

DISSERTATION

COMPETITION FROM NEIGHBORING TREES IN EUCALYPTUS
MONOCULTURE AND IN MIXED SPECIES NATIVE FOREST RESTORATION
PLANTATIONS

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ABSTRACT

COMPETITION FROM NEIGHBORING TREES IN EUCALYPTUS MONOCULTURE AND IN MIXED SPECIES NATIVE FOREST RESTORATION PLANTATIONS

Competition has been recognized as a crucial factor in determining stand structure and productivity. However, competition is not a simple pattern. Its intensity and importance vary with structures of neighboring tree size and composition, and nutrient gradients. Our studies examined the influence of neighborhood uniformity on growth of individual trees in Eucalyptus monoculture, and competition between pioneer and non-pioneer species in mixed native species restoration plantations by developing a number of alternative neighborhood growth models. Our analyses showed that neighborhood uniformity of tree sizes had significant effects on growth of individual clonal Eucalyptus trees and these effects increased with increasing age of stand because stand and neighborhood tree size became less uniform with age. For competition from pioneer trees to non-pioneer trees, competition from neighboring trees had strong effects on the growth of individual non-pioneer trees, and the intensity of competition from neighboring trees varied with focal tree species guild and degrees of silviculture interventions. For example, non-pioneer legumes experienced competition as a function of neighboring tree sizes and distances only. Non-pioneer non-legumes experienced competition as a function of neighboring tree sizes and distances, and also by the identity of neighboring species guilds. The non-pioneer non-legumes experienced stronger competition in the intensive silviculture treatment, probably resulting from the neighboring species guild of

pioneer non-legumes, unlike the non-pioneer legumes. Although intensive silviculture initially enhanced forest stand productivity (both density and tree size), strong competition from fast-growing lowered the later growth of individual non-pioneer trees. Our analyses suggested implications to: (i) increase and maintain stand uniformity to increase stand stem productivity and quality; and (ii) control strong, even exclusive completion in some cases from pioneer trees to non-pioneer trees through matching species to be mixed and managing their abundance.

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CHAPTER 1

INTRODUCTION

Understanding factors affecting growth of individual trees is central to both forest ecology and forest management (Canham et. al. 2004, Uriarte et. al. 2004, Boyden et. al. 2008). The growth of trees depends on obtaining resources from the environment (Binkley et. al. 2004), and the success of each tree in obtaining resources typically depends on the level of competition with neighboring trees (Grace and Tilman 1990, Wilson and Tilman 1991). Competition for limited resources likely intensifies with increasing neighboring tree sizes and density (Bonan 1988, Weiner 2001, Weiner and Damgaard 2006), but intensity of competition is often modified by neighboring structure and focal trees' physiology and morphology (Schwinning and Weiner 1998, Choler et. al. 2001, Callaway et. al. 2002, Boyden et. al. 2005, 2008). The modification in competition from neighbors may influence growth of focal trees and species coexistence, thus stand productivity and stand species populations.

Competition for limited resources between trees is usually asymmetric, with larger trees obtaining disproportionately more resources, suppressing smaller trees (Schwinning and Weiner 1998, Weiner 2001). Asymmetric competition increases the variation in tree sizes within stand, creating classes of dominant and suppressed trees. Individual trees adjust to neighbors and environments by modifying morphology and physiology, or shifting resource allocation (Schwinning and Weiner 1998, Boyden et. al. 2008). These responses may reduce or increase competition from neighboring trees, further affecting growth of individual trees and stand dynamics. The links between neighborhood structure and competition needs further exploration as a basis for

understanding how neighborhood structures (tree size and species composition) modify intensity of competition (Schwinning and Weiner 1998).

Spatially explicit models/neighborhood models of growth of individual trees offer several advantages over the other approaches to studying plant interactions (Radosevich 1988). Neighborhood models capture the demography of component tree species (Pacala et. al. 1996, Law and Dieckmann 2000, Canham et. al. 2004); provide a tool for synthesizing competition processes into spatial and temporal predictions of system dynamics (Gratze et. al. 2004, Canham et. al. 2004); and improve understanding of competition processes in forest stands (Weiner 1984, Daniels et. al. 1986, Wagner and Radosevich 1991, Canham et. al. 2004). We adopted and extended neighborhood models developed by Canham et. al. (2004) because this flexible approach to neighborhood modeling can be used to account for individual tree growth in response to focal tree size and neighborhood competition (e.g. Uriarte et. al. 2004, Coomes et. al. 2007, Boyden et. al. 2008, Baribault et. al. 2011).

My dissertation examined the influence of neighborhood tree size uniformity to growth of individual trees of Eucalyptus in a clone Eucalyptus plantation, and competition from pioneer trees to non-pioneer trees in mixed native species restoration plantations by developing a number of alternative neighborhood models of growth of individual trees. The dissertation includes two studies. One was conducted in a plantation stand of more than 10,000 clonal Eucalyptus trees in Brazil. Chapter 2 investigated effects of neighborhood uniformity on growth of individual trees, this chapter titled “Neighborhood uniformity influences growth of individual Eucalyptus trees”. The second project study (chapter 3) examined interactions between species guilds under different

silvicultural interventions (regular/traditional and intensive treatments) in a 5 ha experimental trail of 20 mixed native species restoration plantations in Brazil. Chapter 3 was entitled “Competition between pioneers and non-pioneers species in tropical forest restoration”.

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CHAPTER 2

NEIGHBORHOOD UNIFORMITY INFLUENCES GROWTH OF INDIVIDUAL EUCALYPTUS TREES

Summary

We used neighborhood models to test and quantify the influence of uniformity on growth of individual trees, in association with the effects of tree size and neighborhood competition. We modeled growth of 8800 focal trees in a 9 ha stand by Bayesian methods to test our hypothesis and quantify the effects of size, and neighborhood competition and uniformity. Our analyses showed that the size of focal trees was important, and this size effect was moderated by the effects of neighborhood competition and the uniformity of tree sizes within the neighborhood. The importance of the size of the focal tree was evident in the maximum potential growth of $15.6 \text{ kg month}^{-1}$ for the optimal trees, declining $0.16\text{-}5.3 \text{ kg month}^{-1}$ for actual tree sizes in the stand. Neighborhood competition lowered potential growth of focal trees by 10-42%, for a 26% average effect across the stand. For a given size focal tree and a given level of neighborhood competition, the uniformity of tree sizes within the neighbor influenced potential growth by -2% (very uniform neighbors) to -10% (for heterogeneous neighbor sizes), with a stand average of -4.3% and this trend increases as non-uniformity increases. Small trees were more sensitive to neighborhood competition, and big trees were more sensitive to neighborhood uniformity. Our analysis is the first analysis using neighborhood model to test and quantify the effect of neighborhood tree size structure/neighborhood uniformity

on growth of individual trees. Our results suggested some foundations for creating and maintaining a highly uniform stand of *Eucalyptus* clonal plantations.

Keywords: Bayesian, Eucalyptus clone, Growth of individual trees, Neighborhood model, Neighborhood competition, Neighborhood structure/uniformity.

1. Introduction

Understanding of the factors that control stem growth is central to forest ecology (Uriarte et. al. 2004, Canham et. al. 2006, Grams and Andersen 2007, Coomes et. al. 2007), providing quantitative insights into biomass and stem quality in intensively managed plantations (Boyden et. al. 2008; Stape et. al. 2010; Aspinwall et. al. 2011). The growth of trees depends on obtaining resources from the environment (Binkley et. al. 2004), and the success of each tree in obtaining resources typically depends on the level of competition with neighborhood trees (Grace and Tilman 1990, Wilson and Tilman 1991). Competition for resources likely becomes more severe as the number and size of nearby trees increases (Bonan 1988, Weiner 2001; Canham et. al. 2004, Uriarte et. al. 2004, Boyden et. al. 2005, 2008). The positive feedbacks of competition typically leads to increasing variance of tree sizes within a stand (Bonan 1988, Weiner 2001), and the increasing variation in tree sizes may alter both tree-to-tree competition and stand-level production.

Competition among individuals has been recognized as a key factor in variation of growth rates, leading to variation in tree sizes within stands (Weiner 1985, 1988, Bonan 1998, 1991, Weiner and Thomas 1986, Hara and Wyszomirski 1994, Schwinning and

Weiner 1998, Weiner et. al. 2001). The mechanisms giving rise to the patterns of competition are not clear (Schwinning and Weiner 1998, Weiner et. al. 2001). The relative importance of features such as “size-asymmetry” (Weiner 1990, Schwinning and Weiner 1998), “size-symmetry” (Lundqvist 1993), and “neighborhood competition” (Bonan 1991) remain controversial. In crowded, intensively managed *Eucalyptus* plantations, Boyden et. al. (2008) examined the effects of competition on stem growth of individual trees of a single clonal genotype, and from seeds. They found that a medium sized focal tree (75kg wood mass) from the heterogeneous size clone treatment and the same size tree from seed origin responded differently to the same level of neighborhood competition. When standardized neighborhood competition index was less intense than 0.5, the clone-origin trees grew better than the seed-origin trees of the same size did, but this pattern reversed when competition was stronger. Binkley et. al. (2010) reported declining stand-level productivity with increasing variation in tree sizes within monoculture stands of *Eucalyptus*, as a result of declining efficiency of resource use (defined as stem growth per unit of light absorption). The pattern of uniformity and growth is clear, but the mechanisms remain largely unknown.

Uniformity of a stand or a group of trees can be characterized in a variety of ways, such as the standard deviation or coefficient of variation (CV). Smaller CV's represent more uniform stands and/or groups. The CV or uniformity is not a mechanistic factor that affects growth of tree or stand, it is only a statistical description of a stand or group of trees. The influence of stand uniformity reported by Boyden et. al. (2008) and Binkley et. al. (2010) was detected in a set of experiments expressly designed to develop a wide range of uniformity within clonal plots that would typically be found in seed-

origin stands. Would the influence of the uniformity of neighborhood trees be detectable within an operational plantation of *Eucalyptus*?

We developed spatially explicit models of individual tree growth as a function of the size of focal trees, the sizes and distances of neighboring trees, and the uniformity of sizes of trees in the neighborhood. Our neighborhood models were extensions of the models developed by Canham et. al. (2004). This neighborhood model approach is very flexible and can be used to capture other effects to stem growth of individual trees that are not the effects of size and neighborhood competition (e.g. Uriarte et. al. 2004, Coomes et. al. 2007, Boyden et. al. 2008, Baribault et. al. 2011).

We developed the spatially explicit models for nearly 9,000 focal trees in a 9-ha stand with more than 10,000 trees to test the hypothesis that the growth of individual trees declines as the variance in size among neighboring trees increases. The effect of uniformity was tested by modeling the influence of focal tree size, the sizes and distances to focal tree of neighboring trees, and the uniformity of size of neighboring trees.

2. Materials and methods

2.1. Site description

This stand of *Eucalyptus* plantation is located in Aracruz, Espirito Santo, Brazil (40°05W, 19°49 S), on an Ultisol soil with 37% clay and pH=4, at the altitude of 12m. The annual average temperature is 23.6°C (not different between the dry season - 22.3°C and the wet season - 24.4°C). Rainfall averages 1360 mm yr⁻¹, with double the rainfall in the wet season as in the dry season (870mm and 490 mm, respectively). The potential evapo-transpiration is 1200 mm yr⁻¹. This stand was established in March 2001 with

Clone # 3918 at a density of 1100 trees ha⁻¹ (3x3m spacing). The objective of this plantation was to create a uniform, highly productive stand.

2.2. Data collection and allometry

All trees in the stand were mapped and measured for diameters at breast height (DBH) and total heights (HT) at the ages of 17th month and 48th month. The canopies of Eucalyptus trees are usually fully developed by one to one and half years after planting and this interval spans the period of maximum stand-level growth (Stape et. al. 2010).

Stem biomass was calculated as:

$$M=0.004*(DBH^{1.959})*(HT^{1.512}) \quad (n = 128, r^2 = 0.98) \quad (1)$$

where M is stem mass in kg, DBH is in cm at 1.3m of stem height and HT is total tree height in meter.

2.3. Model development and hypotheses

We modeled average growth per month of stem biomass of 8816 focal trees for 21 months (age 17- 48 months) in the 9 ha stand. The model is an extension of one developed by Canham et. al. (2004) and successfully applied to analyze growth of individual trees of both temperate species (e.g. Papaik et. al. 2006, Baribault and Kobe 2011) and tropical species (e.g. Uriarte et. al. 2004). Boyden (Boyden. et. al. 2005, 2008) used this neighborhood model to analyze competition effects of growth of individual *Eucalyptus* in Brazil and Hawaii. We therefore adopted and modified this model with four terms (1) Maximum potential growth (Maxgr), (2) initial focal tree size (stem), (3) neighborhood competition (based on size and distances of neighbors) and (4) the uniformity of sizes among neighborhood trees. The last 3 terms were developed as scalars ranging from 0 to 1.

$$\text{Growth} = \text{Maxgr} \times \text{Size Effect} \times \text{Competition effect} \times \text{Uniformity effect} \quad (2)$$

where Growth is kg month^{-1} , Maxgr is maximum growth in kg month^{-1} (the expected growth at the optimal size – X_0 value as defined in the section of size effect); Size effects (S) is focal tree size effects, the multiplication of maximum growth (Maxgr) and S indicates a potential growth of an individual tree (without competition); Competition effect (C) and uniformity effects (U) are negative exponential functions (scaling from 0 to 1). We developed a set of 9 alternative models to test our hypothesis. Each model represents a set of factors, details of factor testing are given in table 2.1.

Size effects (S) on growth– Growth of a tree typically depends strongly on initial tree size (Bella 1971, Hegyi 1974, Canham et. al. 2004, Uriarte et. al. 2004, Boyden et. al. 2008). We used a lognormal function to characterize the size effects:

$$S = \exp \left[-0.5 * \left\{ \frac{\ln \left(\frac{\text{Mass}_k}{X_0} \right)}{X_b} \right\}^2 \right] \quad (3)$$

where *Mass* is stem mass, X_0 represents the stem mass at which maximum growth rate is expected to occur based on data, and X_b is breath of the function. This function is flexible and both theoretically and empirically supported (Zeide 1993, Uriarte et. al. 2004).

Neighborhood competition effects – neighborhood competition has long been recognized as a main driver in structuring growth of individual trees. A number of neighborhood indices was developed to investigate effects of neighborhood competition on growth of individual trees (e.g, Bella 1971, Hegyi 1974, Lorimer 1983, Wimberly and Bare 1996, Wagner and Radosevich 1998, Vettenranta 1999, Berger and Hildenbrandt 2000, Canham et. al. 2004, Uriarte et. al. 2004), including *Eucalyptus* trees (Boyden et. al. 2005, 2008). All the indices developed in these studies were size- and distance-dependent, either a function of focal tree size along with neighboring sizes and distances,

or with only the size and distances of neighbors. In this study we adopted the neighborhood competition index that was previously shown to effectively represent neighborhood competition on biomass stem growth of Eucalyptus (Boyden et. al. 2008).

The formula of neighborhood competition index (NCI), is given by:

$$NCI_k = \sum_i^n \frac{Mass_{ik}^\alpha}{d_{ik}^\beta} \quad (4)$$

where $Mass_{ik}$ is neighboring tree stem mass number i^{th} of focal tree number k^{th} , d_{ik} is distance of neighboring tree number i^{th} to focal tree number k^{th} , n is total number of neighboring trees in a fixed radius; α and β are estimated by the analyses and determine the shapes of the effects of the stem volume (α) and the distance (β) to the neighbor on NCI. The index of NCI was translated into its effects on growth of focal tree by using a negative exponential function of the NCI:

$$C1 = \exp\left(-C * \frac{NCI_k}{NCI_{max}}\right) \quad (5)$$

where $C1$ is neighborhood competition effects, NCI_k is the neighborhood competition index for focal tree k^{th} and NCI_{max} is the maximum value of NCI for all focal trees in the stand. The use of the ratio of NCI_k to NCI_{max} standardizes the neighborhood effects and facilitate comparisons across focal trees in the stand.

Uniformity effects – our analysis of the effects of neighborhood structure to a focal tree tests the hypothesis that greater stand uniformity leads to greater growth by either increasing resource-use efficiency or shifting allocation to stem growth (Binkley et. al. 2010, Ryan et. al. 2010, Stape et. al. 2010). We expected that greater neighborhood uniformity would lead to less influence on the stem growth of individual trees for any given NCI. We characterized uniformity as the Coefficient of Variation (Weiner et. al.

1986, Binkley et. al. 2010); small CVs indicate more uniform sizes among neighbors.

The CV of the Neighborhood for each focal tree was calculated as:

$$CV_k = \frac{\sqrt{\frac{1}{n} \sum_{i=1}^n (Mass_{ik} - \overline{Mass}_k)^2}}{\overline{Mass}_k} \quad (6)$$

where $Mass_{ik}$ is stem mass of neighboring tree number i^{th} of focal tree number k^{th} , \overline{Mass}_k is mean neighborhood mass of focal tree k^{th} in a fixed radius, n is total number of neighboring trees in a fixed radius. Neighborhood CV/Neighborhood uniformity is translated into its effects on growth by using a negative exponential function of CV:

$$U1 = \exp\left(-U * \frac{CV_k}{CV_{max}}\right) \quad (7)$$

where $U1$ is neighborhood uniformity effects, CV_k is a neighborhood coefficient of variation of focal tree k and CV_{max} is a maximum value of CV for all focal trees in the stand. Similar to the NCI ratio the ratio of CV_k to CV_{max} standardizes and facilitates comparisons across focal trees in the stand.

We also added focal tree sizes (at 17 months), scaled by λ to $C1$ and by γ to $U1$, to test whether the effects of neighborhood competition and uniformity are dependants on focal tree sizes. The forms of the effects of competition and uniformity are:

$$C2 = \exp\left(-C * Mass_k^\lambda * \frac{NCI_i}{NCI_{max}}\right) \quad (8)$$

$$U2 = \exp\left(-U * Mass_k^\gamma * \frac{CV_k}{CV_{max}}\right) \quad (9)$$

where $C2$ and $U2$ are neighborhood competition and neighborhood uniformity effects, respectively; and λ and γ are estimated from the analyses. If λ and γ are negative, small trees are more sensitive to neighborhood competition and uniformity than large trees, and vice versa.

To investigate the role of neighborhood radius on competition and uniformity indices, we fitted all the models for the fixed radii of 4, 5, 6, 7, and 8 meters to select the best radius. We limited to the radius of up to 8 meters only, because this plantation was of high density, each focal tree was surrounded by an average of 21 neighbors (ranging from 14 to 24 neighbors).

2.4. Parameter estimation and model selection

We used the program R (R development Core Team 2010) to search for and calculate neighboring trees and distances for and Coefficients of variation (CV) for each focal tree, and package R2jags and JAGS 3.1.0 (Just Another Gibbs Sampler) to estimate parameters. To account for heteroscedasticity and non-normality in the residuals, we used a log-transform of growth to fit the models (Boyden et. al. 2008) and uninformative priors for parameter estimation to maximize likelihood. We fitted a total number of 41 models, the simplest model required estimation of 3 parameters and a variance, and the most complex model required estimation of 9 parameters and one variance. The definitions of parameters and their prior distributions are given in table 2.2.

First, we ran all the models with 10,000 iterations, with the burn in of first 5,000 iterations. We used Rhat value to assess the convergence of models (Gelman and Hill 2007). If any parameter of any model has Rhat >1.05, this model had not converged, and we then increased iterations to 20,000. If Rhat values remained above 1.05 after fitting with the 20,000 iterations, we modified the model (both parameters' priors and equations). We also calculated Akaike's Information Criterion (AIC) to use for model selection and adjusted correlation (R^2 squared) of predicted growth versus observed growth to determine goodness-of-fit.

We used the method of information theory to guide the selection of the best model from a set of candidate models. The principle to be used for this method is that the model that loses the least information relative to the truth is the best model among a set of models to be considered (Burnham and Anderson 2001). There are a number of criteria for selection of the best model from a set of candidate models, for example, Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), and Deviance Information Criterion (DIC). In this study, we used AIC to select the best model from our candidate models. AIC entails ranking models based on the information lost when using a model to approximate the truth, and using the principle of parsimony, models are penalized for having more parameters. Lower AIC values indicate stronger model performance (Burnham and Anderson 2001).

3. Results

3.1. Model selection, parameter estimation and hypothesis testing

All models and their parameters converged well (Rhat less than 1.05), with AIC values ranging from 1533 (biggest value, least information) to 1120 (smallest value, highest information). The R^2 values varied only 3% (ranging from 0.43 to 0.46) among the models and across the neighborhood radii (Table 2.3).

Radius strongly influenced the models; as the radius increased, AIC value dramatically decreased, from 1305 (smallest AIC of the radius of 4 meters) to 1120 (smallest AIC of the radius of 8 meters, Table 2.3). AIC decreased as the radius increased, but it leveled off as the radius reached to 7 meters (Table 2.3). We also found that the parameters of the best model of the radii of 7 meters (results not shown) and 8

meters were very slightly different and R^2 s were almost stable. We selected the radius of 8 meters for further modeling.

Both neighborhood competition and uniformity affected stem growth of focal trees, and neighborhood competition had a stronger effect than neighborhood uniformity. Adding the term of neighborhood uniformity (U1 or U2) into the simplest, basic model (including only the term of size effects) decreased AIC values from 1532 to 1505 (Table 2.3). Adding the terms of the effects of neighborhood competition dropped AIC more dramatically from 1532 to 1125. Adding the term of the effects of neighborhood uniformity to this model, AIC value decreased slightly (but significantly) to the smallest value of 1120.

We selected the model number 9 of the radius of 8 meters as the most parsimonious model, with the smallest AIC value of 1120 and highest R^2 of 0.46. This model is one of the best goodness of fit and the most complex model from 9 alternative candidate models. This model includes the terms of size effects, competition effects and uniformity effects and all of the 9 parameters (details in Table 2.4).

Our analyses supported our hypothesis that the neighborhood uniformity significantly influenced to stem growth of individual trees, beyond the stronger effects of focal tree size and neighborhood competition. We also observed that neighborhood radius significantly decreased AIC, improving the performance of the models, thus neighborhood competition was size- and distance-dependent.

3.2. Effects of Size (stem biomass) on potential growth

Focal tree size and stem growth were strongly correlated; the correlation coefficient (R^2) of the simplest model (size effects only) was 0.43. Increasing the number

of terms in the model by adding the effects of neighborhood competition and uniformity increased R^2 slightly to the maximum R^2 of 0.46 (Table 2.3). Stem growth of individual trees exponentially increased with tree size (Fig. 2.1a), peaked at the maximum growth of $15.6 \text{ kg month}^{-1}$ at the tree size of 346 kg, after that stem growth gradually decreased even as tree size increased. The reduction in the maximum stem growth, caused by focal tree size, ranged from 70% to 96% (Fig. 2.1b), leading to a large variation in potential stem growth. The potential stem growth of individual trees ranged from $0.16 \text{ kg month}^{-1}$ to $4.75 \text{ kg month}^{-1}$ (Fig. 2.1c).

3.3. Effects of neighborhood competition (Effects of neighboring tree size and distance)

Scales of neighboring size and distance strongly influenced neighborhood competition index (α and β from the best model of each radius). Alpha (α) increased from 2.13 (radius of 4 meters) to the peak of 2.5 (radius of 7 meters) and then slightly decreased to 2.3 (radius of 8 meters), but β dramatically decreased from the maximum value of 4 as the radius of 4 meters to the minimum value of 0.33 as the radius of 8 meters (Fig.2.2), indicating neighborhood competition index increased as the radius increased; the neighborhood competition index depended strongly on neighboring tree sizes and distances to focal tree. The values of α , the scale of neighboring tree size, were always larger than 2 for all radii tested, indicating neighboring tree size had strong, asymmetric influences on focal tree growth (Canham et. al. 2004).

Smaller trees were more sensitive to neighborhood competition. For example, neighborhood competition reduced a maximum of stem growth of a large tree of 15 kg (~10 cm dbh) about 30% as neighborhood competition was the most severe, while the

same degree of neighborhood competition reduced stem growth of a small tree of 0.5 kg (~3 cm dbh) by almost 70% (Fig. 2.3a).

We used α and β from the best model to predict and map neighborhood competition index and neighborhood competition effects for all focal trees in the stand. The standardized competition index ranged from 0.2 to 1 (Fig.2.3b). This index was translated into neighborhood competition effects (Fig. 2.3c). The Fig. 2.3c shows that variation in NCI altered potential stem growth of individual trees from 10% where the competition was the least severe to the maximum of 42% where the competition was the most severe.

3.4. Effects of neighborhood uniformity

One of the goals of the clonal plantation was to create a high uniformity stand, but uniformity varied substantially across the stand. The smallest value of standardized neighborhood uniformity was of 0.2 – the most uniform and the biggest value was of 1 – the least uniform as illustrated in Fig.2.4. Neighborhood uniformity significantly influenced stem growth of focal trees, though the effects were weaker than neighborhood competition effects. Focal tree size was also sensitive to the effects of neighborhood uniformity, but it was opposite to the effects of neighborhood competition: larger focal trees are more sensitive to neighborhood uniformity (Fig. 2.5a). Low neighborhood uniformity decreased the growth of small tree (0.5 kg) by about 2%, compared to a reduction of more than 10% for large tree (15 kg) . We used parameters from the most parsimonious model and neighborhood uniformity index to predict the influence of the uniformity on the stem growth of all the focal trees in the stand as illustrated in Fig.2.5b. The Fig. 2.5b shows differences in uniformity altered growth by 2% where was higher

uniform to almost 10% where was less uniform. Integrating across the entire area of the stand, the total loss in potential growth as a result of imperfect uniformity was 4.3 % (weighted by potential growth – total potential growth of the stand: 26,192 kg month⁻¹; total loss of the stand due to imperfect uniformity: 1,150 kg month⁻¹).

4. Discussion

Our analysis supported the hypothesis that neighborhood uniformity significantly influences to growth of individual trees, beyond the strong effects of focal tree size and neighborhood competition. Our best neighborhood model with the term of neighborhood uniformity has goodness of fit – R^2 of 0.46, which is higher than any R^2 of any neighborhood model developed by Boyden (Boyden et. al. 2008) for *Eucalyptus* trees, which did not included neighborhood uniformity. This is first study using neighborhood model to test and quantify the effects of neighborhood uniformity on growth of individual trees in association with the other effects of focal tree sizes and neighboring tree sizes and distances.

Our results of neighborhood analysis on the roles and effects of focal tree size on growth of individual trees are consistent with those observed by Canham et. al. (2004) for temperate tree and by Uriarte et. al. (2004) for tropical trees: the growth of individual trees was strongly depended on their initial size – growth increases with tree size, then peaks at optimal tree size (X_0 value), after that growth decreases even tree size increases. The maximum estimated potential growth was of 15.6 kg month⁻¹ at the optimal tree size of 346 kg (X_0 value). The maximum potential growth dramatically declined as a result of size effects, ranging 70% - 96%, leading potential growth of individual tree widely

ranging 0.66 - 4.75 kg month⁻¹, averaging 2.97 kg month⁻¹, equaling ~ 40Mg ha⁻¹ year⁻¹. The annual potential growth of 40 Mg ha⁻¹ year⁻¹ is very close to the current annual increment (ages 1.5 -6.0 years) – a biological productivity, estimated by Stape (Stape et. al. 2010). Tree size at which the maximum estimated potential growth occurred was 346 kg – X0 value, this value is over 20 times larger than the biggest tree size at 17th month (15 kg) and equals to the size of a 6 years old tree (see Stape et. al. 2010 and Binkley et. al. 2010). This value would not be both biologically and practically supported for a Eucalyptus tree of 17 months old. One of advantages of Bayesian method (used in this study) is that it can combine existing knowledge with data to yield more scientific meaningful parameters. However we did not have any existing information on maximum potential growth and tree size in this period for estimation of parameters, we used uninformative priors. In this case, Bayesian method is similar to the maximum likelihood method. Therefore, the value of X0 could be overestimated, likely leading to underestimating the effects of neighborhood competition and uniformity on growth of individual trees.

Our analysis indicated neighborhood competition had strong effects on the potential growth of individual trees. Declines in potential growth caused by neighborhood competition effects ranged 11-42%, or about 26% if averaged cross over the stand. The pattern of competition effects on growth of individual trees from our analyses is consistent with the findings of Boyden et. al. (2008): neighborhood competition had stronger effects on growth of small trees than large trees. The biggest tree of 15 kg at 17th month in our study was significantly sensitive to neighborhood competition, but the biggest tree of 125 kg at 44th in Boyden's study had little or no sensitivity to

neighborhood competition (Boyden et. al. 2008). This may be a result of strong advantage of size effects and strongly asymmetric competition, leading to increasing size variation. Tree size distribution shifted from almost normal (a little right skew), more uniformity at 17th month to strong left skew distribution of tree sizes at 48th month– less uniformity (data not shown). This pattern was matched with Weiner’s findings for uniform spatial distribution of plants (Weiner et. al. 2001), suggesting that size variation would increase with density and age in a size asymmetric competition environment, such as this study.

Although neighborhood uniformity had the least effects on growth of individual tree among the effects of size and neighborhood competition, this effect would be more intense as the stand becomes older, usually less uniform as results of tree size advantages and asymmetric neighborhood competition. Ryan et. al. (2010) tested the effects of stand uniformity by creating a series of stands which were different in stand uniform degrees, and concluded that stand uniformity could reduce stand stem growth up to 14%, due to lower efficiency of light use (stem growth per unit of light absorbed). This reduction in stand-level growth was almost 3 times bigger than our estimated effects of neighborhood uniformity, probably owing to the much higher degree of uniformity across our plantation than in the intentionally low-uniform treatments examined by Ryan et. al.(2010). Our analyses showed interesting results that focal trees were sensitive to neighborhood uniformity, but larger trees were more sensitive to neighborhood uniformity than small trees. Binkley et. al. (2010) reported that dominant trees capture more resources and use them more efficiently and Ryan et. al. (2010) concluded that uniform stands allocate more resources to stem growth than less uniform stands. In this case, although

larger/dominant tree may capture more resources and utilize resources more efficiently, it may allocate more resources to its canopy and underground production compared to the same size of that tree in high uniform neighborhoods. Dominant/large tree allocates more resources to its canopy production would be likely due to unstressed development of its canopy. Canopy of dominant tree might not be suppressed by canopies of neighboring lower trees, it allocates more resources to develop its canopy as much as it can to capture more resources. On the other hand, because of its large canopy and dominance over its neighbors, dominant/large tree may suffer more from physical forces such as wind-throw and rains, leading to requirements of allocating more resources to the underground to support its large canopy. Consequently it would allocate less resource for stem growth than those which have same size living in homogeneous neighbors.

Overall if living in a heterogeneous neighborhood, a small tree is more sensitive to neighborhood competition, while big tree is more sensitive to neighborhood uniformity, that all reduce growth of individual trees. Therefore it is necessary to create stand uniformity from the beginning and then more importantly is to maintain it during the course of stand development. Some silviculture treatments should be considered including site preparations and altering planting density. Site preparation including fertilization can promote homogeneous site condition across stand, thus would facilitate size uniformity before the onset of competition, after that variation in tree sizes is mainly controlled by neighborhood competition, which is determined by planting density and tree sizes. Lower density would keep neighborhood competition low and less asymmetric, thus maintaining stand more uniform.

Table 2.1. Models and factors to be tested

| Model | Max growth | Factor Testing | | | | Summary | |
|-------------------------|------------|------------------|-------------|----|-------------|---|---|
| | | Size effects (S) | NCI effects | | NUI effects | | |
| | | | C1 | C2 | U1 | | U2 |
| 1. Growth =Maxgr*S | ✓ | ✓ | | | | Size effects | |
| 2. Growth=Maxgr*S*U1 | ✓ | ✓ | | | ✓ | Size and Uniformity without sensitivity | |
| 3. Growth=Maxgr*S*U2 | ✓ | ✓ | | | | ✓ | Size and Uniformity with sensitivity |
| 4. Growth=Maxgr*S*C1 | ✓ | ✓ | ✓ | | | | Size and Competition without sensitivity |
| 5. Growth=Maxgr*S*C2 | ✓ | ✓ | | ✓ | | | Size and Competition with sensitivity |
| 6. Growth=Maxgr*S*C1*U1 | ✓ | ✓ | ✓ | | ✓ | | Size, Competition and Uniformity without sensitivity |
| 7. Growth=Maxgr*S*C2*U1 | ✓ | ✓ | | ✓ | ✓ | | Size, Competition with sensitivity and Uniformity without sensitivity |
| 8. Growth=Maxgr*S*C1*U2 | ✓ | ✓ | ✓ | | | ✓ | Size, Competition without sensitivity and Uniformity with sensitivity |
| 9. Growth=Maxgr*S*C2*U2 | ✓ | ✓ | | ✓ | | ✓ | Size, Competition and uniformity, both with sensitivity |

Table 2.2. List of parameters and their distributions which they were developed

| Parameters | Definition | Distributions |
|-----------------|---|------------------|
| 1. $\ln.\maxgr$ | log transform of Maximum growth | Normal (0,.0001) |
| 2. C | Coefficient of Neighborhood effect | Uniform (0,5) |
| 3. U | Coefficient of Uniformity effect | Uniform (0,5) |
| 4. $X0$ | Stem biomass at which Maxgr occurs | Normal (0,.0001) |
| 5. Xb | Breath of the function | Normal (0,.0001) |
| 6. α | Shape of effect of neighboring size on focal | Uniform (0,5) |
| 7. β | Shape of effect of neighboring distance to focal growth | Uniform (0,5) |
| 8. λ | Sensitivity of focal size to neighborhood competition | Uniform (-5,5) |
| 9. γ | Sensitivity of focal size to neighborhood uniformity | Uniform (-5,5) |

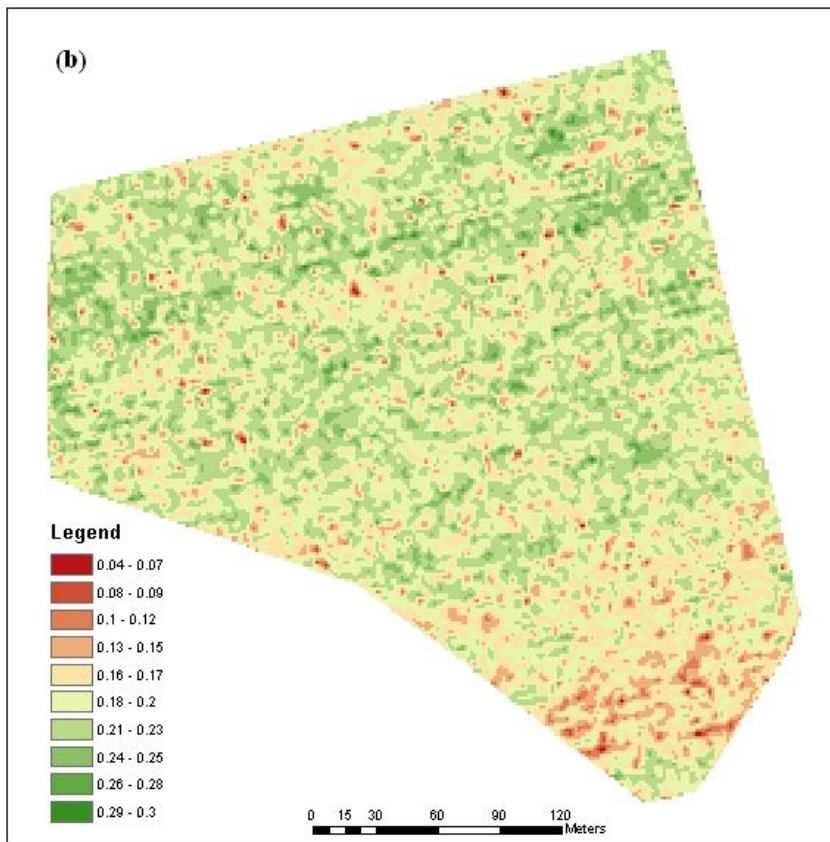
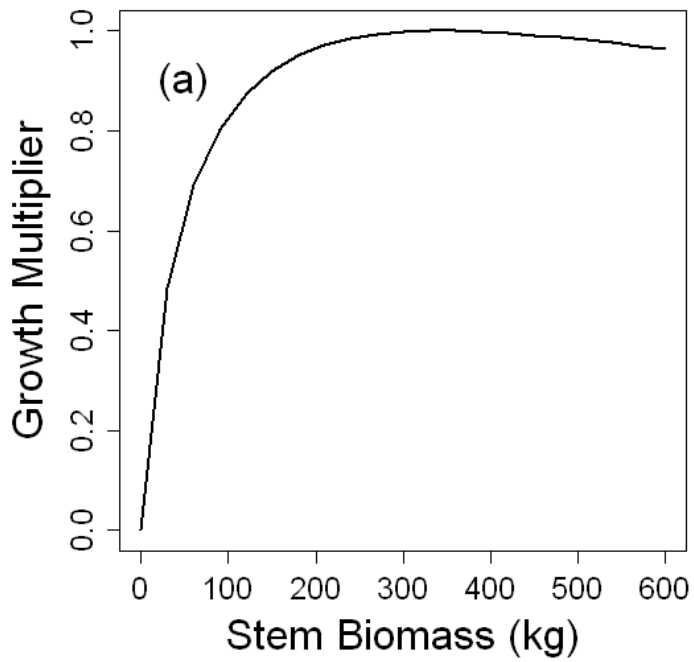
Table 2.3. Akaike's Information Criterion (AIC) and Correlation Coefficients (R^2) and number of parameters of 9 nested models of 5 different radii (from 4 meter to 8 meter). The model with lowest AIC is the most parsimonious, and the model with the highest R^2 has the best goodness of fit.

| Model | Para- meter | 4 meter | | 5 meter | | 6 meter | | 7 meter | | 8 meter | |
|--|----------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|
| | | AIC | R^2 | AIC | R^2 | AIC | R^2 | AIC | R^2 | AIC | R^2 |
| 1. Growth=Maxgr*S | 3 | 1532.5 | 0.43 | 1532.5 | 0.43 | 1532.5 | 0.43 | 1532.5 | 0.43 | 1532.5 | 0.43 |
| 2. Growth=Maxgr*S*U1 | 4 | 1530.6 | 0.43 | 1523.8 | 0.43 | 1524.6 | 0.43 | 1513.3 | 0.43 | 1508.9 | 0.43 |
| 3. Growth=Maxgr*S*U2 | 5 | 1534.3 | 0.43 | 1528.5 | 0.43 | 1525.6 | 0.43 | 1512.0 | 0.43 | 1505.1 | 0.43 |
| 4. Growth=Maxgr*S*C1 | 6 | 1323.2 | 0.45 | 1320.8 | 0.45 | 1285.5 | 0.45 | 1170.5 | 0.46 | 1129.4 | 0.46 |
| 5. Growth=Maxgr*S*C2 | 7 | 1306.5 | 0.45 | 1305.5 | 0.45 | 1276.9 | 0.45 | 1167.0 | 0.46 | 1125.1 | 0.46 |
| 6. Growth=Maxgr*S*U1*C1 | 7 | 1320.5 | 0.45 | 1314.4 | 0.45 | 1281.2 | 0.45 | 1168.7 | 0.46 | 1126.3 | 0.46 |
| 7. Growth=Maxgr*S*U1*C2 | 8 | 1304.7 | 0.45 | 1299.5 | 0.45 | 1271.9 | 0.45 | 1164.8 | 0.46 | 1121.7 | 0.46 |
| 8. Growth=Maxgr*S*U2*C1 | 8 | 1321.4 | 0.45 | 1312.8 | 0.45 | 1280.8 | 0.45 | 1168.9 | 0.46 | 1125.8 | 0.46 |
| 9. Growth=Maxgr*S*U2*C2 | 9 | 1305.5 | 0.45 | 1298.2 | 0.45 | 1270.9 | 0.45 | 1164.5 | 0.46 | 1120.2 | 0.46 |
| Ranking (Min AIC, Max R^2) | | 1304.7 | 0.45 | 1298.2 | 0.45 | 1270.9 | 0.45 | 1164.5 | 0.46 | 1120.2 | 0.46 |

Note: (i) AIC varied with radius: AIC dramatically declined with increasing neighborhood radius, but the marginal gain in R^2 was slight (AIC and R^2 were from the best models of each radius); (ii) AIC varied across models in a radius: A striking decline in AIC, but slight increase in R^2 , as adding the term of neighborhood competition to the simplest model. When adding one more term of neighborhood uniform to the model, AIC slightly decreased, but this decrease still made significantly difference among the models, while R^2 remained almost unchanged.

Table 2.4. Parameter estimation for the best model (model No 9 of radius 8 meter)

| Parameters | Definition | Value & 95% credible interval (CI) |
|----------------|---|------------------------------------|
| 1. Maxgr: | Maximum growth | 15.6 (12.5, 19.0) |
| 2. C: | Coefficient of neighborhood competition effects | 0.85 (0.61, 1.11) |
| 3. U: | Coefficient of neighborhood uniformity effects | 0.03 (0.001, 0.09) |
| 4. X0: | Stem volume at which Maxgr occurs | 346.0 (240.9, 459.5) |
| 5. Xb: | Breath of the function | 2.3 (1.9, 2.5) |
| 6. α : | Shape of effects of neighboring tree size on focal tree | 2.3 (1.8, 2.8) |
| 7. β : | Shape of effects of neighboring tree distance on focal tree | 0.33 (0.02, 0.76) |
| 8. λ : | Sensitivity of focal tree size to neighbors | -0.25 (-0.38, -0.10) |
| 9. γ : | Sensitivity of focal tree size to neighborhood structure | 0.52 (0.10, 1.01) |



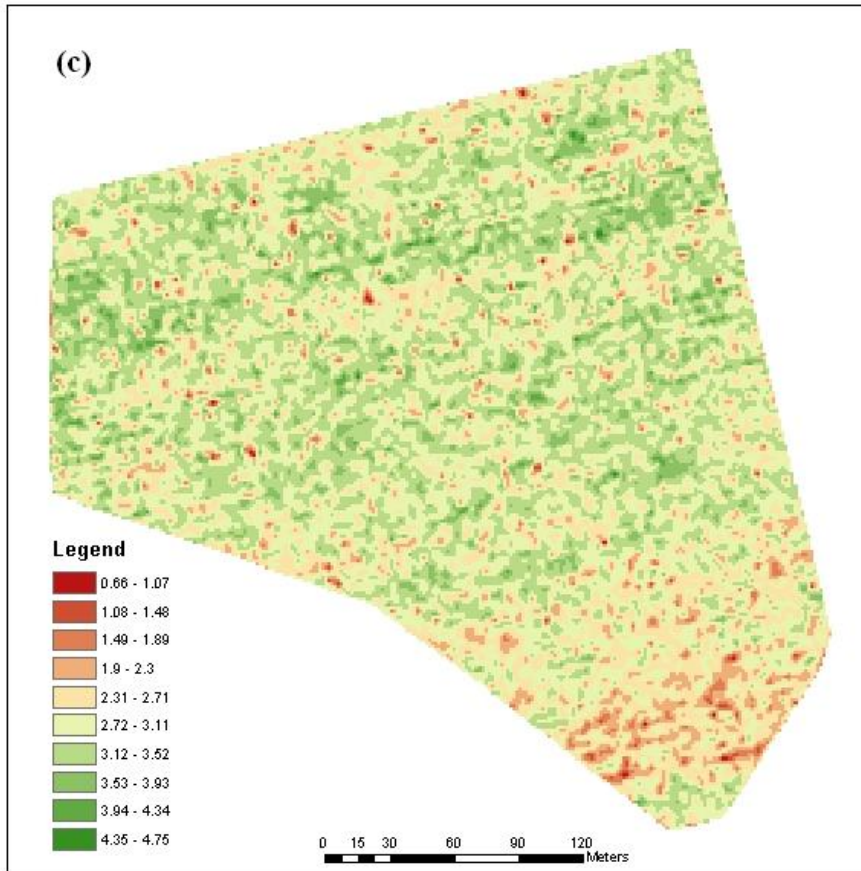


Fig.2.1. (a) Focal tree size effects on potential growth. The potential growth exponentially increased with tree size (tree size less than 100 kg) and peaked at tree size by 300-350 kg (X_0), and then decreased; (b) Map of distribution of size effects on maximum growth – prediction of relative effects of focal tree size on maximum growth. A large decline in the maximum growth, caused by size effect. This decline ranged by 70-96%; (c) Map of distribution of potential growth – prediction of multiplication of maximum growth with size effects. Potential growth widely ranged due to strong effects of tree size. The green color is higher growth than the red one. This "cause" is somewhat circular in reasoning, as some areas with low growth owing to smaller tree sizes have smaller tree sizes because of lower (earlier) growth; in part, this effect maps site fertility or the influence of silvicultural treatments such as variations in effectiveness of fertilization or weed control

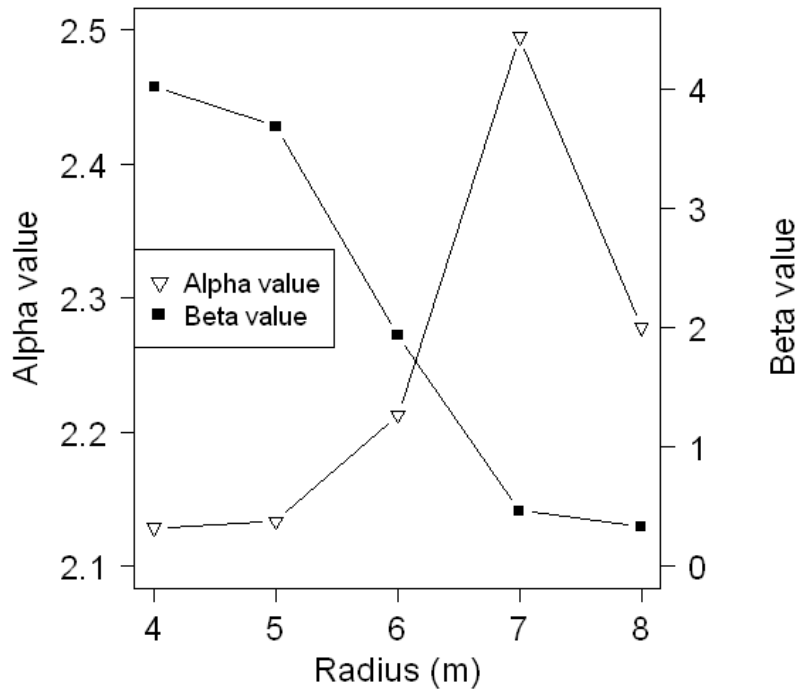
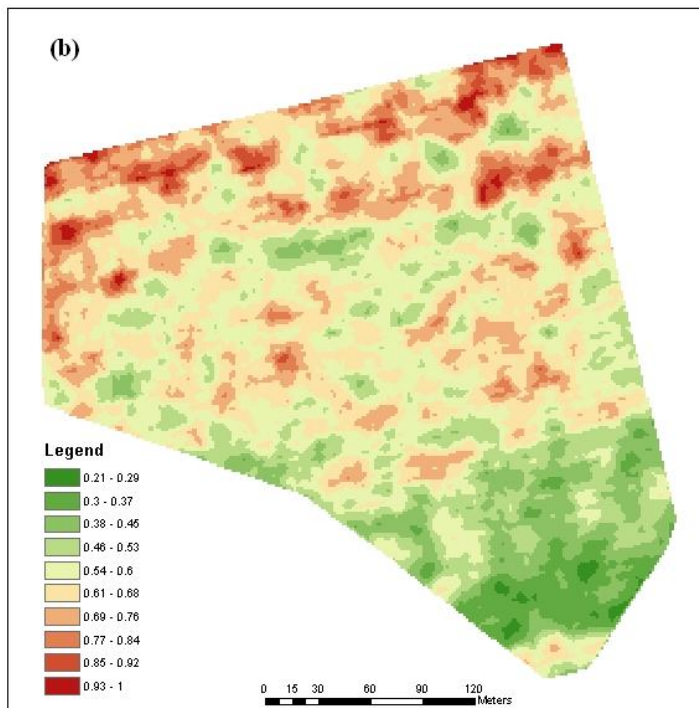
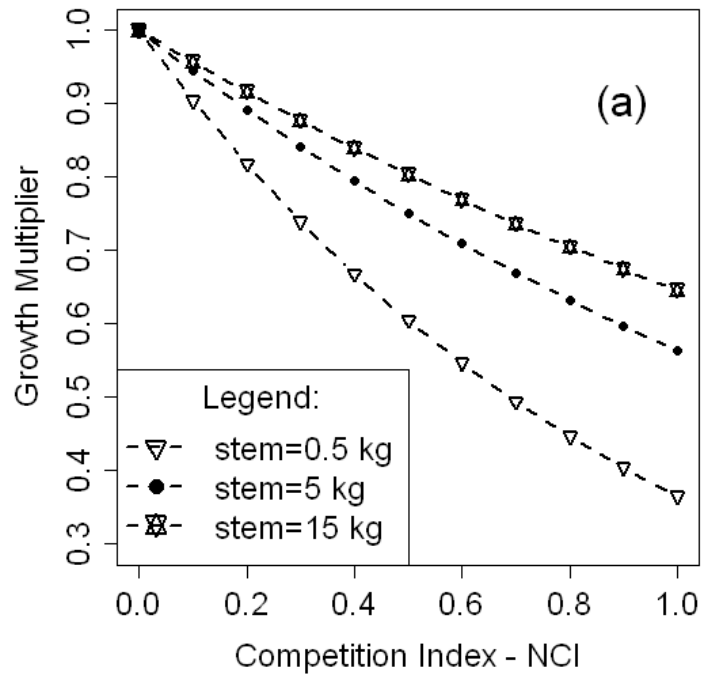


Fig.2.2. Scales of neighboring size (α) and neighboring distance (β) along radius. Both scales of neighboring tree size and distance depend on the neighborhood radius. As the radius increased, the effects of neighboring tree size and distance to focal trees changed dramatically. This would indicate that neighborhood competition index is size- and distance-dependent.



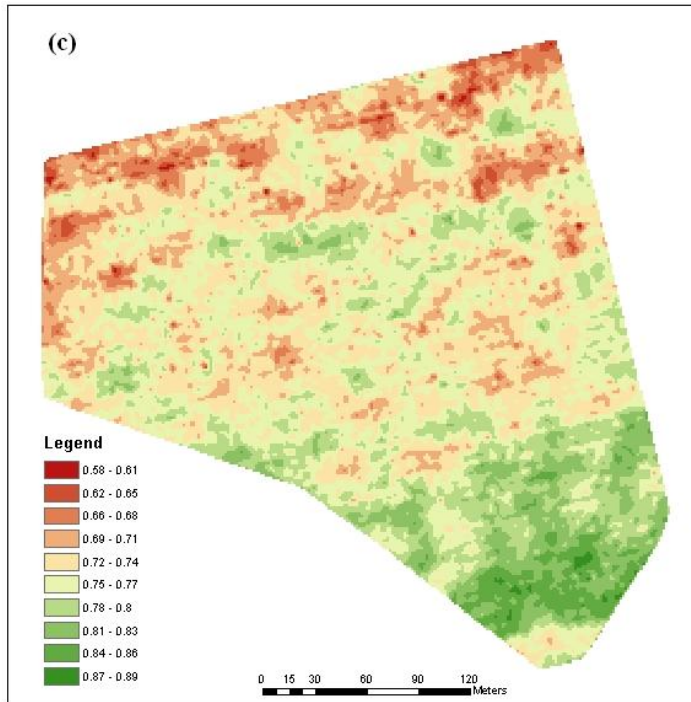


Fig. 2.3. (a) Competition effects on potential stem growth. Tree size was very sensitive to neighborhood competition. The larger focal trees were less affected by neighborhood competition than smaller trees; (b) Map of distribution of neighborhood competition index (NCI). NCI tends to be more intense in areas of bigger trees. NCI was calculated based on the parameters of the most parsimonious models. The green color is less severe competition, and the red is the most severe competition; (c) Map of neighborhood competition effects. Neighborhood competition effects were translated from NCI. The dark green color indicates the least effect, the red color is the strongest effect. This map differs from Fig. 2.3b by representing the effect of neighborhood competition on focal tree growth, rather than the intensity of competition.

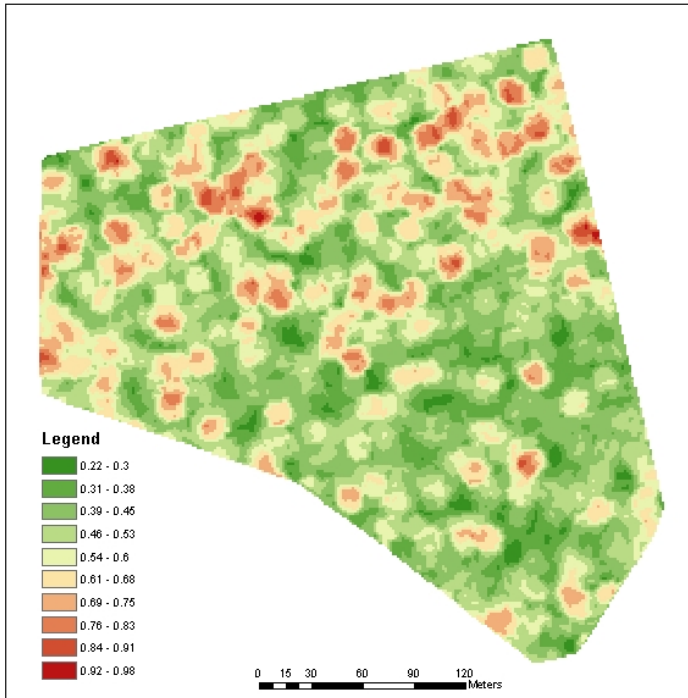


Fig. 2.4. Map of Neighborhood Uniformity Index (NUI). Higher NUI tended to be concentrated more on areas of bigger trees. NUI was standardized by neighborhood coefficient of covariance. The small NUI indicates high neighborhood uniformity - the green color and the red is the most heterogeneous

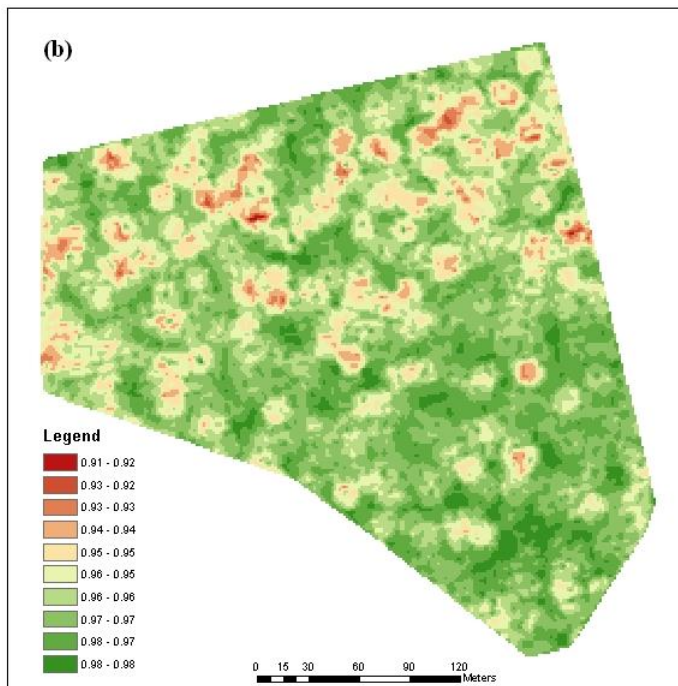
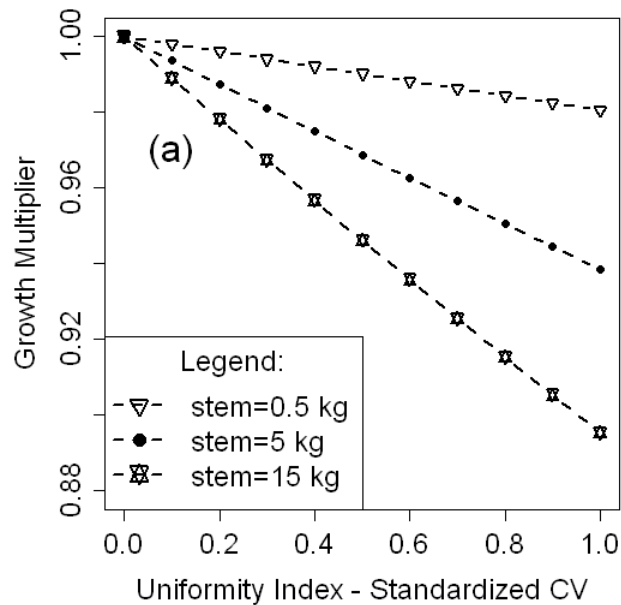


Fig.2.5. (a) Effects of neighborhood uniformity on potential growth. Tree size is sensitive to neighborhood uniformity effects. The bigger trees more sensitive to neighborhood uniformity than the smaller tree; (b) Distribution of neighborhood uniformity effects. Neighborhood uniformity effects were translated from NUI by a negative exponential function. The dark green color indicates the least effects by neighborhood uniformity, while the red color indicates the most effects. This map differs from Fig. 2.4 by representing the effect of neighborhood uniformity on focal tree growth, rather than the degrees of neighborhood uniformity.

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CHAPTER 3

COMPETITION BETWEEN PIONEER AND NON-PIONEER SPECIES IN TROPICAL FOREST RESTORATION PLANTATIONS

Summary

Interactions between species are very crucial to determine forest structures and dynamics. The intensity and importance of species interactions depend on species composition and vary with productivity gradients. We tested and quantified the competition between two focal species guilds of non-pioneer legumes and non-pioneer non-legumes with four neighboring species guilds across silviculture treatments by developing a set of alternative neighborhood models. Competition from neighboring trees had strong effects on the growth of individual trees of non-pioneer species, and the intensity of competition from neighboring trees varied with focal tree species guilds and silviculture. For example, non-pioneer legumes experienced competition as a function of neighboring tree sizes and distances only. Non-pioneer non-legumes experienced competition as a function of neighboring tree sizes and distances, and also by the identity of neighboring species guilds. The non-pioneer non-legumes experienced stronger competition in the intensive silviculture, unlike the non-pioneer legumes. Although intensive silviculture initially enhanced forest stand productivity (both density and tree size), strong competition from fast-growing trees lowered the later growth of individual non-pioneer non-legume trees. Our results suggested some implications for management: (i) abundance of pioneer trees should be controlled during developments of forest stand to reduce competition from pioneer trees on target species of non-pioneers; (ii) assembly

of pioneers and non-pioneers should follow a general rule that abundance of pioneers decrease with increasing productivity gradients.

Keywords: Competition, pioneer, non-pioneer, legume, non-legume, focal/neighboring species guild, neighborhood competition index/effects, restoration, native species, traditional/intensive silviculture, relative strength of competition.

1. Introduction

Environmental and livelihood benefits develop when degraded lands are restored to native forests (ITTO 2002, Lamb et. al. 2005, Carnus et. al., 2006). One of solutions to the recovery of native forests is the active restoration of degraded areas by mixing a number of native species together (ITTO 2002, Lamb and Gilmour 2003, Lamb et. al. 2005, Carnus et. al., 2006). Attempts to establish mixed native species plantations in tropical regions have shown both negative and positive responses to inter-specific competition (Parrotta and Knowles 1999, Binkley et. al. 2003, Petit & Montagnini 2004, Piotto et. al. 2004, Erskine et. al. 2006, Wuethrich 2007). Wuethrich (2007) reported that only 2 of 98 publicly funded reforestation projection projects in Brazil were successful; rapid domination by fast-growing, non-pioneer trees typically led to suppression or elimination of many other species. This failure might be due to lack of understanding of species resource needs and interaction between species, thus leading to competitive exclusion of target species. The assembly and composition of species to be mixed play important role in determining the success of mixed plantations (Kelty, 2006), so that one species does not dominate and completely suppress other species; ideally, inter-planted

species can both temporally and spatially complement in their use of resources such as light, water, and soil nutrients (Carnus et. al., 2006).

Goals for native forest restoration often focus on successful establishment and growth of long-lived (non-pioneer) species. Inter-planting fast-growing, short-lived (pioneer) species, or nitrogen-fixing species, can sometimes facilitate these non-pioneer species (Parrotta et. al. 1997, Aston et. al. 2001, Binkley 2003, Lamb et. al. 2005, Boyden et. al. 2005, Carnus et. al., 2006, Kelty 2006), especially if the inter-planted species enrich the soil (Binkley 2003, Rothe and Binkley 2001) or somehow differ in resource partitioning (Grace and Tilman 1990, Tilman et. al. 1997, Hooper and Vitousek 1997, Chesson 2000; Lehman and Tilman 2000, Aston et. al. 2001, Amarasekare 2003, Carnus et. al. 2006, Kelty 2006). However, simple competition for resources may be so strong that any potential benefit of inter-planted species may be small or non-existent (Grace and Tilman 1990, Binkley 2003, Boyden et. al. 2005, Carnus et. al., 2006, Kelty 2006).

Our study was conducted in restoration plantations of Brazil's Atlantic forests, designed to test a number of factors, including two levels of silvicultural treatments on restoration outcomes. The plantations were mixed plantings of 20 native species (10 pioneer and 10 non-pioneer species), with a number of legumes species in both species groups (Campoe et. al. 2010). At age 3.5 years, Campoe et. al. (2010) reported very large differences in survival, growth, stem production and light area index (LAI) among species and across silvicultural treatments. Intensive management increased seedling survival, stem wood production, leaf area index, and efficiency of resource use for most species, leading to a higher site productivity. Interactions, however, among species were not examined. Interactions among species often vary with productive gradients in a way

that inter-specific competition increases with increasing productivity, and vice versa (Keddy et. al. 1997, Grime 2001). In some cases, competition may be developed for belowground resources (Tilman 1988, Wilson and Tilman 1991). These interactions of enhanced resource supply and changing intensity of competition with intensive silviculture may play an important role in the long-term success of non-pioneer native species. These restoration plantations provide a great opportunity to explore how silvicultural treatments affect species interactions, and the long-term value (or cost) of including fast-growing pioneer and legume species in native forest restoration plantations.

We used spatially explicit neighborhood models to examine interactions between trees, because these models offer several advantages over the other approaches to studying plant interactions (Radosevich 1988). Neighborhood models provide a tool for synthesizing competition processes into spatial and temporal predictions of system dynamics (Gratze et. al. 2004); and improve understanding of competition processes in forest stands (Weiner 1984, Daniels et. al. 1986, Wagner and Radosevich 1991). Our overall objective was to test and quantify interactions between pioneer and non-pioneer species across traditional and intensive silviculture. We hypothesized that: (i) focal species guilds of non-pioneers would experience less competition from neighboring pioneers relative to neighboring non-pioneers; (ii) neighboring groups of legume species offer less competition than non-legumes; and (iii) pioneers would become stronger competitors relative to neighboring non-pioneers in intensive silviculture.

2. Material and methods

2.1. Study area and data collection

Site description

The trial was installed in March, 2004, at the University of São Paulo's Anhembi Forest Research Station (22°43'22"S, 48°10'32"W), at the elevation of 460 m on a 2% slope. The research station is located within the Atlantic Forest biome. Mean, maximum and minimum monthly temperature averages 19.1 °C, 24.2 °C, and 14.1 °C, and rainfall averages 1170 mm year⁻¹, with 75% falling between October and March. During the dry season (May to August), the water deficit is about 50 mm. The soil is an acidic (pH 4.0) Typic Hapludox, comprised of 5% silt, 13% clay and 82% sand, with relatively low organic matter (1% in the top 20 cm).

Experimental design

Twenty tree species native to Sao Paulo and Bahia, Brazil (Table 3.1) were used; 10 were chosen to represent light demanding pioneer species, and 10 represented shade tolerant, non-pioneer species (Campoe et. al. 2010). Tree species were randomly mixed in experimental plots, after controlling African grass (*Brachiaria decumbens*) through cultivation and application of 5 L ha⁻¹ of glyphosate (0.2%) on all treatments. Control of leaf-cutter ants (*Atta* sp. and *Acromyrmex* sp.) was accomplished by systematic placement of baits (0.3% of sulfuramid), throughout the experimental area. The 2x2x2 factorial design used two ratios of pioneer species to non-pioneer species (A, 50:50, B, 67:33); two levels of spacing (3 m × 1 m, 3300 trees ha⁻¹, and 3 m × 2 m, 1,667 tree ha⁻¹); and the two levels of silvicultural management (traditional and intensive). The traditional treatment had weed control and fertilization (27 kg N, 21 kg P, 11 kg K, and 24 kg Ca ha⁻¹) at 6 and 12 months only. The intensive treatment applied weed control at 3 month

intervals, and fertilization once each year (cumulative application of 81 kg N, 62 kg P, 33 kg K, 452 kg Ca and 180 kg ha⁻¹). Each combination of treatments was replicated 4 times in randomized blocks; each plot was 42 m × 30 m (1260 m²) to provide a buffer, with an interior plot of 36 m × 22 m (792 m²) on which measurements were made.

Data collection

Heights and diameters (at 0.3 m height) were measured on all trees every 6 months for first 4 years and then once a year. The species were classified into 4 guilds based on shade tolerance (light-demanding pioneer versus shade-tolerant non-pioneer), and legumes versus non-legumes (Table 3.1). We used stem basal area (based on diameters at 0.3 m height) to model mean annual growth of individual trees for each guild of non-pioneer species. For multi-stem trees, we summed the basal area of all stems and removed those trees with negative growth increments (from 2008 to 2011, age 4 to 7 years). Data was summarized in table 3.2.

2.2. Model development

The long-term goal of native forest restoration is often the successful establishment and development of long-lived (non-pioneer) species. Therefore, we evaluated the influence of neighboring trees on the focal species guilds of non-pioneers. Pioneer trees were tested for their influence on growth of non-pioneer trees (in categories of pioneer legumes and pioneer non-legumes). Given the goal of long-term development of non-pioneer species, we did not examine pioneer species as focal trees themselves. Our preliminary analyses showed strong differences in response to silviculture and to competition for the legume and non-legume subgroups of non-pioneers. Therefore we analyzed two subgroups of non-pioneers separately (3 non-pioneer legume species and 7

non-pioneer non-legume species), and did not pursue analysis of the entire non-pioneer group.

We used spatially explicit neighborhood models (Canham et. al. 2004, Uriarte et. al. 2004a&b, Boyden et. al. 2008) with a fixed radius of 5 meters to model mean annual basal area growth of individual trees for each focal species guild of two focal species guilds of non-pioneer legumes and non-legume non-pioneers in the period of 3 years (from July 2008 to June 2011) in relationship with four neighboring species guilds as given in table 3.1. Our basic model included 3 terms: (1) maximum growth expected for a tree under any condition, (2) size effects of focal trees, and (3) neighborhood competition effects. The generalized form of the model for each focal species guild was:

$$\mathbf{Growth=Maxgr \times S \times NC} \quad (1)$$

where Growth is mean annual basal area growth over 3 years (2008-2011), Maxgr is the maximum annual basal area growth year⁻¹ (the expected growth at the optimal size – X_o value as defined in the section of size effect); S is focal tree size effects, the multiplication of maximum growth (Maxgr) and S indicates a potential growth of an individual tree (without competition); NC is neighborhood competition effects. S and C are negative exponential functions as further defined in the sections of size and neighborhood competition effects, respectively. Both S and NC are a scalar ranging from 0 to 1, hence reducing potential stem growth.

In order to test how silviculture affects growth and competition of each focal species guild, we varied terms of maximum growth (Maxgr), leading to varying potential growths, and neighborhood competition coefficient (parameter C as defined in the section of neighborhood competition effects) by silvicultural treatments. We developed a set of 8

alternative models to test a number of factors and hypotheses, details of factors testing are given in table 3.3.

Size effects on growth – Growth of an individual tree typically relates to its size at the beginning of a growth period (e.g., Bella 1971, Hegyi 1974, Lorimer 1983, Zeide 1993, Canham et al. 2004, Uriarte et al. 2004a&b, Boyden et al. 2008). We used a lognormal function to characterize initial size effects for each focal species guild:

$$S = \exp \left[-0.5 * \left\{ \frac{\ln \left(\frac{Ba}{X_0} \right)}{X_b} \right\}^2 \right] \quad (2)$$

where Ba is stem basal area of focal tree, X_0 represents the stem basal area at which maximum growth rate is expected to occur based on the data, and X_b is breadth of the function that controls the rate of achieving that maximum growth (Baribault and Kobe 2011). This function is flexible and well supported theoretically and empirically (Zeide 1993, Canham et. al. 2004, Uriarte et al. 2004).

Neighborhood competition effects – neighborhood competition commonly influences tree growth, and a number of neighborhood indices have been developed to characterize the influence of neighbors (e.g, Canham et. al. 2004, Uriarte et. al. 2004a, Boyden et. al. 2005 and 2008). We adopted 2 general neighborhood competition indices (NCIs), which were previously shown to effectively represent neighborhood competition on both sapling and adult tropical forest trees (Uriarte et. al. 2004a &b, Boyden et. al. 2008). Neighborhood competition index for each focal species guild was:

$$NCI1_k = \sum_j^S \sum_i^n \lambda_{jk} \frac{Ba_{ik}^\alpha}{d_{ik}^\beta} \quad (3)$$

Where $NCI1_k$ is neighborhood competition index of focal tree number k^{th} of the focal species guild, Ba_{ik} is neighboring tree stem basal area number i^{th} of focal tree number k^{th} ,

d_{ik} is distance of neighboring tree number i^{th} to focal tree number k^{th} , n is total number of neighboring trees in a fixed radius; α , β , and λ estimated for each focal species guild by the analyses. α and β determine the shape of effects of neighboring stem basal area (α) and distance (β) to the neighbor. The influence of the identity of neighboring species group was determined as λ (species competition coefficient). If all neighboring species groups have equal or same effects on focal trees, we modified equation 3 (NCI1) by assuming that all the λ s equal to 1, leading to removal of λ from equation 3 and simplifying NCI:

$$NCI2_k = \sum_i^n \frac{Ba_{ik}^\alpha}{d_{ik}^\beta} \quad (4)$$

To test whether the sensitivity of focal trees to their neighborhood competition decreased or increased with focal tree size, we added a term of sensitivity of focal tree size to neighborhood competition indices 1 and 2 (equation 3 and 4), creating two more neighborhood competition indices:

$$NCI3_k = Ba_k^\gamma \sum_j^S \sum_i^n \lambda_{jk} \frac{Ba_{ik}^\alpha}{d_{ik}^\beta} \quad (5)$$

$$NCI4_k = Ba_k^\gamma \sum_i^n \frac{Ba_{ik}^\alpha}{d_{ik}^\beta} \quad (6)$$

γ is shape of sensitivity of focal tree size to its neighborhood competition and was also estimated by the analyses. If $\gamma < 0$ the smaller trees are more sensitive to neighborhood competition than the bigger trees, and vice versa. In order to explore the influence of silviculture on growth and neighborhood interactions, we fit growth models separately for the focal species guilds receiving traditional versus intensive silviculture.

All the indices of NCI were translated into effects on growth by using a negative exponential function of NCI:

$$NC_i = \exp\left(-C * \frac{NCI_i}{NCI_{max}}\right) \quad (7)$$

where C is neighborhood competition coefficient estimated for each focal species guild from the models, NCI_i is the neighborhood competition index of focal tree number i^{th} for the focal species guild and NCI_{max} is the maximum value of NCI of all the focal trees of the focal species guild in the stand. The use of the ratio of NCI_i to NCI_{max} standardizes the neighborhood effects and facilitate comparisons across focal trees of the focal species guild in the stand.

Model implementation and model selections

We used the program R (R development Core Team 2010) and packages of R2jags and JAGS 3.1.0 (Just Another Gibbs Sampler) to fit and estimate parameters. The simplest model required estimation of 5 parameters and a variance; the most complex model required estimation of 8 parameters and one variance, of which 3 parameters (Maxgr, C and λ) were treated as random effects. To account for heteroscedasticity and non-normality in the residuals, we used a log-transform of growth to fit the models (Boyden et. al. 2008) and uninformative priors for parameter estimation to maximize likelihood. The parameters and their prior distributions are given in table 3.4.

We ran all the models with 2,000 iterations and burn-in of first 1,000 iterations and used Rhat value to assess the convergence of models (Gelman and Hill, 2007). We also calculated adjusted correlation (R^2) of predicted growth versus observed growth to determine goodness-of-fit.

We used information theory methods to guide the selection of the best model from sets of candidate models. The principle for this method is that the model that loses the least information relative to the truth is the best model among a set of models to be

considered (Burnham and Anderson, 2001). There are a number of criteria for selection of the best model from a set of candidate models, such as Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), and Deviance Information Criterion (DIC). We used DIC to select the best model from our candidate models, because we focused on analyses of random effects of silvicultural treatments and species group identity on growth of individual trees, in which there were some difficulties and uncertainties in the determination of the number of parameters of models. DIC, a measure of deviance and effective number of parameters in a model (a difference between the posterior mean of deviance and the deviance at the posterior means of the parameters), is similar to AIC (Spiegelhalter et. al., 2002) and is interpreted similarly (Gelman and Hill, 2007). Thus DIC entails ranking models based on the information lost when using a model to approximate the truth, and using the principle of parsimony, models are penalized for having more complexity. Smaller DIC values indicate better supported by the data (Spiegelhalter et. al., 2002).

3. Results

3.1. Silviculture effects on stand structure and growth

Intensive silviculture enhanced stand basal area and uniformity, population density and tree size. Intensive silviculture increased stand density ~10% and tree size ~20%, leading to higher density of species guilds, total stand basal area (~30%) and mean annual increments (MAI) of both stand and species guilds, compared to the traditional treatment (Table 3.2). Intensive silvicultural treatment also increased relative abundance of non-pioneer species (40.3% versus 37% in traditional silviculture) and stand

uniformity by reducing coefficients of variation (CV) of individual tree sizes (~119 %, compared to 154% for traditional silviculture). The latter pattern was also observed with current annual increment – CAI (Table 3.2). Larger tree size and higher density in intensive silviculture indicated that intensive silviculture increased stand productivity.

In contrast to these cumulative properties, current increments were actually lower with intensive silviculture at the levels of both individual trees and stands, with the exception of non-pioneer legume species (Table 3.2). We did not have an opportunity to explore why growth was lower in the treatment with intensive weeding and fertilization early in the plantation's development. One possibility would be a size-related decline because the trees were so much larger at the beginning of the current growth period.

3.2. Effects of neighboring species guilds on focal species guilds

Effects of neighboring species guilds on focal trees varied with focal species guilds (Table 3.5). The best growth model for non-pioneer legume guild did not include a term of species/guild competition coefficient – parameter λ (Table 3.5, model # 1 in Appendix S.1), indicating that all four neighboring guilds of pioneer legumes, pioneer non-legume, non-pioneer legume and non-pioneer non-legumes were equal in relative strength of competition on the focal species guild of non-pioneer legumes. Neighborhood competition index (NCI) of the focal species guild of non-pioneer legumes was only determined by neighboring tree sizes and distances. The same pattern was observed across silvicultural treatments for this focal species guild (Table 3.5, model#1 for both treatments in Appendix S.2). Contrary to the focal species guild of non-pioneer legumes, the best growth model for the focal species guild of non-pioneer non-legumes did include parameter λ (Table 3.5, model #8 in Appendix S.1), suggesting that each of the four

neighboring species guilds would have distinctive per capital effects on the focal trees of non-pioneer non-legume guild. This indicates that neighborhood competition index (NCI) of the focal species guild of non-pioneer non-legumes was not only determined by neighboring tree size, distance, but also by identity of neighboring species guilds. Effects of neighboring guild identity on the focal species guild of non-pioneer non-legumes were also observed in both intensive (Table 3.5, model #2 in Appendix S.2) and in traditional silviculture (Table 3.5, model #4 in Appendix S.2).

We used λ from the best models (Table 3.6) to further investigate relative strength of competition of each neighboring species guild among four neighboring species guilds on the focal species guilds as illustrated in Fig. 3.1. For the focal species guild of non-pioneer legumes, we assumed all λ s equal to 1 as illustrated in Fig. 3.1a. In contrast, each of four neighboring species guilds differed in its relative strength of competition on the focal species guild of non-pioneer non-legumes, but their ranking in relatively competitive strength among neighboring species guilds varied with silviculture (Table 3.6, Fig. 3.1b). The neighboring species guilds of pioneer legumes and pioneer non-legumes were the 1st and 2nd weakest competitors, respectively, for the focal species guild of non-pioneer non-legumes in traditional treatment (Fig. 3.1b, column: Traditional), but they became stronger relative to the other neighboring species guild and shifted their ranking to the 1st (pioneer non-legumes) and 3rd (pioneer legumes) strongest competitors in intensive silviculture (Fig 3.1b, columns: Traditional and Intensive). These variations in relative strength of competition with focal species guilds and silviculture indicated that per capital effects of species identity were focal species guild-dependent and/or nutrient/productivity gradient-dependent.

3.3. Silviculture effects on potential growth and neighborhood competition

Silviculture intensity significantly affected on the focal species guild of non-pioneer non-legumes, but not non-pioneer legumes (Table 3.5). Although observed data showed that the focal species guild of non-pioneer legumes slightly positively responded to intensive silviculture (bigger observed growth in intensive silviculture than in traditional silviculture, Table 3.2), the best growth model for this focal species guild only included terms of fixed maximum growth (parameter Maxgr) and neighborhood competition coefficient (parameter C), which did not vary with silviculture treatments (Table 3.6, model #1 in Appendix S.1). This indicates that silviculture did not significantly affect on potential growth (Fig. 3.2a) and neighborhood competition (Fig. 3.3a) of the focal species guild of non-pioneer legumes, resulting in no significant effects on individual growth of the focal species guild of non-pioneer legumes (Fig. 3.4a).

In contrast to behaviors of non-pioneer legume guild to silviculture, silviculture had significant effects on the focal species guild of non-pioneer non-legumes (Table 3.5, model #8 in Appendix S.1). Silviculture varied both maximum growth (parameter Maxgr) and neighborhood competition coefficient (parameter C) in a way that intensive silviculture decreased Maxgr and C (Table 3.6), leading to lower potential growth in intensive silviculture treatment than in traditional silviculture (Fig.3.2b) and decreasing the importance of neighborhood competition effects – the degree to which neighborhood competition affecting on growth of focal trees (Fig.3.3b). Combining the effects of focal tree size and neighborhood competition effects, individual growth of the focal species guild of non-pioneer non-legumes was still higher in traditional silviculture than in intensive silviculture. However the difference in growth in intensive and traditional

silviculture decreased and even disappeared for small focal tree sizes, as neighborhood competition index increased (Fig. 3.4b). This indicates that competition from neighboring trees would be the main factor leading to growth reduction of individual trees (especially smaller ones) with intensive silviculture.

Although intensive silviculture slightly enhanced initial tree size of the focal species guild of non-pioneer non-legumes (Table 3.2, Fig. 3.5), both observed and predicted current individual growth of this focal species guild was less in intensive silviculture than in traditional silviculture (Table 3.2, Fig.3.4b), indicating that non-pioneer non-legumes were more strongly suppressed in intensive silviculture than in traditional silviculture. Our analyses showed that higher density and larger tree size of pioneers in intensive than in traditional silviculture (Table 3.2, Fig. 3.5). Moreover the prediction of neighborhood competition index as illustrated in Fig. 3.6 showed that distribution of neighborhood competition index was right skew in intensive silviculture – more intense, but it was left skew in traditional silviculture – less intense. This all indicates that intensive silviculture intensified competition, resulting in stronger pressure on non-pioneer non-legume trees in intensive silviculture.

Silvicultural treatments also varied the functions of neighborhood competition index of the focal species guild of non-pioneer non-legumes (Table 3.5, model #2 versus model #4 for intensive and traditional silviculture, respectively, Appendix S.2). When analyzing with pooled data, we found that the best model for non-pioneer non-legume guild included the term of focal tree size with parameter γ -sensitivity of focal tree size to neighborhood competition (Table 3.5). However this focal guild differed in its behaviors in responses to neighborhood competition across silvicultural treatments (Table 3.5). In

traditional silviculture, the best growth model for this focal guild included parameter of negative γ (Table 3.5, and 3.6), indicating that bigger trees were suffered less competition effects than smaller trees. Oppositely, in intensive silviculture, the best growth model did not include parameter γ (Table 3.5, model #2 in Appendix S.2), indicating that neighborhood competition did not depended focal tree size, only determined by neighboring tree sizes and distances (Table 3.5). Silvicultural treatments altered mode of neighborhood competition from focal tree size dependence (traditional silviculture) to focal tree size independence (intensive silviculture). Our study was not designed to explore the mode of competition between non-pioneer and pioneer trees. Pioneer trees increased in size with intensive silviculture proportionally more than non-pioneer non-legume tree sizes (Table 3.2, Fig. 3.5). Campoe et. al. (2010) reported that leaf area index (LAI) in intensive silviculture (LAI~1.7) was over 3 times bigger than in traditional silviculture (LAI~0.5) after 3 years. This all indicates that non-pioneer non-legume trees were much more suppressed by larger pioneer trees with intensive silviculture, suggesting that much stronger competition from pioneer trees for light would intensify competition with neighboring trees.

3.4. Hypothesis tests

That the two focal species guilds of non-pioneer legumes and non-pioneer non-legumes responded differently to silviculture and to neighboring species guilds, none of our hypotheses was supported for both focal species guilds.

Our first hypothesis predicted that neighboring species guilds of pioneer legumes and pioneer non-legumes would exert less competitive pressure on non-pioneer focal species. This hypothesis was supported for the focal species guild of non-pioneer non-

legumes under traditional silviculture (Fig. 3.1a, column: Traditional). The hypothesis was refuted for the non-pioneer legumes (Fig. 3.1a) and for non-pioneers non-legume in the intensive silviculture treatment (Fig.3.1b, column: Intensive). Our second hypothesis predicted that legumes would offer weaker competition to non-pioneer focal trees than non-legumes. This prediction was supported for the focal species guild of non-pioneer non-legumes with neighboring species guild of pioneer legumes (Fig. 3.1b), but not for the focal species guild of non-pioneer legumes, or for the neighboring species guild of non-pioneer legumes on either focal species guild. The final hypothesis speculated that neighboring species guilds of pioneers increased their strength of competition relative to the other neighboring species guilds with site productivity. This expectation was supported for the focal species guild of non-pioneer non-legumes (Fig. 3.1b), but this hypothesis was refuted for the focal species guild of non-pioneer legumes (Fig. 3.1a).

4. Discussion

Our analyses showed that interactions between pioneer and non-pioneer species guilds in restoration plantations on abundant pastures depended on focal species guilds, neighboring species guilds and varied with site productivity and/or silvicultural interventions. For the focal species guild of non-pioneer non-legumes, we found that each neighboring species guild differed in relative strength of competition effects on growth of the focal species guilds of non-pioneers (Table 3.5, Fig. 3.1b). This finding is consistent with those reported in both temperate forests (Canham et. al.2004, Zhao 2006, Papaik et. al. 2009) and in a number of seedling species in tropical forests (Uriarte et. al. 2004b, Comita and Hubbell 2009). However relative strength of competition among four

neighboring species guilds became less distinctive, more neutral in intensive silviculture, where was higher productivity. This is because the neighboring species guilds of pioneer legumes and pioneer non-legumes became stronger relative to the neighboring species guilds of non-pioneer legumes and non-pioneer non-legumes in intensive silviculture. A number of studies in tropical forests (Harms et. al. 2000, Uriarte et. al. 2004b) found that interspecies competition becomes more intense as trees get bigger. In addition, Choler et. al. (2001), Callaway et. al. (2002), Boyden et. al. (2005) reported that intensity of inter-specific competition usually increases with increasing productivity gradients. This would explain why the competitors of neighboring species guilds of pioneer legumes and pioneer non-legumes became stronger relative to the other neighboring species guilds, leading to less difference in relative strength of competition among the four neighboring species guilds in intensive silviculture.

In contrast to the focal species guild of non-pioneer non-legumes, the focal species guild of non-pioneer legumes did not respond to neither silviculture nor neighboring species guilds. Competition from neighboring trees to focal trees of non-pioneer legumes was not dependant on identity of neighboring species guilds, indicating no effects of species identity on focal trees, or all neighboring species guilds had neutral effects on focal trees. From empirical evidence that although most of studies show the existence of hierarchical competition in template species forest trees (Canham et. al. 2004, Zhao et. al. 2006, Papaik et. al. 2009), neutral responses of tropical forest tree species to their neighbors were reported by a number of studies (Hubbell 2001, Uriarte et. al. 2004, Comita and Hubbell 2009). Some possible explanations for the neutral responses of the focal species guild of non-pioneer legumes would be: (i) its ability to fix

nitrogen so that it can be very flexible to self-adjust to neighbors; (ii) this focal guild only competed with its neighbors for soil resources, this underground competition is often size-symmetric, thus not dependant on its size and neighboring species identity.

The relation between competition and nutrient gradients has been a long debate (Wilson and Tilman 1991). Competition between individual plants was observed to be increased intensity with increasing nutrient (Keddy et. al. 1997, Grime 2001). In contrast, some ecologists reported that it does not vary with environment (Newman 1973, Tilman 1988, Wilson and Tilman 1991), but it shifts from below ground to above groups as nutrients become more available (Tilman 1988, Wilson and Tilman 1991). Our analyses showed that bigger initial tree size (both focal and neighboring trees) and higher density appeared in intensive silviculture (Table 3.2), but both observed and predicted current growths of the focal species guild of non-pioneer non-legumes was lower in intensive treatment than in traditional one (Fig 3.4b). Additionally, our prediction showed that neighborhood competition index was higher in intensive silviculture than in traditional silviculture (Fig. 3.6). This all indicates that competition was more intense in intensive silviculture than in traditional silviculture, supporting that intensity of competition increases with increasing nutrients (Keddy et. al. 1997, Grime 2001), reinforcing our findings that intensity of inter-specific competition increases with productivity gradients for the focal species guild of non-pioneer non-legumes. In contrast, we found that higher reduction in growth with increasing neighborhood competition index in traditional silviculture than intensive silviculture for the focal species guild of non-pioneer non-legumes (Fig 3.4b), indicating neighborhood competition was more important in the traditional silviculture than in the intensive silviculture (*sensu* Welden and Slauson,

1986). However, the focal species guild of non-pioneer legumes was not affected by silvicultural interventions (Table 3.6, Fig. 3.4b), suggesting that competition did not vary with nutrient gradients. Additionally, the focal species guild of non-pioneer legumes had smallest size compared to the other guilds' tree sizes (Table 3.2, Fig. 3.5), indicating they did not compete with others for light, but they were one of the strongest competitors for the focal species guilds of both non-pioneer legumes and non-pioneer non-legumes (Fig. 3.1). It can infer that competition between this focal guild with its neighbors shifted from above ground to below ground (Tilman 1988, Wilson and Tilman 1991). Intensity and importance of competition from neighboring trees to focal trees are focal species guild-dependent (Fig. 3.4).

One of objectives of mixing pioneers with non-pioneers in restoration plantations is to promote establishment of non-pioneer species through positive effects of pioneer species by providing shade and/or nutrients for non-pioneer species. In our study, we found neighboring species guilds of pioneers had very small effects (less 20%) on the focal species guild of non-pioneer non-legumes relative to per capital effects of the neighboring species guilds of non-pioneers, but no facilitation effect was detected on growth of individual trees. This would be due to (1) facilitation was more pronounced for survival than growth, specially for seedling life-stage (Goldberg et. al. 1999); (2) in our study both pioneer and non-pioneer species were planted at the same time, thus pioneer trees could not provide shade for non-pioneer trees which are usually shade-tolerance; (3) non-pioneer trees may have turned to shade-intolerant (from shade-tolerant species) during analysis period. This all would lead to a speculation that positive effects could be

occurred if time sequence of mixing pioneers and non-pioneers be taken into account (Kelty 2006).

Both theoretical (Heuhausser and Pacala 1999, Bolker et. al. 3002) and empirical (Wuethrich 2007) evidences show that when inter-specific competition is stronger relative to intra-specific competition, two species cannot coexist under equilibrium conditions. Our analyses showed that the neighboring species guilds of pioneer non-legumes became the strongest competitor for the focal species guild of non-pioneer non-legumes in intensive silviculture. With their much larger size (Fig. 3.5) and high abundance (~ 30% for pioneer non-legumes and 60% for both pioneer legume and pioneer legumes guilds, Table 3.2), the neighboring species guild of pioneer non-legumes would strongly suppress non-pioneer non-legume trees under intensive silviculture. This would imply that neighboring species guild of pioneer non-legumes would become a superior competitor and potentially exclude non-pioneer non-legume trees in intensive treatment. Over coming decades, shifts in competition may result from a variety of factors (such as insect or disease impacts on some species, wind-throw, and varying life spans among species), so the pioneer species may not totally exclude non-pioneer species in the long run. However, goals of restoring non-pioneer species do not appear to be fostered by relatively high densities of pioneer species.

Overall interactions between pioneer and non-pioneer species were complex. These interactions depended both neighboring species and focal species guilds and varied with silvicultural interventions. Some implications would be considered based on our results: (1) Monitoring and controlling abundance of pioneers should be carried out to avoid negative effects or even competition exclusion from pioneers on non-pioneers

during stand development; (2) Assembly of pioneers and non-pioneers along productivity gradients should follow a general rule that abundance of pioneers decreases with increasing productivity gradient. Although effects of shading on performance (mortality and growth) of non-pioneers are still debatable, some trials of planting non-pioneers under canopies of pines (Aston et. al. 1997), Acacia (McNamara et. al. 2006) showed promising results for seedlings of a number of non-pioneer species. Further studies should be carried out to test effects of shading on performance of non-pioneers under canopy of pioneers.

Table 3.1. Species groups/guilds classified based on species' characteristics (shade tolerance - non-pioneer species versus intolerance – pioneer species, and legume versus non-legumes)

| Pioneer (P) | | Non-pioneer (NP) | |
|---|-----------------------------------|----------------------------------|----------------------------------|
| Pioneer legume (PL) | Pioneer non-legume (PNL) | Non-pioneer legume (NPL) | Non-pioneer non-legume (NPNL) |
| 1. <i>Acacia polyphylla</i> | 1. <i>Luehea divaricata</i> | 1. <i>Hymenaea courbaril</i> | 1. <i>Ficus guaranitica</i> |
| 2. <i>Erythrina mulungu</i> | 2. <i>Croton urucurana</i> | 2. <i>Myroxylon peruiferum</i> | 2. <i>Tabebuia impetiginosa</i> |
| 3. <i>Peltophorum dubium</i> | 3. <i>Guazuma ulmifolia</i> | 3. <i>Poecilanthe parviflora</i> | 3. <i>Chorisia speciosa</i> |
| 4. <i>Enterolobium contortisiliquum</i> | 4. <i>Heliocarpus americanus</i> | | 4. <i>Jacaranda cuspidifolia</i> |
| 5. <i>Pterogyne nitens</i> | 5. <i>Schinus terebinthifolia</i> | | 5. <i>Lafoensia pacari</i> |
| | | | 6. <i>Cariniana estrellensi</i> |
| | | | 7. <i>Cedrela fissilis</i> |

Table 3.2. Basal area and growth at stand level in 11 years (total basal area and mean growth of all plots) and tree level in 8 and 11 years (mean basal area for tree level and coefficient of variation - CV)

| Treatments; Species guilds/groups | N | Species relative abundance (%) | Stand level | | Tree level | | | | | |
|--------------------------------------|------|---|---|--|---|-----------|---|-----------|---|-----------|
| | | | 2011 Basal area (cm ²) | CAI* (cm ² yr ⁻¹) | 2008 mean basal area (cm ²) | CV (%) | 2011 mean basal area (cm ²) | CV (%) | CAI (cm ² yr ⁻¹) | CV (%) |
| Intensive silviculture | 1175 | 100.0 | 148089.8 | 14001.7 | 90.3 | 120 | 126.0 | 119 | 11.9 | 155 |
| Pioneer legume | 363 | 30.9 | 71913.6 | 7397.3 | 137.0 | 100 | 198.1 | 102 | 20.4 | 133 |
| Pioneer non-legume | 344 | 29.3 | 51008.6 | 3689.5 | 116.1 | 89 | 148.3 | 84 | 10.7 | 125 |
| Non-pioneer legume species | 129 | 11.0 | 4583.7 | 780.8 | 17.4 | 125 | 35.5 | 114 | 6.1 | 114 |
| Non-pio. non-legume species | 339 | 28.9 | 20583.9 | 2134.0 | 41.8 | 109 | 60.7 | 107 | 6.3 | 136 |
| Traditional silviculture | 1011 | 100.0 | 103346.7 | 16925.3 | 52.0 | 152 | 102.2 | 154 | 16.7 | 185 |
| Pioneer legume | 331 | 32.7 | 57433.7 | 10119.8 | 81.8 | 134 | 173.5 | 135 | 30.6 | 154 |
| Pioneer non-legume | 306 | 30.3 | 29193.0 | 4054.8 | 55.6 | 111 | 95.4 | 95 | 13.3 | 106 |
| Non-pioneer legume species | 79 | 7.8 | 1723.6 | 352.3 | 8.4 | 129 | 21.8 | 120 | 4.5 | 125 |
| Non-pio. non-legume species | 295 | 29.2 | 14996.4 | 2398.4 | 26.4 | 167 | 50.8 | 145 | 8.1 | 195 |

Note: * Current annual increment in period of 2008 to 2011

Table 3.3. Summary of models and factors to be tested. Four neighborhood competition indices nested in two silvicultural treatments (traditional and intensive).

| Model | Maximum growth | | Size effects (S) | Neighborhood Competition effects | | | | | | Tested factors | |
|-------------------------------|------------------|---------------------------|------------------|----------------------------------|----------------------|--------------------------------|------|------|------|----------------|--|
| | Pooling (Maxgr1) | Partial pooling* (Maxgr2) | | Competition coefficients (C) | | Neighborhood competition index | | | | | |
| | | | | Pooling (C1) | Partial pooling (C2) | NCI1 ** | NCI2 | NCI3 | NCI4 | | |
| Without silvicultural effects | | | | | | | | | | | |
| 1 | ✓ | | ✓ | ✓ | | ✓ | | | | | No sensitivity (γ); identity (λ) |
| 2 | ✓ | | ✓ | ✓ | | | ✓ | | | | No sensitivity (γ); no identity (λ) |
| 3 | ✓ | | ✓ | ✓ | | | | ✓ | | | With sensitivity (γ), identity (λ) |
| 4 | ✓ | | ✓ | ✓ | | | | | | ✓ | Sensitivity (γ); no identity (λ) |
| With silvicultural effects | | | | | | | | | | | |
| 5 | | ✓ | ✓ | | ✓ | ✓ | | | | | No sensitivity (γ); identity (λ) |
| 6 | | ✓ | ✓ | | ✓ | | ✓ | | | | No sensitivity (γ); no identity (λ) |
| 7 | | ✓ | ✓ | | ✓ | | | ✓ | | | With sensitivity (γ), identity (λ) |
| 8 | | ✓ | ✓ | | ✓ | | | | | ✓ | Sensitivity (γ); no identity (λ) |

* Coefficients were partially pooled (or treated as random effects) by traditional and intensive silvicultural treatments. The coefficients were indexed 1 for traditional silvicultural treatment and 2 for intensive silvicultural treatment.

Table 3.4. List of parameters and their distributions from which they were developed.

| Parameter | Definition | Distribution |
|-----------------|---|-------------------------|
| 1. $\ln.\maxgr$ | log transform of Maximum growth (Maxgr) | Normal (0,.00001) |
| 2. C | Coefficient of Neighborhood competition effect | Normal (0,.00001)I(0,) |
| 3. $X0$ | Stem basal area at which Maxgr occurs | Normal (0,.00001) I(0,) |
| 4. Xb | Breadth of the function | Normal (0,.00001) I(0,) |
| 5. α | Shape of neighboring size effect to focal tree | Uniform (0,10) |
| 6. β | Shape of neighboring distance effect to focal tree | Uniform (0,10) |
| 7. γ | Sensitivity of focal size to neighborhood competition | Uniform (-5,5) |
| 8. λ | Shape of neighboring species group effect to focal tree (species competition coefficient) | Uniform(-1,1) |

Note: these distributions are fairly uninformative to maximize likelihood.

Table 3.5. Summary of factors tested (based on best model)

| Pooled data; data by treatments; Species guilds | Silviculture effects | | Neighborhood Competition Index | | | |
|---|-------------------------|------|---|------|--|------|
| | | | Sensitivity of focal tree size (γ) | | Neighboring group identity (λ) | |
| | W/out | With | W/out | With | W/out | With |
| Pooled data | | | | | | |
| Non-pioneer legume species | ✓ | | ✓ | | ✓ | |
| Non-pio. non-legume species | | ✓ | | ✓ | | ✓ |
| Intensive silviculture | | | | | | |
| Non-pioneer legume species | | | ✓ | | ✓ | |
| Non-pio. non-legume species | | | ✓ | | | ✓ |
| Traditional silviculture | | | | | | |
| Non-pioneer legume species | | | ✓ | | ✓ | |
| Non-pio. non-legume species | | | | ✓ | | ✓ |

Table 3.6. Parameter values with their 95% credible intervals from the best model of each focal species guild.

| Species guilds/ groups | Maximum growth (Maxgr) | | Size effects (S) | | Competition coefficients | |
|---------------------------------|-------------------------|-----------------------|---------------------------|-------------------|--------------------------|---------------------|
| | Traditional Maxgr[1] | Intensive Maxgr[2] | X0 | Xb | Traditional (C[1]) | Intensive (C[2]) |
| <i>Pooled data</i> | | | | | | |
| Non-pioneer legume species | 38.5 (24.1, 59.3) | - | 1573.4 (589.1, 2865.3) | 2.6 (2.3, 2.8) | 0.55 (0.1, 1.1) | - |
| Non-pio. non-legume species | 54.3 (33.9, 84.9) | 25.3 (17.5, 35.0) | 2128.1 (1027, 3555.6) | 3.0 (2.7, 3.3) | 3.6 (2.9, 4.5) | 2.1 (1.1, 3.0) |
| <i>Intensive silviculture</i> | | | | | | |
| Non-pioneer legume species | - | 38.8 (20.6, 70.1) | 1523.3 (511.2, 2984.3) | 2.6 (2.3, 2.8) | - | .61 (.05, 1.4) |
| Non-pio. non-legume species | - | 27.7 (16.2, 44.5) | 1657.2 (694.6, 2917.9) | 2.4 (2.2, 2.7) | - | .86 (.25, 1.6) |
| <i>Traditional silviculture</i> | | | | | | |
| Non-pioneer legume species | 36.0 (14.3, 73.9) | - | 1166.7 (225.4, 2596.9) | 2.5 (2.2, 2.9) | .57 (.04, 1.3) | - |
| Non-pio. non-legume species | 48.4 (29.0, 80.8) | - | 1588.5 (586.7, 2976.5) | 3.1 (2.7, 3.6) | 3.3 (2.6, 4.1) | - |

Note: PL: Pioneer Legumes; PNL: Pioneer Non-Legumes; NPL: Non-Pioneer Legumes; NPNL: Non-Pioneer Non-Legumes

Table 3.6. (continued)

| Species guilds/ groups | γ | α | β | Lambda (λ) – Species competition coefficients | | | | Variance |
|---------------------------------|----------------------|-------------------|-------------------|--|-------------------------|-------------------------|--------------------------|-------------------|
| | | | | PL ($\lambda[1]$) | PNL ($\lambda[2]$) | NPL ($\lambda[3]$) | NPNL ($\lambda[4]$) | |
| <i>Pooled data</i> | | | | | | | | |
| Non-pioneer legume species | - | .65 (.13,.99) | 0.53 (.04,.99) | - | - | - | - | .80 (.73,.89) |
| Non-pio. non-legume species | -.18 (-.27, -.09) | .63 (.38,.86) | .19 (.01,.62) | .45 (.09,.89) | .62 (.2,.97) | .55 (.04,.98) | .67 (.23,.99) | .88 (.83,.93) |
| <i>Intensive silviculture</i> | | | | | | | | |
| Non-pioneer legume species | - | 0.68 (.12,.99) | .47 (.02,.96) | - | - | - | - | .77 (.68,.87) |
| Non-pio. non-legume species | - | .64 (.17,.96) | .33 (.01,.93) | .44 (.03,.94) | .68 (.19,.99) | .49 (.02,.97) | .40 (.02,.93) | .92 (.86, 1.0) |
| <i>Traditional silviculture</i> | | | | | | | | |
| Non-pioneer legume species | - | .50 (.03,.97) | .56 (.04,.99) | - | - | - | - | .88 (.76, 1.0) |
| Non-pio. non-legume species | -.19 (-.28, -.09) | .37 (.19,.61) | .30 (.01,.93) | .17 (.01,.49) | .25 (.04,.62) | .64 (.11,.99) | .74 (.32,.99) | .83 (.76,.89) |

Note: PL: Pioneer Legumes; PNL: Pioneer Non-Legumes; NPL: Non-Pioneer Legumes; NPNL: Non-Pioneer Non-Legumes

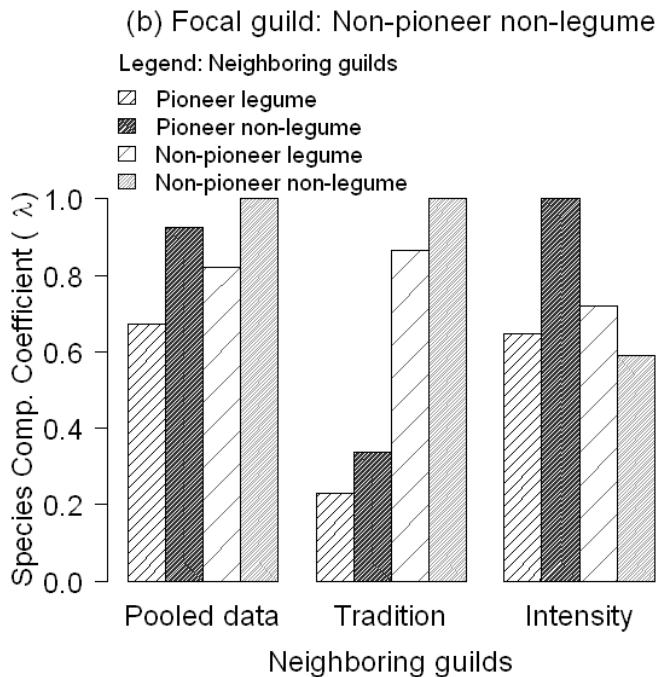
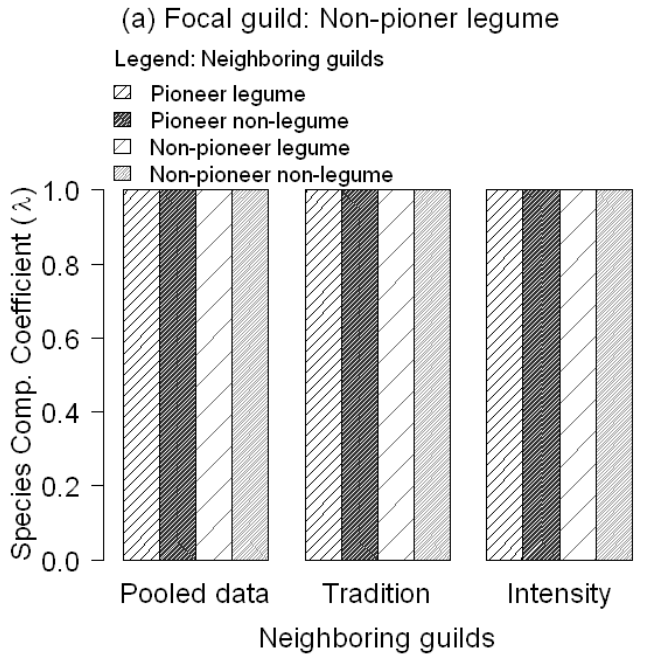


Fig.3.1. Relative effects of neighboring species guilds on focal guilds of non-pioneer legumes (a) and non-pioneer non-legumes (b), estimated by best model. λ was standardized by scaling λ_i by λ_{max} for each focal species guild. Non-pioneer non-legumes differed in responses to its neighboring species guilds, and its responses to neighboring species guilds varied with silviculture, but those patterns were not observed for non-pioneer legumes.

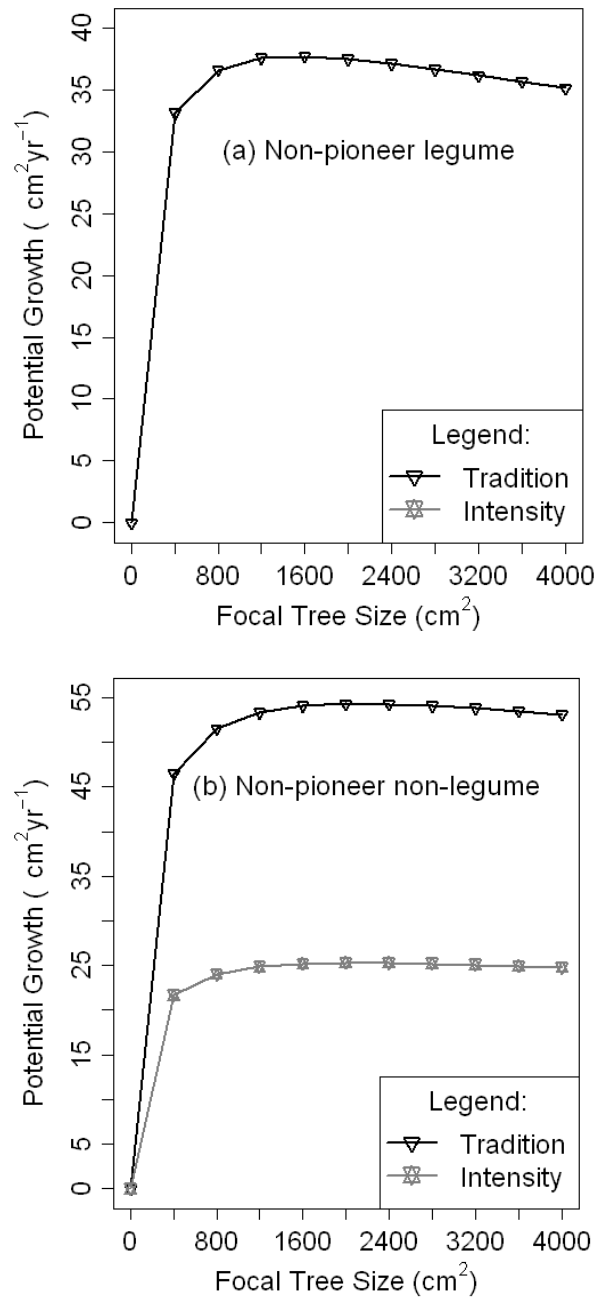


Fig.3.2. Size and silviculture effects on potential growth of the focal species guilds of non-pioneer legumes (a) and non-pioneer non-legumes (b). Potential growth of both non-pioneer legumes and non-pioneer non-legumes was strongly influenced by focal tree sizes, but silviculture only influenced on potential growth of non-pioneer non-legumes.

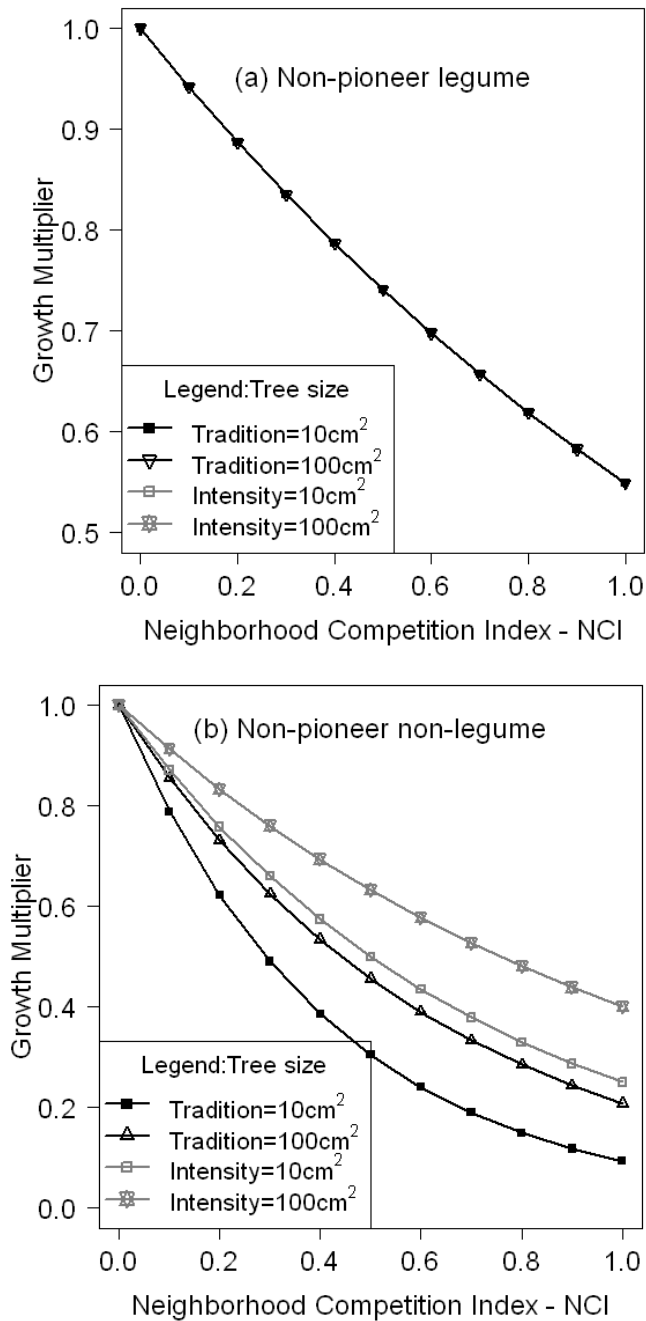


Fig. 3.3. Effects of Neighborhood competition on potential growth of small and big tree sizes of 10 cm² and 100 cm² of the focal species guilds of non-pioneer legumes (a) and non-pioneer non-legumes (b). Neighborhood competition strikingly reduced potential growth of individual trees of non-pioneer legumes and non-pioneer non-legumes. While neighborhood competition index is a function of focal tree size for non-pioneer non-legumes, it did not include focal tree size for non-pioneer legumes. Silviculture only varied neighborhood competition effects on non-pioneer non-legumes.

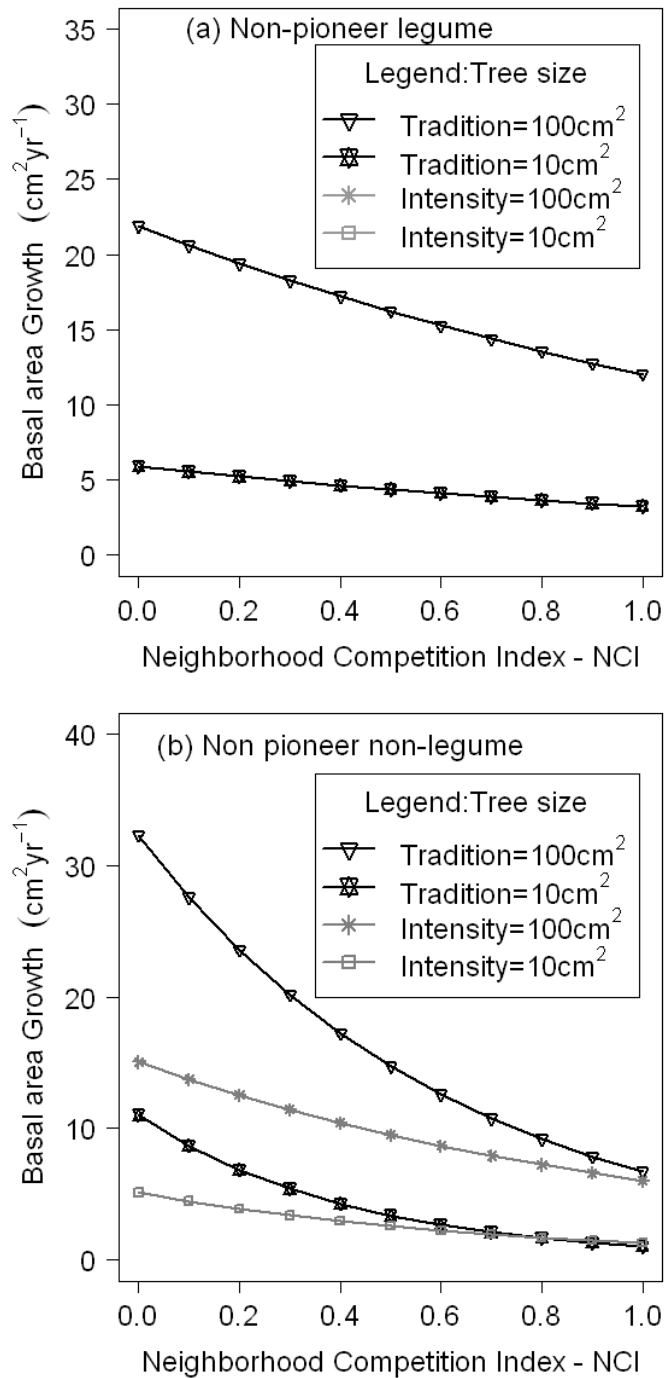


Fig.3.4. Effects of neighborhood competition on growth of small tree size of 10 cm² and big tree size of 100 cm² for the focal species guilds of non-pioneer legumes (a) and non-pioneer non-legumes (b). Individual tree growth of both focal guilds was strongly influenced by its size and neighborhood competition. However two focal guilds differed in responses to silviculture, while silviculture strikingly affected on non-pioneer non-legumes, it did not affect on non-pioneer legumes.

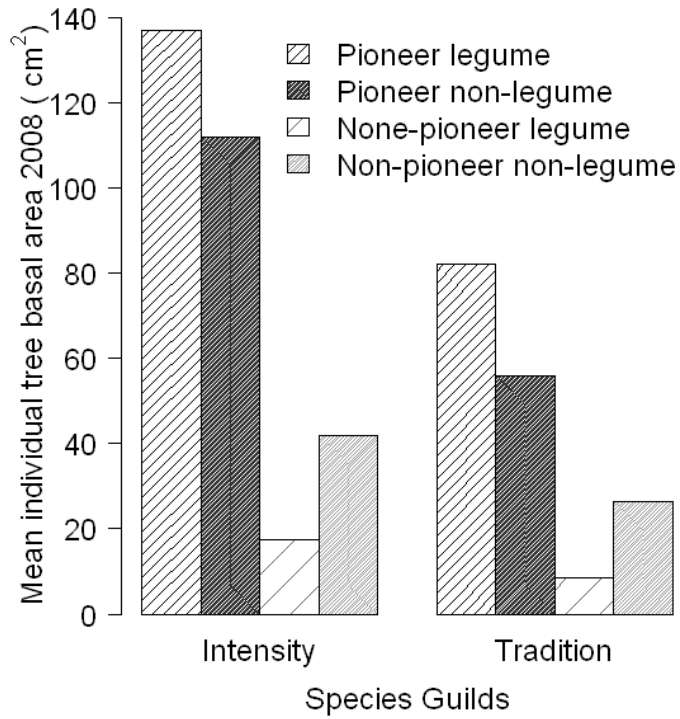


Fig. 3.5. Basal area of species guilds. Striking differences in basal area of pioneer legumes and pioneer non-legumes in traditional and intensive silviculture, probably leading to a stronger suppression on non-pioneers, consequently resulting in a change of mode of neighborhood competition of non-pioneer non-legumes.

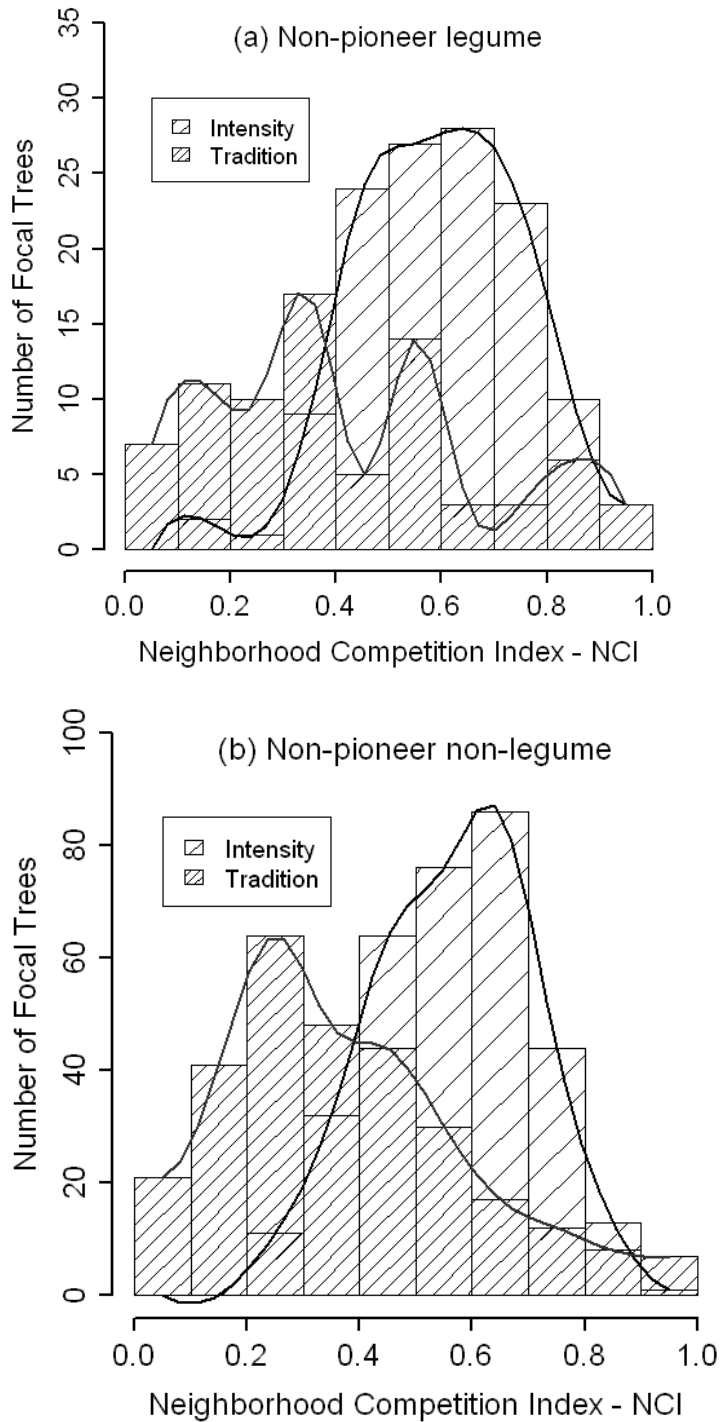


Fig. 3.6. Distribution of neighborhood competition index estimated from best models for the focal species guilds of non-pioneer legumes (a) and non-pioneer non-legume (b). Intensive silviculture clearly increased neighborhood competition index of both focal guilds of non-pioneer legumes and non-pioneer non-legumes.

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Appendix

Table S.1. Deviance Information Criterion (DIC), adjusted correlation coefficients (R^2) and difference in DICs between candidate models with smallest DIC (Δ_i) of focal groups of non-pioneer legume and non-pioneer non-legumes. The model with lowest DIC is the most parsimonious; the model with the highest R^2 has the best goodness of fit.

| Model | Focal guild of non-pioneer legumes | | | Focal guild of non-pioneer/non-legumes | | |
|----------|------------------------------------|--------------|-------------|--|---------------|------------|
| | R^2 | DIC | Δ_i | R^2 | DIC | Δ_i |
| 1 | 0.72 | 498.8 | 0.00 | 0.52 | 1632.5 | 24.5 |
| 2 | 0.71 | 498.9 | 0.10 | 0.52 | 1637.1 | 29.1 |
| 3 | 0.71 | 505.3 | 6.46 | 0.53 | 1616.5 | 8.5 |
| 4 | 0.71 | 504.3 | 5.46 | 0.53 | 1618.4 | 10.4 |
| 5 | 0.71 | 501.0 | 2.16 | 0.53 | 1619.0 | 11.0 |
| 6 | 0.72 | 501.4 | 2.56 | 0.53 | 1621.1 | 13.1 |
| 7 | 0.71 | 507.5 | 8.74 | 0.54 | 1608.5 | 0.5 |
| 8 | 0.71 | 507.7 | 8.86 | 0.54 | 1608.0 | 0.0 |
| Ranking* | 0.72 | 498.8 | | 0.54 | 1608.0 | |

* ranking by min DIC and max R^2 .

Table S.2. Deviance Information Criterion (DIC), adjusted correlation coefficients (R^2), and difference in DICs between candidate models with smallest DIC (Δ_i) of the focal groups of non-pioneer legumes and non-pioneer non-legumes separated by silvicultural treatments. The model with lowest DIC is the most parsimonious; the model with the highest R^2 has the best goodness of fit.

| Model | Focal group of Non-pioneer legumes | | | Focal group of Non-pioneer/non-legumes | | |
|--------------------------|------------------------------------|--------------|------------|--|--------------|------------|
| | R^2 | DIC | Δ_i | R^2 | DIC | Δ_i |
| Intensive silviculture | | | | | | |
| 1 | 0.74 | 297.8 | 0.0 | 0.51 | 878.4 | 1.2 |
| 2 | 0.74 | 298.4 | 0.5 | 0.51 | 877.2 | 0.0 |
| 3 | 0.73 | 303.2 | 5.4 | 0.51 | 885.3 | 8.1 |
| 4 | 0.73 | 304.5 | 6.7 | 0.51 | 887.6 | 10.2 |
| Ranking* | 0.74 | 297.8 | | 0.51 | 878.4 | |
| Traditional silviculture | | | | | | |
| 1 | 0.66 | 206.5 | 0.0 | 0.55 | 745.4 | 16.5 |
| 2 | 0.66 | 207.2 | 0.7 | 0.56 | 744.2 | 15.3 |
| 3 | 0.65 | 212.0 | 5.5 | 0.56 | 734.2 | 5.3 |
| 4 | 0.65 | 214.0 | 7.5 | 0.58 | 728.9 | 0.0 |
| Ranking* | 0.66 | 206.5 | | 0.58 | 728.9 | |

* ranking by min(DIC) and max (R^2)