0.0001) and different effect of heterogeneity on yield depending on genotype (p-value for "Gini × Genotype" interaction < 0.0001; coefficients shown in Appendix A1).

2.4. DISCUSSION

By isolating the effect of structural heterogeneity from genetic diversity, this study showed that stand heterogeneity, represented by Gini's coefficient, was negatively related to stand production, in accordance our hypothesis (2) and with other studies (Stape et al., 2010; Luu et al., 2013; Binkley et al., 2010; Ryan et al., 2010; Aspinwall et al., 2011). In general (fixed component of Gini 1 model), a 10-unit increase in heterogeneity was associated with a productivity loss of approximately 17 m³ ha^{-1} for the widest spacing of 667 trees ha^{-1} and 23 m³ ha^{-1} for the closest spacing of 1667 trees ha^{-1} by the end of the 7-year rotation.

In relative terms this reflects a reduction in productivity of approximately 5%-7%, respectively, for each 10-unit increase in Gini. For example, in a stand with a planting density of 1667 trees ha^{-1}, increasing from a Gini of 10 to a Gini of 40 units, a realistic range in our dataset, was associated with a mean volume yield decrease of 20%. This reduction is consistent with the 18% decrease in mean annual increment in experiments where structural heterogeneity was directly manipulated by staggering the age of planting within a given stand (Stape et al., 2010).

This large reduction in growth is probably correlated with similarly large changes in other ecosystem functions that are correlated with productivity such as carbon sequestration, nutrient cycling, transpiration and water-use efficiency (annual wood growth per unit annual transpiration). For example, based on regional relationships between growth and water use for plantations in northeastern Brazil (Stape et al., 2004), a 20% reduction in productivity at the age of 7 years, e.g. from 50 m³ ha^{-1} year^{-1} to 40 m³ ha^{-1} year^{-1}, would likely decrease stand transpiration by about 11.5% (from 902 mm year^{-1} to 798 mm year^{-1}) and decrease water-use efficiency by about 12.5% (from 2.83 to 2.47 kg of above ground biomass per m^3 of water).

These large differences not only have implications for regional water supply but also for responses to droughts. Less heterogeneous stands are more productive and are likely to use more water, but they will probably also be more water-use efficient based on the general positive correlations between forest growth, transpiration and water-use efficiency (Stape et al., 2004; Binkley, 2012; Otto et al., 2014).

As we posed in our hypothesis (4), there were two opposing effects influencing productivity as planting density increased: planting density directly increases stand yield by increasing the number of stems and basal area. However, heterogeneity also increased with planting density due to the intensification of competition for resources (Boyden et al., 2008; Aspinwall et al., 2011) and this increase in heterogeneity reduced productivity. In this study the former usually had the larger effect, so that productivity generally increased with increasing planting density (Figure 2.3).

This dominating effect of stand density is consistent with meta-analyses and inventory studies showing that stand density can have a much stronger influence on forest growth than species diversity (Paquette and Messier, 2011; Vilà et al., 2013). However, it is important to note that species diversity associated with structural heterogeneity sometimes often have a positive effect on productivity (Lei et al., 2009; Wang et al., 2011; Paquette and Messier, 2011; Vilà et al., 2013; Zhang and Chen, 2015), whereas in this

study, where genetic diversity was reduced to zero, structural heterogeneity had a negative effect on growth.

There were also exceptions where the negative heterogeneity effect was actually greater than the positive spacing effect on growth. For example, assuming no mortality, the smallest difference in planting density, between the 667 trees ha^{-1} and 833 trees ha^{-1} treatments, is 166 trees ha^{-1}. Close to the rotation length (seven years), the maximum Gini for the density 833 trees ha^{-1} was 33, found in Experiment E1, and the minimum Gini found in the 667 trees ha^{-1} treatment, in this same experiment, was 21. Based on the estimated coefficients of the model Yield 1, this 12-unit difference in the Gini's coefficient has an effect of 21.4 m³ ha^{-1} while the difference in density (a difference of 166 trees ha^{-1}) has an effect of 8.4 m³ ha^{-1}. That is, in this case, increasing the number of trees did not offset the negative effect of heterogeneity.
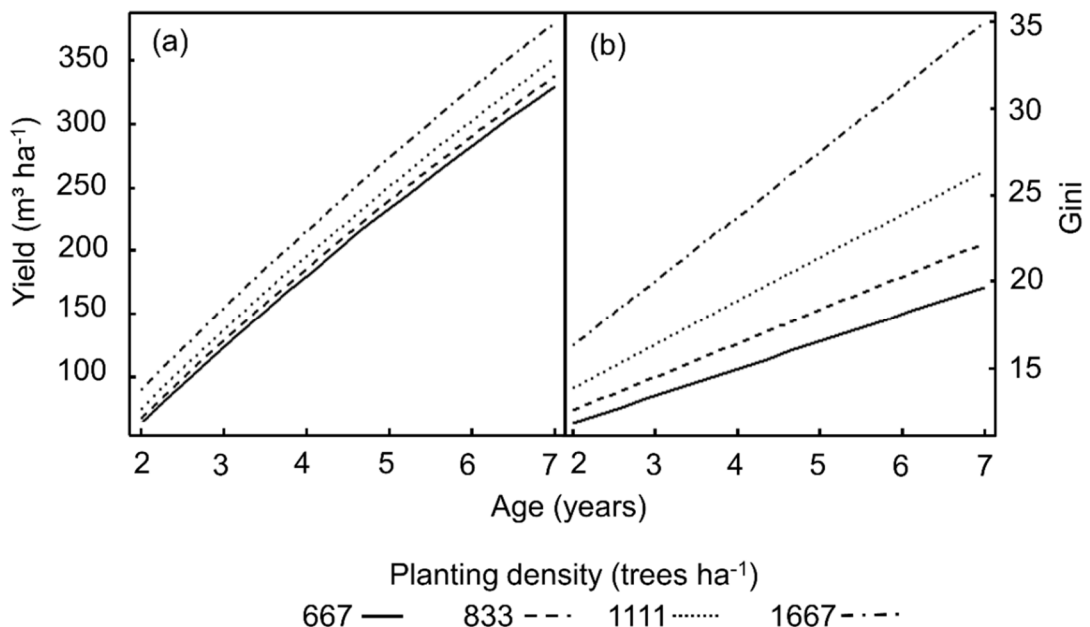

Figure 2.3. Yield (a) and Gini's coefficient (b) throughout time for four planting densities in a genotype × spacing trial of *Eucalyptus* in northeastern Brazil

Even though this is not the rule, it illustrates the fact that the effect of stand heterogeneity on productivity is not necessarily always smaller than the effect of planting density. When choosing closer spacings, opting for genotypes that are less likely to form heterogeneous stands could minimize any loss in production due to tree competition and suppression.

Despite the clones deployed in these experiments may be considered very genetically related, they differed in production, in tree size variability. The relationship between structural heterogeneity and productivity was also influenced by genotype.

These findings corroborate our hypothesis (3). As expected, the most uniform genotypes were generally the most productive (Figure 2.4). Similarly, Aspinwall et al. (2011) examined genotype and uniformity in *Pinus taeda* stands and also observed that the most uniform genotypes were generally the most productive.

These results have important management implications. Given that forest plantation companies typically use a greater collection of genotypes (but not in the same stand), the effect of genotype on stand uniformity and production may be even greater. This suggests the potential for future selection of genotypes that are able to form more uniform and productive stands.
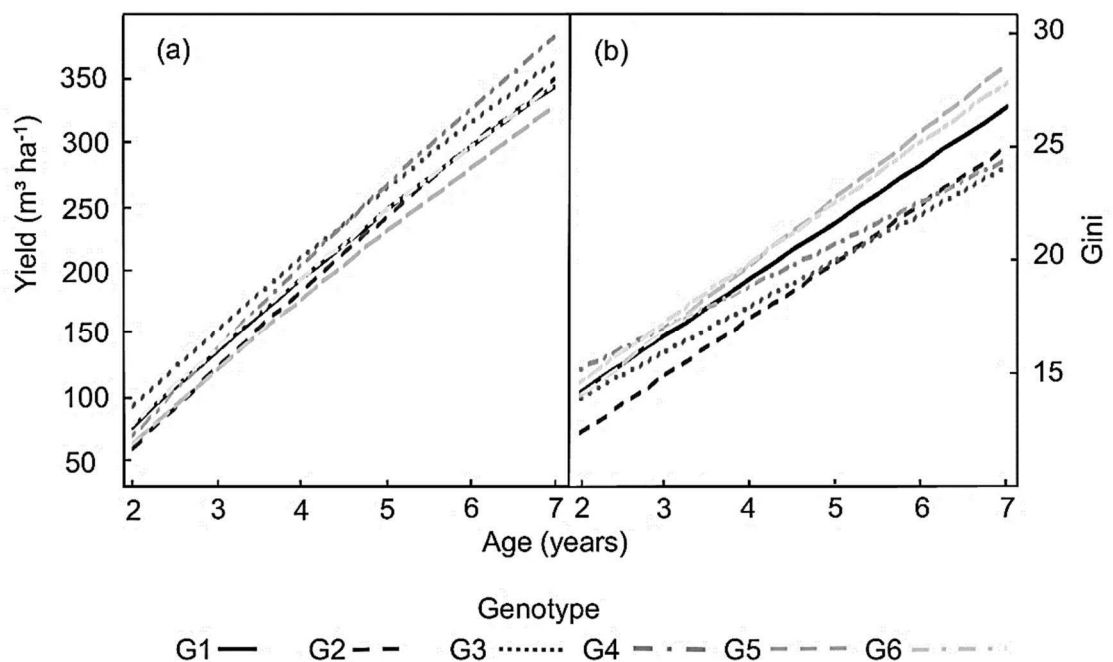

Figure 2.4. Yield (a) and Gini's coefficient (b) throughout time for six genotypes in a genotype × spacing trial of *Eucalyptus* in northeastern Brazil

The within-genotype variability also has ecological implications. Our results contrast with the often expected increase in productivity associated with increases in structural diversity of mixed-species stands compared with monocultures. That is, greater productivity of mixtures is often attributed, in part, to the structural heterogeneity that results from inter-specific differences in growth and allometry (Kelty, 1992; Forrester et al., 2006), or with the plasticity of a given species that allows it to modify its allometry (or physiology, phenology) when growing in a mixture that is complementary to other species (Bauhus et al., 2004; Pretzsch, 2014).

This study shows that in the absence of genetic diversity, structural heterogeneity by itself is not necessarily as useful as indicated by some studies that confound genetic and structural diversity.Tree-level studies in monospecific stands have shown that the

reduction in stand-level productivity with increasing heterogeneity occurs because there is a decrease in growth, resource use and use efficiency of suppressed trees that outweighs any increase in the growth and resource-use efficiency of the dominant trees (Stape et al. 2010; Campoe et al. 2013; Luu et al. 2013).

The contrasting effects of structural heterogeneity on growth with, versus without, the presence of genetic diversity, and also inter-genotype differences in this study, are likely to reflect shifts in this balance between the positive response of dominant trees and the negative response of suppressed trees. The balance will also likely be influenced by the fact that within a stand there can be large variability in soil nutrients, soil moisture and light availability (Schume et al., 2004; Boyden et al., 2012).

The faster growing and less heterogeneous genotypes may have traits, such as rapid root development, that make them less responsive to micro-site heterogeneity. In stands where there is genetic diversity, such as mixed-species stands, the greater genetic diversity may increase the probability that trees in lower resource supply micro-sites have traits that enable them to make more efficient use of their environment than trees of a similar dominance class in stands with less genetic diversity. We suggest that greater insight into the driving mechanisms of structural heterogeneity-productivity relationships could be obtained by combining tree- and stand-level analyses with process-based analyses (e.g. Binkley et al., 2010). In addition, *Eucalyptus* species are generally very shade intolerant, so it would be of great interest to repeat these experiments with shade tolerant species.

In conclusion, we found a negative association between the heterogeneity in tree sizes and volume yield for monoclonal *Eucalyptus* plantations in northeastern Brazil. Increases in structural heterogeneity reduced productivity by as much as 20% over a seven-year rotation period and is likely to have a similar impact on other ecosystem services that are correlated with productivity. The most uniform genotypes tended to have greater productivity than the most heterogeneous ones. Closer spacings were associated with greater heterogeneity, however, productivity generally increased with closer spacings because the greater number of stems generally had a greater positive effect on productivity than the negative effect of greater heterogeneity. The negative relationship between heterogeneity and productivity contrasts with the positive relationship observed in some studies in forests with genetic diversity. An understanding of the mechanisms behind these contrasting effects would improve our knowledge about how forest structure and genetic diversity influence forest growth and other ecosystem functions and services.

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APPENDIX A1

Fixed components of the models for Gini's coefficient and stem volume yield and their effect sizes. Gini = plot-wise Gini's coefficient for the over-bark stem volume of individual trees; age = age from planting in years; density = number of trees per hectare; ()= standard error; * = Genotype G1 set as the baseline level; the number in the models' names represent whether the variable density (1) or genotype (2) was used as fixed effect.

Fixed component		Models		
	Gini 1	Gini 2	Yield 1	Yield 2
Intercept*	8.56311 (2.76397)	9.03589 (2.57434)	-102.93380 (11.44290)	-55.20333 (7.91105)
Age	0.13086 (0.66498)	2.53161 (0.65961)	72.41484 (9.31299)	74.90272 (8.58877)
Density	0.00019 (0.00075)	-	0.02825 (0.00687)	-
Genotype G2	-	-1.80971 (0.74823)	-	-34.08279 (3.79506)
Genotype G3	-	0.73820 (0.88306)	-	-30.76564 (5.22834)
Genotype G4	-	2.33223 (1.08651)	-	-53.42374 (5.90317)
Genotype G5	-	-1.02270 (1.44250)	-	-22.96544 (6.09971)
Genotype G6	-	0.21859 (2.66980)	-	-8.57528
Gini	-	-	1.2666 (0.43198)	0.31006 (0.29770)
Age²	-	-	-1.67396 (0.22622)	-1.41932 (0.22712)
Density × Age	0.00216 (0.00015)	-	0.00474 (0.00187)	-
Density × Gini	-	-	-0.00059 (0.00029)	-
Genotype × Age G2	-	0.01063 (0.15808)	-	4.40599 (0.91504)
Genotype × Age G3	-	-0.48707 (0.17696)	-	0.59657 (1.08417)
Genotype × Age G4	-	-0.66732 (0.21609)	-	8.96963 (1.22880)
Genotype × Age G5	-	0.41799 (0.30280)	-	-0.74620 (1.37127)
Genotype × Age G6	-	0.12739 (0.86029)	-	-0.40480 (2.24392)
Genotype × Gini G2	-	-	-	0.39879 (0.19378)
Genotype × Gini G3	-	-	-	2.32586 (0.24958)
Genotype × Gini G4	-	-	-	1.47993 (0.31774)
Genotype × Gini G5	-	-	-	0.57467 (0.26721)
Genotype × Gini G6	-	-	-	-0.01531 (0.32103)
Age × Gini	-	-	-0.36879 (0.060280)	-0.44562 (0.05183)

3. CAPÍTULO 2

DEVELOPMENT OF STAND STRUCTURAL HETEROGENEITY AND GROWTH DOMINANCE IN THINNED *Eucalyptus* STANDS IN BRAZIL*

Abstract

Higher tree size heterogeneity in forests has been linked to lower productivity, especially in monocultures. Thinning the stand can directly manipulate tree size variability, thereby changing growth partitioning across tree dominance classes and consequently changing the development of stand structural heterogeneity compared to its course in unthinned stands. We used three thinning-intensity experiments to assess how stand heterogeneity and growth dominance develop through time and across different thinning intensities in *Eucalyptus* stands in one of the most productive regions of Brazil. The experiments were established along a three-site gradient in productivity. The plots were thinned from below at ages 58 and 146 months. The thinning intensities tested were 20%, 35% and 50% of basal area removal and an additional treatment of 35% removal plus pruning at 27 months. Thinning reduced stand heterogeneity and growth dominance as well as their development through time and this reduction was greater the more intense the thinnings were. Stand structural heterogeneity and growth dominance both increased before and after the first thinning, but the rates of increase after the first thinning were lower than they were before the first thinning. After the second thinning, heterogeneity tended to remain constant, whereas growth dominance tended to decrease, reaching negative values. This was contrary to our expectations of observing the same trends in both variables. Our results show that thinning from below not only reduces heterogeneity and growth dominance by removing the smaller trees, but can also slow the development of stand heterogeneity and growth dominance in Eucalyptus stands and potentially other monocultures.

Keywords: Tree size inequality; Gini's coefficient; Growth dominance; Growth partition; Asymmetric competition.

3.1. INTRODUCTION

Stand structure is a key feature of forests because of its relationship with forest functioning. An assessment of stand structure, and how it develops through time, can indicate which processes are likely to be driving stand dynamics. It can reveal, for instance, which individuals or cohorts are contributing the most to stand growth and how resources are being partitioned between individuals or cohorts. Many studies have shown a correlation between variability in stand structure and forest productivity (e.g. Binkley et al., 2002; Lei et al., 2009; Forrester and Bauhus, 2016; Bourdier et al., 2016; Soares et al., 2016) and some have even suggested how different tree cohorts might therefore respond to climate change (Trouvé et al., 2014; Fernández-de-Uña et al., 2015).

Stand structure, in terms of size heterogeneity, arises from differences in individual tree growth, which are driven by three components: the amount of resources available, the proportion of these resources that the trees are able to acquire and the efficiency with which trees use them to grow (Monteith, 1977; Binkley et al., 2004). Among the myriad of factors that may affect those components (e.g. Zenner and Hibbs, 2000; Little et al., 2003; Boyden et al., 2012; Skovsgaard and Vanclay, 2013), competition plays a crucial role as it affects the trees access to resources.

For example, faster growing trees are able to increase resource acquisition by growing bigger crowns and root systems, and increasing resource use-efficiency, while decreasing the availability of resources for the suppressed trees, e.g. by partially or totally shading other crowns (Binkley et al., 2002, 2010, 2013; Campoe et al., 2013; Forrester et al., 2013a). These trees become dominant in the stand as the trees differentiate into size classes according to the level of suppression and their ability to cope with competition (Schwinning and Weiner, 1998).

The contributions of individual tree growth can be assessed at the stand level by the proportional contribution of the trees' growth relative to their size, known as the growth dominance coefficient (Binkley et al., 2003; Binkley et al., 2006; West, 2012). In addition to the ecological contribution of understanding changes in growth dominance patterns through time and between species and forest types (Binkley et al., 2006; Doi et al., 2010; Fernández et al., 2011; Tschieder et al., 2012; Binkley and Kashian, 2015), this coefficient may also work as a tool for understanding the response to silvicultural treatments, such as thinning (Doi et al., 2010; Bradford et al., 2010; Trouvé et al., 2014).

The link between growth dominance and stand structural heterogeneity is that the development of tree size inequality is determined by the different growth rhythms of the trees, especially in relation to their size. That is, in the absence of structural changes

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resulting from natural disturbances or silvicultural treatments, growth dominance determines tree size inequality. When the biggest trees grow disproportionately faster than smaller trees, heterogeneity increases. When growth is proportional to tree size, heterogeneity remains the same. When smaller trees grow disproportionately faster than bigger trees, structural heterogeneity decreases and the stand becomes more uniform in terms of tree size.

Elucidating the dynamics of forest stands as affected by stand structural heterogeneity has relevant implications for silvicultural decisions, such as thinning regimes. For example, in plantations of *Eucalyptus globulus*, *E. grandi*s and *E. nitens* in Australia, the effect of stand structure was as strong, or even stronger, than site quality in determining the thinning response (Forrester et al., 2013b). In these areas, the relative and the absolute thinning responses, of the 200 largest-diameter trees per hectare, were higher in stands with smaller coefficients of variation in diameter and with diameter distributions containing higher proportions of trees in the larger size classes than in the smaller size classes.

Therefore, thinning responses may not only result from the response to greater resource availability, but also to the change in stand structure and the partitioning of resources between the retained individual trees (Forrester et al., 2013b). However, the effect of thinning on structural heterogeneity and growth dominance has received little attention.

Thinning from below can be expected to reduce structural heterogeneity and growth dominance because it systematically reduces the variability in individual tree sizes and growth rates by removing the smaller trees within the stand. Thinning might also be expected to slow the rates at which structural heterogeneity and growth dominance increase through time because it reduces competition; the greater the thinning intensity, the slower the increase in structural heterogeneity and growth dominance. Therefore, we posed the following predictions: (i) stand structural heterogeneity and growth dominance are immediately reduced by thinning; (ii) the more intense the thinning, the greater the decrease in the level of heterogeneity and growth dominance, as well as in their development through time; (iii) stand structural heterogeneity and growth dominance increase rapidly until the first thinning, after which the rate of increase declines, and after a second thinning, the heterogeneity and growth dominance remain constant through time; (iv) stand structural heterogeneity and growth dominance are directly related and therefore should display the same pattern of development through time and across thinning treatments.

3.2. MATERIAL AND METHODS

3.2.1. Site and data description

We used data from a thinning experiment in *Eucalyptus* stands established in 1995 in the state of Bahia, northeastern Brazil. The stands comprised monoclonal plantations of hybrids of *E. grandis* x *E. urophylla*. The experiment was installed at three sites (A, B and C), with altitudes of 285 m, 290 m and 150 m and an annual rainfall of 900 mm year^{-1}, 1100 mm year^{-1} and 1200 mm year^{-1}, respectively.

There was a gradient of productivity, which increased from site A to site C (Figure 3.1), such that the mean annual increment at the age of about 58 months (before the first thinning) was 27 m^3 ha^{-1} year^{-1}, 31m^3 ha^{-1} year^{-1} and 35 m^3 ha^{-1} year^{-1}, respectively for site A, B and C.

The equations shown in the figure are:

$$Hd_A = e^{\left(3.5095 - 24.3844 * \left(1/Age\right)\right)} \quad R^2 = 0.96 \quad S_{yx} = 0.04 \text{ m}$$

$$Hd_B = e^{\left(3.5690 - 26.1667 * \left(1/Age\right)\right)} \quad R^2 = 0.95 \quad S_{yx} = 0.05 \text{ m}$$

$$Hd_C = e^{\left(3.6655 - 29.0767 * \left(1/Age\right)\right)} \quad R^2 = 0.96 \quad S_{yx} = 0.04 \text{ m}$$
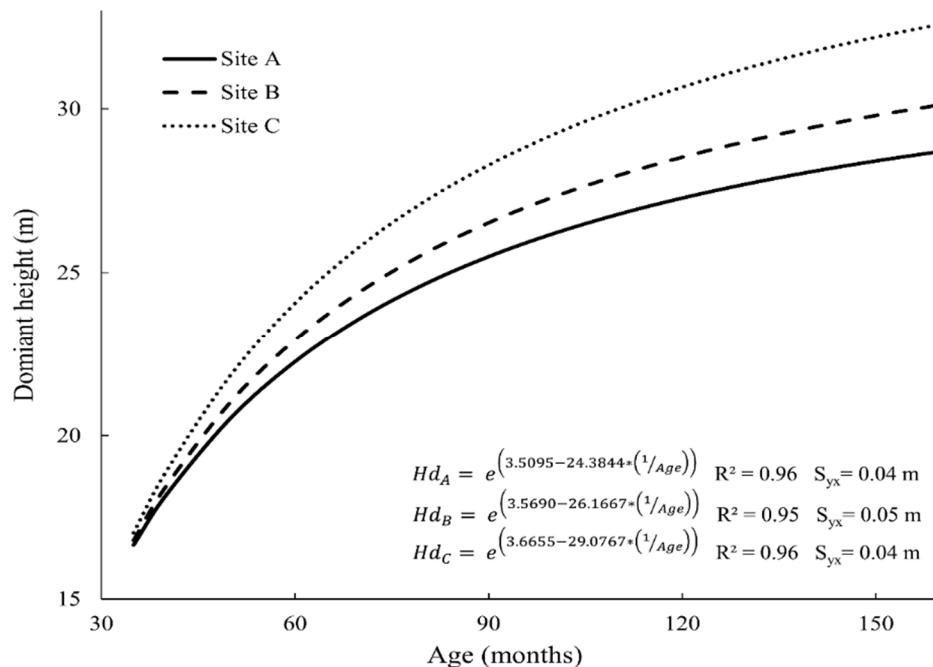
Figure 3.1. Total height of dominant trees (Dh) as a function of age in the three *Eucalyptus* thinning experiments. The dominant trees are the tallest 100 trees per ha. R^2 = coefficient of determination, S_{yx} = residual standard error. The three curves are statistically different from each other (P-values < 0.0001 for all pairwise contrasts of intercepts and slopes for the log-transformed equations, analysis not shown).

The experiment was implemented in a randomized block design with two blocks per site. Within block, each treatment was replicated twice, so that each treatment had 12 plots in total (3 sites × 2 blocks per site × 2 replicate within each block). The plots had an area of approximately 2600 m² (~ 46 m × ~ 56 m) with initial tree spacing of 3 m × 3 m.

The treatments corresponded to different percentages of basal area removed in each thinning event, namely: 20%, 35%, 50%. There was also an additional 35% treatment where the remaining trees were pruned to a height of 6.0 m at the age of 27 months. Thinning was performed at 58 and 146 months, with each plot receiving the same thinning intensity at 146 months as it did at age 58 months. At Site C, the experiment was felled before reaching the age of the second thinning. No control treatment (i.e. non-thinned plots) was present. The trees that were removed by thinning were those with the smallest heights and or diameters, or crooked, forked or broken trees. The thinning schedule was determined by the percent entries method as in Nogueira et al. (2001). In a previous study using these experiments, Nogueira et al. (2015) found that thinning improved tree and stand growth, but pruning had no effect.

3.2.2. Measurements and analysis

Each plot was measured approximately at the ages of 26, 40, 50, 58, 60, 75, 87, 100, 111, 114, 136, 146, 158, 164 months, except in Site C where the last measurement was performed at the age of 87 months. The total height (Ht) of the first 15 trees in each plot, the total height of the five largest-diameter trees (Dh) and the diameter at 1.3 m height (dbh) of all trees in the plot were recorded. The heights of the unmeasured trees were estimated using the equation:

$$\ln(\text{Ht}) = \beta_1 + \beta_2 \times \ln(\text{Age}) + \beta_3 \times \text{Age} + \beta_4 \times \ln(\text{SI}) + \beta_5 \times \text{SI} +$$
$$\beta_6 \times \ln(\text{dbh}) + \beta_7 \times \text{dbh} + \varepsilon \qquad \text{Equation 3.1}$$

Site index is a predictor in Equation 1 and was estimated using the dominant height measurements. This was done by firstly estimating the dominant height as a function of the stand age with Equation 2. Then, Equation 2 was rearranged into Equation 3, according to the guide-curve method (Clutter et al., 1983) to estimate site index.

$$\ln(\text{Dh}) = \alpha_o + \alpha_1 \times \left(\frac{1}{\text{Age}}\right) + \ln(\varepsilon) \qquad \text{Equation 3.2}$$

$$\ln(\text{SI}) = \ln(\text{Dh}) + \alpha_1 \times \left(\frac{1}{60} - \frac{1}{\text{Age}}\right) + \ln(\varepsilon) \qquad \text{Equation 3.3}$$

In the equations above: *Ht* is the tree height, *SI* is the site index, $\alpha_o, \alpha_1, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7$ are coefficients estimated by ordinary least squares and ε

is the random error assumed to be $\varepsilon \sim N(0, \sigma^2)$. Equations 1 and 2 were fitted to data separately for each of the three sites. Tree volume was estimated using Equation 4, previously fitted for each site by Nogueira et al. (2015) (Appendix A2.1):

$$\ln(V) = \phi_0 + \phi_1 \times \ln(dbh) + \phi_2 \times \ln(Ht) + \varepsilon \qquad \text{Equation 3.4}$$

The individual tree volumes were used to calculate Gini's coefficient, a commonly used proxy for stand structural heterogeneity (Weiner and Thomas 1986; Lexerød and Eid 2006; Wang et al. 2011; Pretzsch and Schütze 2014; McGown et al. 2016). This coefficient is a measure of inequality derived from the Lorenz curve. It can range, theoretically, from zero to one, but we multiplied it by 100 for better visualization. The closer Gini's coefficient is to zero, the more homogeneous the individual tree volumes.

To model the development of heterogeneity, we used mixed-effect models with Gini's coefficient as the response variable. We started with the full model in which the predictors in the fixed components were: *time*, *thinning treatment*, *growth period* and all their interactions. *Growth period* is a dummy variable and indicates whether the measurements are from the period *before the first thinning*, *after the first thinning* or *after the second thinning*. *Thinning treatment* refers to the aforementioned thinning intensities and was entered as a categorical variable. *Time* refers to the period in months elapsed from the start of each given *growth period*. To conform with the nested structure of the experiments, the initial random component of the model consisted of *Plot*, nested within *Block* nested within *Site*.

Model selection was performed by firstly selecting the best random structure in the presence of the full set of fixed effects (main effects and interactions). This selection was based on log-likelihood tests on the removal of the levels of the nested structure. Once the best random structure was obtained, a series of partial (sequential) F-tests were performed comparing the nested models, removing terms one by one, starting from the highest order interaction. When testing the random component, the model was fitted by restricted maximum likelihood procedure (REML), whereas when testing the fixed structure, the model fit was made through maximum likelihood (ML). These steps were according to Pinheiro and Bates (2000) and Zuur et al. (2009). The analyses were performed using the package "nlme" (Pinheiro et al., 2015) in R 3.2.2 (R Core Team, 2015). Final goodness-of-fit was assessed using the following statistics: the proportion of the total variance explained by only the fixed component of the models (marginal R^2) and by the full structure (conditional R^2) calculated with the piecewiseSEM package

(Lefcheck, 2016), the root mean squared error (RMSE), and the Pearson's correlation coefficient between estimates and observed values ($r_{y\hat{y}}$).

To test the hypothesis regarding growth dominance, we used mixed-effect models with the plot-wise growth dominance coefficient (GDC) as the response variable. The GDC is an index inspired by Gini's coefficient. It is calculated by ordering the trees in ascending order of a size variable (volume in this study) and plotting the cumulative percent initial values on the x axis against the cumulative percent increments on the y axis. In this experiment, there was no record of tree identity between measurements. Therefore, after ordering the trees we grouped them in groups of five, assuming that there was a greater likelihood of a change in the tree order within a group than trees changing between the groups. The GDC was then calculated as the relative difference between the area under the conceptual perfect equality curve (1:1) and the area under the actual inequality curve. This statistic was calculated according to West (2012) using the function "trapz" from the package "caTools" (Tuszynski, 2014) to perform the integration of the Lorenz curves by trapezoidal approximation, so that the GDC was calculated as:

$$GDI = 1 - \sum_{i=1}^{n}(x_i - x_{i-1})(y_i + y_{i-1}) \qquad \text{Equation 3.5}$$

where *x* is the cumulative percent volume and *y* is the cumulative percent increment in volume. Therefore, the GDC ranges from -1 to 1, but we also multiplied it by 100, as for Gini's coefficient. If all groups of trees grow in proportion to their size, the GDC equals 0; positive values indicate that the biggest trees contribute disproportionally more to stand total volume growth than smaller trees; and negative values indicates the opposite, such that smaller trees grow disproportionally more than bigger trees in relation to tree size. Figure 3.2 illustrates three examples of plots and their respective GDC's (negative, close to zero and positive). All of the initial fixed and random effects, as well as the steps for model selection were performed as for the Gini model.
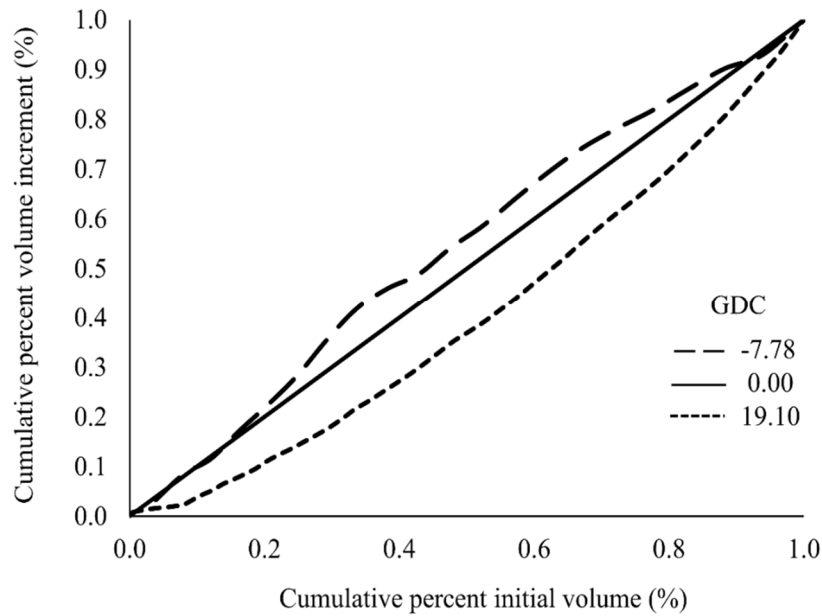
Figure 3.2. Examples of growth dominance curves (actual data from the studied experiments) and their respective growth dominance coefficients (GDC). The values of GDC -7.78 and 19.10 refer, respectively to a plot 164 months old which was thinned twice with an intensity of 35% of basal area removal; and a plot 136 months old which was thinned once at an intensity of 20% of basal area removal.

In both Gini and GDC models, the intercepts are interpreted as the estimated level of stand structural heterogeneity or growth dominance immediately after thinning. The slopes are the rates of change (i.e. rate of increase, rate of decrease or no change) of those variables through time within the given growth period. Therefore, to infer whether the thinning treatments had an effect on Gini or GDC, the treatments' intercepts, as well as the slopes, were compared to each other within a given growth period. To assess whether there was a change in the levels of Gini and GDC, as well as in their development, across the growth periods, the intercepts across the growth periods were compared to each other, per treatment, and the same was performed with the slopes. For such comparison, we used pairwise t-tests at 5% significance level.

3.3. RESULTS

The thinning clearly affected the yield such that the yield declined with increasing thinning intensity (Figure 3.3a). Mortality was very low, so thinning was almost exclusively responsible for any changes in stand density (Figure 3.3b).

The final model for Gini's coefficient included the fixed main effects *Thinning treatment*, *Time*, *Growth period* and all the two- and three-way interactions. The three-

35

way interaction was kept, though not statistically significant, as it allows the slope of each thinning treatment through time to vary between growth periods. In the absence of the threeway interaction, all of the other interactions were significant (i.e. p-values less than 0.0001 for the interactions ''Thinning intensity × Time" and ''Time × Growth period" and equal to 0.0011 for ''Thinning intensity × Growth period"). The random component comprised random intercepts and slopes (in relation to *Time*) with the full nested structure (*Plot* within *Block* within *Site*). A summary of the model fits is shown in Table 1.
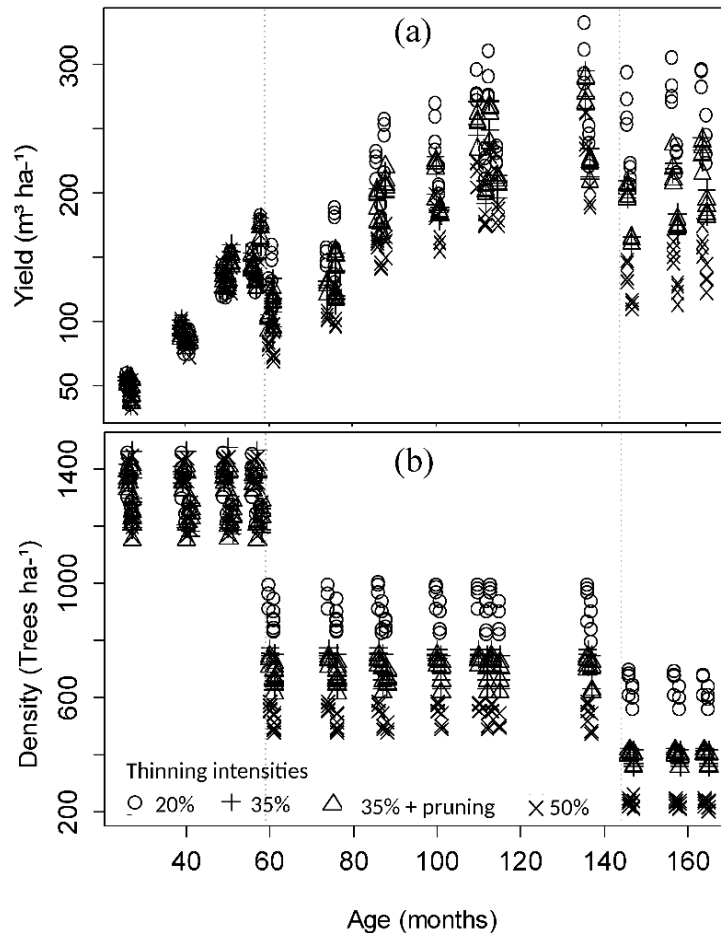

Figure 3.3. Observed values of yield (a; m³ ha^{-1}) and density (b; trees ha^{-1}) against age for the thinning intensities of 20%, 35%, 35% plus pruning up to 6 m and 50% of basal area removal in *Eucalyptus* plantations in northeastern Brazil. Vertical dotted lines mark the two thinnings.

As expected, given that thinning was applied from below, thinning reduced stand heterogeneity. After the drop in heterogeneity that resulted from thinning, the development of heterogeneity through time differed between the growth periods (P-value for the interaction *Growth period × Time* < 0.0001). All of the treatment's slopes before the first thinning were greater than their respective slopes in the other growth periods

(results not shown), i.e., the rate of increase in heterogeneity was the greatest before thinning was applied (Figure 3.4).

After the first thinning, heterogeneity continued to increase but at a much slower rate (Figure 3.4). The only statistically different treatment within this period was the 20% basal area removal, which presented a faster increase in heterogeneity (greater slope) than the others (refer Appendix A2.2 for the pair-wise slope coefficient comparisons between treatments). In terms of the intercept, that is, the estimated level of heterogeneity immediately after the first thinning, the levels of heterogeneity were inversely related to the thinning intensity.

Table 3.1. P-values of the partial F-tests for Gini and GDC models. *Treatment* refers to the thinning weights of 20%, 35%, 35% + pruning and 50% basal area removal; *Growth Period* refers to the periods before first thinning, after first thinning and after second thinning; *Time* is the time in months elapsed from planting or from any of the thinnings. Refer to Appendix A2.1 for the terms' estimated coefficients.

Terms	Model	
	Gini	GDC
Thinning weight	<0.0001	<.0001
Time	<0.0001	0.0382
Growth period	<0.0001	0.0020
Thinning weight × Time	0.3807	0.6656
Thinning weight × Growth period	<0.0001	<0.0001
Time × Growth period	<0.0001	<.0001
Thinning weight × Time × Growth period	0.3765	0.5665
R^2(marginal/conditional)	0.93 / 0.97	0.14 / 0.69
RMSE (m / %)	0.95 / 6.59	2.91 / 89.48
$r_{y\hat{y}}$	0.98	0.73

R² is the proportion of the total variance explained by only the fixed (marginal) component of the model (marginal) and by the full structure (conditional); RMSE is the root mean squared error given in meters and as a percentage of the mean response, and $r_{y\hat{y}}$ is the Pearson's correlation coefficient between estimates and observed values.

The intercepts significantly differed between the thinning intensities, but pruning in the 35% treatment had no effect. Pruning in this experiment was also reported to have no effect on tree growth (Nogueira et al., 2015). The comparison between the 35% plus

pruning treatment against the 50% treatment, though not significant, was close to the significance level (0.08).

After the second thinning, heterogeneity either remained the same or decreased slightly, especially in the 50% basal area removal treatment. However, this decreasing trend was not significant for any of the treatments. When *After second thinning* was set as the baseline level, none of the coefficients for *Time*, either as a main effect or interactions with it, were different from zero (Appendix A2.2; Figure 3.4).

The intercepts, on the other hand, followed the same patterns as before. The 20% treatment presented the highest Gini coefficient immediately after the second thinning. The other treatments where not different from each other (Appendix A2.2) but the significances between the 35% treatments (with and without pruning) against the 50% treatment showed the trend of differentiation between these two thinning intensities.
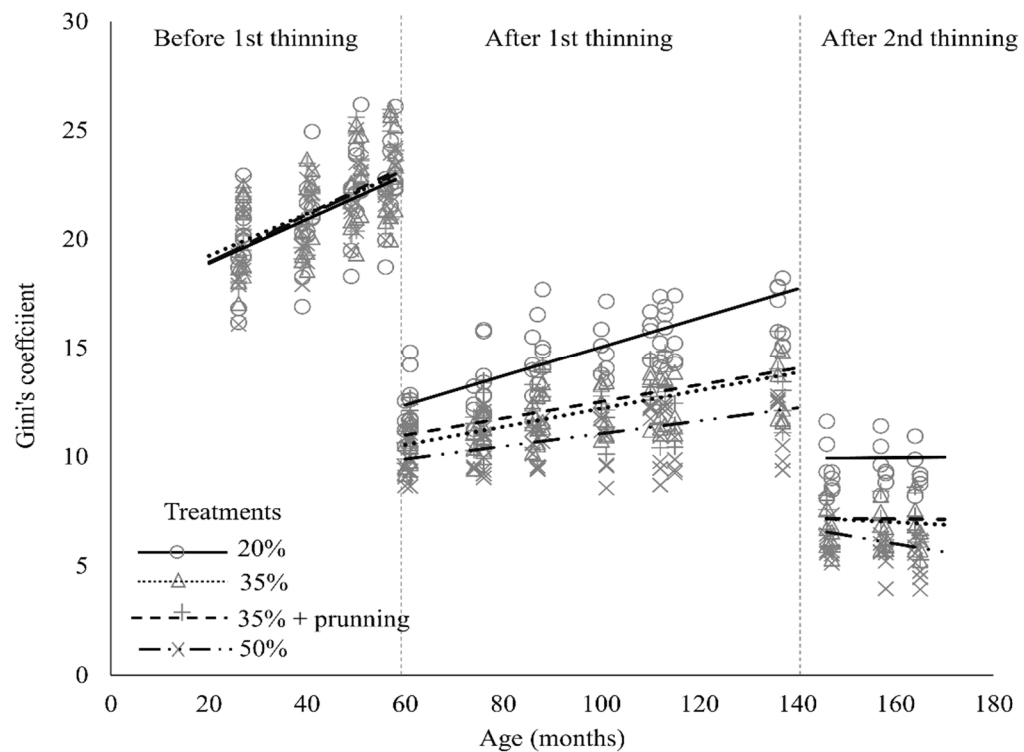

Figure 3.4. Development of heterogeneity (Gini coefficient) in *Eucalyptus* plantations in Brazil. The grey vertical dotted lines correspond to the thinnings.

The final model for GDC had the same structure as the Gini model. It included the fixed main effects *Thinning treatment*, *Time*, *Growth period* and all the two- and three-way interactions (see Table 1 for the partial F-tests summary). Like in the Gini model, the non-significance of the third-order interaction in the GDC model might have

occurred because only one statistically different slope within growth periods was found, i.e. the slope for the 20% basal area removal after the first thinning.

The random component was also comprised of random intercepts and slopes with the full nested structure. The boxplots of the normalized residuals against the sites revealed a very heterogeneous distribution and, hence, we added the variance structure model so that each site can have a different variance (i.e. $\varepsilon_{ij} \sim N\left(0, \sigma_j^2\right)$, where j = sites A, B or C). This model fixes one category as the baseline level and estimates the variance of the other levels as rates of the baseline level. In our model the variance of site B and C were estimated, respectively as 0.87 and 0.59 of site A's variance. This improved the residual dispersion and yielded a better model. The Akaike's information criterion (AIC) was reduced to 2131.70 from 2149.46 when using the models with the variance structure modeling, and the P-value was smaller than 0.001 in the log-likelihood test.

The development of GDC differed between growth periods (P-value for the interaction *Growth period × Time* < 0.0001). Growth dominance increased faster before the first thinning than in the following growth periods. The only exception was the 20% thinning intensity after the first thinning whose slope was not statistically different from before thinning (P-value = 0.48). Even though the curves in Figure 3.5 show a pattern of smaller intercepts and slopes with increasing intensity of the first thinning, only the slope of the 20% treatment was significantly different from zero (Appendix A2.3).

After the second thinning, the curves also revealed a trend of declining intercepts and slopes with increasing thinning intensity, but unlike the other growth periods, all curves had a declining trend. Only the intercept of the 20% treatment was significantly different from zero, but it did not differ from the other intercepts, which did not differ from each other either (Appendix A2.3). There was no statistical difference between the slopes of any treatment (Appendix A2.3). No slope in this period was significantly different from zero, despite of the descending curves shown in Figure 3.5, nor did they differ from each other (Appendix A2.3).
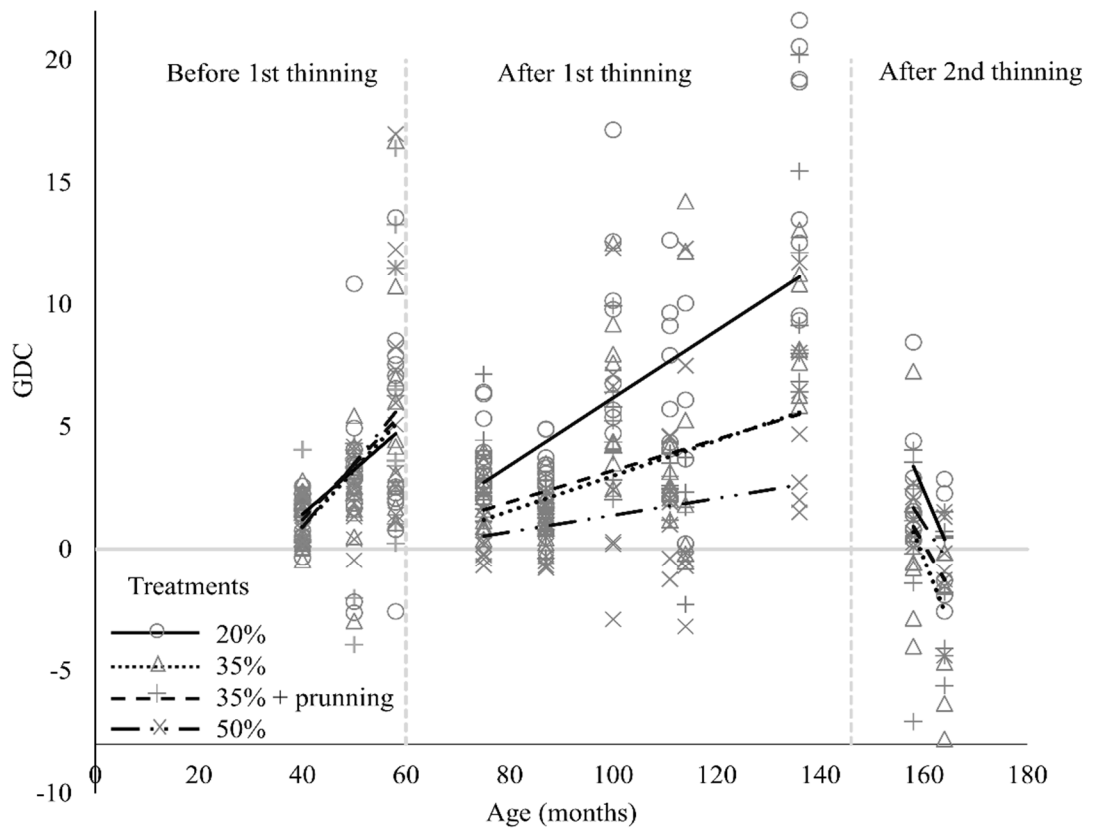
Figure 3.5. Development of the growth dominance coefficient (GDC) in *Eucalyptus* plantations in Brazil. The grey vertical dotted lines correspond to the thinnings.

3.3. DISCUSSION

We used three thinning-intensity experiments in northeastern Brazil to assess how stand heterogeneity and growth dominance develop with time in response to thinning interventions in *Eucalyptus* stands in one of the most productive regions of Brazil. As posed in our hypothesis, stand structural heterogeneity and growth dominance were reduced by thinning from below and this decrease was related to thinning intensity.

Congruent with prediction (i), there was a decrease in stand heterogeneity and growth dominance immediately after thinning. The more intense the thinning, the less heterogeneous the resulting stands, because more small trees were removed. Growth dominance was very close to zero at the beginning of every growth period. This is consistent with the open environment created by thinning and with trees experiencing little competition, thereby enabling them to grow fairly proportionally to their sizes (Binkley et al., 2006; Fernández and Gyenge, 2009).

The decrease in the level of heterogeneity as well as in their development through time was greater the more intense the thinning was (Figures 3.4 and 3.5), consistent with

our prediction (ii). Higher density, as related to more intense competition, has been shown to intensify asymmetric competition in the direction of a greater disproportional growth of the largest trees (Fernández and Gyenge, 2009; Bradford et al., 2010; Keyser, 2012; Trouvé et al., 2014).

Regarding the trends of stand heterogeneity and growth dominance through time, both of these variables tended to increase before and after the first thinning, consistent with our prediction (iii). The rate of increase in heterogeneity decreased after the first thinning, which was also evident for the growth dominance trend, except for the lightest thinning intensity (20% of basal area removal) in which the rate of increase was not different from before the first thinning was applied.

Increasing variability in tree size with age is commonly shown in monospecific even-aged stands (Binkley et al., 2002; Hakamada et al., 2015; Soares et al., 2016) as a result of different individual tree competitive abilities leading to different growth rates (Luu et al., 2013). Thus, the hereby evidenced differences in heterogeneity and growth dominance development across growth periods, and across thinning intensities within a growth period, can be explained by two interacting characteristics, both of which are directly related to individual tree growth rhythms: the variability in tree size at the beginning of the growth period and the level of competition.

Reducing the range in tree size also reduces the variability in the size-inherent ability of a tree to acquire resources and/or to use them more efficiently. For example, for *Pinus ponderosa* in Argentina, a difference in water use efficiency between the largest and the smallest trees was found at a site with a wide range in tree size, while no statistical difference was detected at a site with a narrower range in tree size (Fernández and Gyenge, 2009). The level of competition amplifies the effect of initial tree-size variability because competition can be very size-asymmetric and distance dependent in *Eucalyptus* monoclonal stands (Little et al., 2003; Boyden et al., 2008; Luu et al., 2013)

After the second thinning some trends deviated from what was expected in prediction (iii). Heterogeneity remained constant through time for most treatments, but showed a trend of decrease for the most intense thinning (50% basal area removal for the second time resulting in a stand density of around 220 trees ha^{-1}; Figure 3.4). Growth dominance decreased reaching negative values for all of the thinning intensities, which indicates that non-dominant trees grew slightly disproportionately faster than the dominant trees (e.g. the -7.78 GDC line in Figure 3.1). Therefore, contrary to prediction (iv), stand structural heterogeneity and growth dominance were not perfectly related, though this was revealed only after the second thinning.

This pattern after the second thinning, when heterogeneity and growth dominance generally remained the same or slightly decreased, can be explained by the level of competition in the remaining density. Tree density was reduced to around 620, 380 and 220 trees ha^{-1}, respectively, in the 20%, 35% and 50% basal area removal treatments. At this level of canopy openness, tree competition is likely to be relatively low, and consequently, competition-induced differences in tree growth rate would be minimal. Furthermore, *Eucalyptus* in Brazil are normally intensively cultivated (Gonçalves et al., 2004), which involves the removal of all understory competition. Therefore, in relatively open stands with very small initial variation in tree size, trees were able to grow fairly proportionally to their size (Binkley et al. 2006; Fernández and Gyenge 2009), thereby maintaining or even slightly reducing the level of heterogeneity.

This slight decrease in stand heterogeneity and the trends of decreasing growth dominance, reaching negative values, might have happened because retained trees belonging to intermediate dominance classes may present a greater relative response to thinning than the dominant ones (Forrester et al., 2013b). This can happen because both dominant and non-dominant trees benefit from the increased water and nutrient availability, whereas dominant trees already have the most access to light so increases in light availability should be more relevant to non-dominant trees (Forrester, 2013).

The same reasoning applies to growth dominance patterns. Besides the alleviated competition after thinning, an increase in the relative response of intermediate trees decreases the difference in growth between dominant and intermediate trees, which may reach a level in which the intermediate trees present greater relative growth rates than the dominant trees. For example, in the plot illustrated in Figure 3.2 with a GDC of 7.78, the biggest 25 trees, the second biggest 25 trees and the following 25 trees had a relative growth of 1.83%, 2.26% and 2.65%, respectively.

The reason for differing patterns for Gini's coefficient and the growth dominance coefficient after the second thinning is likely due to the absolute values of the increments. Growth dominance summarizes the distribution of the relative increment among the trees. Intuitively, its trend through time is directly related to Gini's coefficient, but this is not necessarily the case, for example, when there are very small increments. Very small increments that are heterogeneously distributed may reveal a high growth dominance, but they may not correspond to enough absolute increment to actually be reflected in a change in stand structural heterogeneity. This can be seen in our data. Even though all of the treatments presented a decreasing trend in growth dominance (Figure 3.5), only the

greater absolute tree growth (Figure 3.6) in the 50% basal area removal was high enough to cause perceptible changes in stand tree size-inequality.
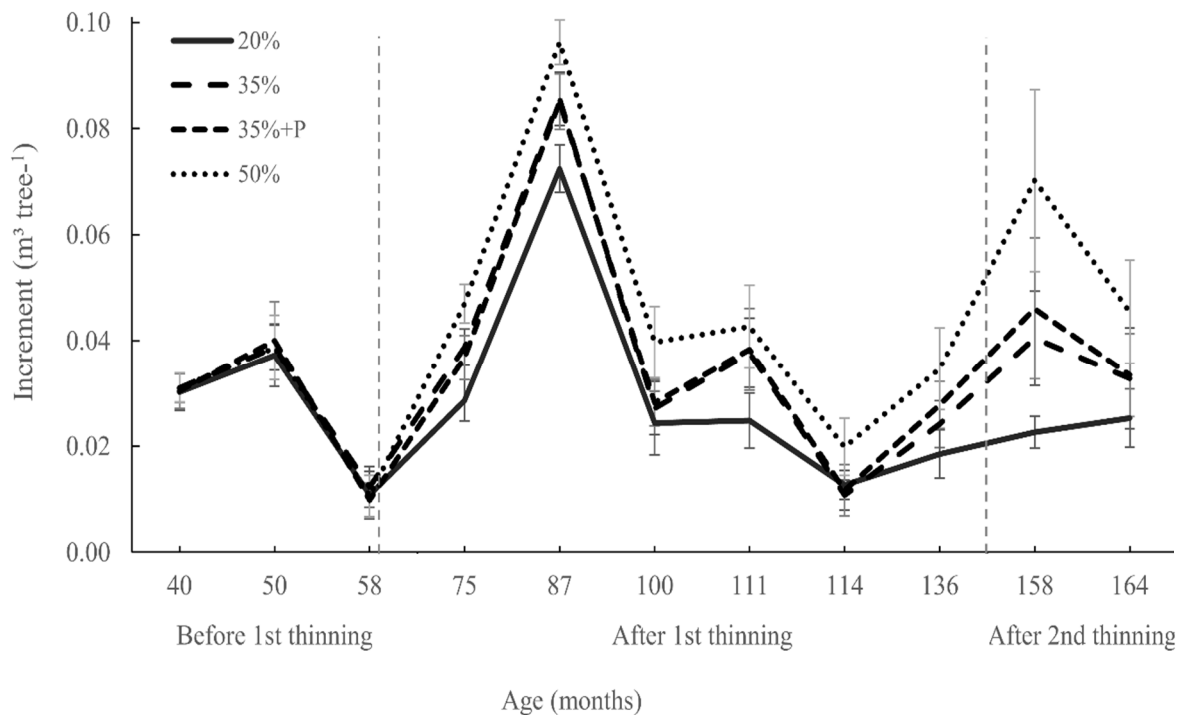

Figure 3.6. Tree mean increment (m³ tree⁻¹) through time in five thinning intensities in northeastern Brazil. Error bars' size is equivalent to one standard deviation.

High stand structural heterogeneity and growth dominance can have negative effects on stand productivity (Binkley et al., 2002; Stape et al., 2010; Aspinwall et al., 2011; Luu et al., 2013; Soares et al., 2016; Bourdier et al., 2016). Therefore, in addition to the well-known effect of thinning that results from greater resource availability and often greater resource use efficiency (Forrester, 2013), part of the response to thinning also depends on the stand structure prior to thinning (Forrester et al., 2013b). It may also depend on how thinning affects stand structure and how growth partitioning changes after the thinning intervention. Consequently, thinning can potentially improve the productivity of very heterogeneous monospecific or monoclonal plantations because it reduces tree-size inequality and the growth dominance of the biggest trees.

In conclusion, we found that thinning from below reduced the level of heterogeneity and growth dominance as well as their development through time, and that this decrease was directly related to thinning intensity. After the second thinning, both heterogeneity and growth dominance were reduced to very low levels, which remained fairly constant through time or even decrease for the more intense thinning intensity,

indicating stand homogenization due to a greater relative thinning response of the intermediate trees.

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APPENDIX 2

A2.1. Parameters estimates and goodness-of-fit statistics for the dominant height, total tree height and tree overbark stem volume equations. $\overline{R^2}$ = adjusted coefficient of determination; S_{yx} = residual standard error (m); * = single equation for the three sites whose parameters' estimates were taken from Nogueira et al (2015); nr = not reported.

Model	Site	Parameter	Estimate	$\overline{R^2}$	S_{yx}
Dominant height	A	α_0	3.5095	0.96	0.04
		α_1	-24.3844		
	B	α_0	3.5690	0.95	0.05
		α_1	-26.1667		
	C	α_0	3.6655	0.96	0.04
		α_1	-29.0767		
Total tree height	A	β_0	5.3029	0.97	0.04
		β_1	0.4838		
		β_2	-0.0033		
		β_3	-3.1357		
		β_4	0.1712		
		β_5	0.8671		
		β_6	-0.0309		
	B	β_0	-2.8436	0.97	0.04
		β_1	0.6057		
		β_2	-0.0045		
		β_3	0.6475		
		β_4	0.0084		
		β_5	0.6604		
		β_6	-0.0194		
	C	β_0	-1.5748	0.97	0.05
		β_1	0.9562		
		β_2	-0.0099		
		β_3	-0.6249		
		β_4	0.0548		
		β_5	0.9837		
		β_6	-0.0402		
Tree volume*	-	ϕ_0	−10.2886	0.98	nr
		ϕ_1	1.7512		
		ϕ_2	1.2352		

A2.2. Gini coefficient model's estimates of the intercepts and slopes for the thinning intensities (20%, 30%, 35%+pruning + 50% of basal area removal) across the growth periods (before 1st thinning, after 1st thinning and after 2nd thinning) and their pair-wise difference within growth period.

Period	Coeff.	Baseline	Contrasting treatments			
			20%	35%	35%+P	50%
Before 1st thinning	Intercept	20%	**16.875(*0.000*)**	-0.432	0.144	0.036
		35%	*0.606*	**17.294(*0.000*)**	0.576	0.468
		35%+P	*0.863*	*0.492*	**16.725(*0.000*)**	-0.108
		50%	*0.966*	*0.576*	*0.897*	**16.834(*0.000*)**
	Slope	20%	**0.101(*0.000*)**	0.004	-0.009	-0.005
		35%	*0.810*	**0.097(*0.000*)**	-0.014	-0.009
		35%+P	*0.617*	*0.459*	**0.111(*0.000*)**	0.004
		50%	*0.789*	*0.611*	*0.816*	**0.106(*0.000*)**
After 1st thinning	Intercept	20%	**12.228(*0.000*)**	1.772	1.317	2.398
		35%	*0.000*	**10.459(*0.000*)**	-0.455	0.626
		35%+P	*0.001*	*0.200*	**10.912(*0.000*)**	1.081
		50%	*0.000*	*0.080*	*0.004*	**9.830(*0.000*)**
	Slope	20%	**0.067(*0.000*)**	0.025	0.029	0.038
		35%	*0.001*	**0.042(*0.000*)**	0.003	0.012
		35%+P	*0.000*	*0.684*	**0.038(*0.000*)**	0.009
		50%	*0.000*	*0.113*	*0.239*	**0.029(*0.000*)**
After 2nd thinning	Intercept	20%	**9.935(*0.000*)**	2.768	2.759	3.376
		35%	*0.000*	**7.170(*0.000*)**	-0.009	0.609
		35%+P	*0.000*	*0.987*	**7.175(*0.000*)**	0.617
		50%	*0.000*	*0.252*	*0.246*	**6.556(*0.000*)**
	Slope	20%	**0.002(*0.951*)**	0.003	0.003	0.040
		35%	*0.737*	**-0.012(*0.678*)**	-0.011	0.027
		35%+P	*0.936*	*0.799*	**-0.001(*0.958*)**	0.037
		50%	*0.310*	*0.350*	*0.340*	**-0.038(*0.174*)**

Intercepts and slopes (obtained by resetting each combination of "*Thinning intenisy × Growth period*" as the baseline level in the model) and their respective P-values (in italic in parenthesis) for the t-test (H_0: coefficient = 0; H_1: coefficient $\neq$ 0) are given in the bold diagonals. The estimated difference in intercepts or in slopes (*Time × Thinning treatment i*) between the baseline level and *treatment i* within growth periods and their P-values are given, respectively, above and below the bold diagonal.

A2.3. Growth dominance coefficient model's estimates of the intercepts and slopes for the thinning intensities (20%, 30%, 35%+pruning + 50% of basal area removal) across the growth periods (before 1st thinning, after 1st thinning and after 2nd thinning) and their pair-wise difference within growth period.

Period	Coefficient	Baseline	Contrasting treatments			
			20%	35%	35%+P	50%
Before 1st thinning	Intercept	20%	**-5.882(0.072)**	2.480	1.963	3.681
		35%	0.561	**-8.361(0.012)**	-0.517	1.201
		35%+P	0.645	0.904	**-7.844(0.019)**	1.718
		50%	0.386	0.779	0.688	**-9.562(0.004)**
	Slope	20%	**0.183(0.017)**	-0.049	-0.043	-0.079
		35%	0.565	**0.232(0.003)**	0.006	-0.029
		35%+P	0.611	0.947	**0.226(0.004)**	-0.035
		50%	0.354	0.732	0.682	**0.261(0.001)**
After 1st thinning	Intercept	20%	**0.392(0.811)**	0.409	-0.134	0.103
		35%	0.750	**-0.017(0.992)**	-0.543	0.037
		35%+P	0.917	0.670	**0.526(0.746)**	0.029
		50%	0.731	0.978	0.652	**-0.051(0.975)**
	Slope	20%	**0.138(0.009)**	0.066	0.074	0.103
		35%	0.027	**0.072(0.169)**	0.008	0.037
		35%+P	0.014	0.789	**0.064(0.222)**	0.029
		50%	0.001	0.207	0.324	**0.034(0.512)**
After 2nd thinning	Intercept	20%	**9.874(0.047)**	2.086	4.159	3.902
		35%	0.755	**7.788(0.107)**	2.073	1.816
		35%+P	0.523	0.745	**5.714(0.210)**	-0.257
		50%	0.563	0.784	0.968	**5.971(0.223)**
	Slope	20%	**-0.499(0.109)**	0.047	-0.131	-0.169
		35%	0.912	**-0.545(0.066)**	-0.177	-0.216
		35%+P	0.748	0.654	**-0.368(0.175)**	-0.039
		50%	0.687	0.598	0.921	**-0.329(0.260)**

Intercepts and slopes (obtained by resetting each combination of "*Thinning intenisy × Growth period*" as the baseline level in the model) and their respective P-values (in italic in parenthesis) for the t-test (H$_0$: coefficient = 0; H$_1$: coefficient ≠ 0) are given in the bold diagonals. The estimated difference in intercepts or in slopes (*Time × Thinning treatment i*) between the baseline level and *treatment i* within growth periods and their P-values are given, respectively, above and below the bold diagonal.

5. CONCLUSÃO GERAL

A heterogeneidade estrutural por si própria, na ausência de diversidade genética e diversidade de espécies, teve um forte efeito negativo sobre a produtividade de madeira. Ambos os fatores espaçamento e genótipo tiveram efeito tanto na heterogeneidade quanto na produtividade.

O desbaste por baixo diminuiu a heterogeneidade estrutural e o efeito de dominância do crescimento, além de retardar o desenvolvimento de ambos. Quanto mais pesado o desbaste, mais pronunciadas foram estas diminuições.

Os resultados e discussões apresentados reforçam que a estrutura do povoamento tem grande influência na dinâmica do crescimento. No caso de povoamentos monoclonais, a menor produção de povoamentos mais desuniformes, mostrada no Capítulo 1, e o crescimento desproporcionalmente menor das árvores menores, mostrado no Capítulo 2, corroboram com as evidências de que o efeito negativo da heterogeneidade estrutural está relacionada à menor produção das árvores suprimidas.

Como discutido, estas árvores têm seu acesso a recursos restringido pelas árvores maiores, além de serem menos eficientes no uso dos mesmos. Assim, práticas que favoreçam o crescimento mais homogêneo das árvores e que evitem o desenvolvimento de forte dominância tem o potencial de permitir que os recursos do sítio sejam utilizados de forma mais eficiente pelas árvores, resultando em povoamentos mais produtivos. Por fim, métricas que descrevam a estrutura bem como a partição do crescimento ao longo do tempo constituem ferramentas úteis na caracterização dos povoamentos, auxiliando o manejo em direção não somente a maior produtividade, mas também a maior eficiência no uso de recursos.