

**DISSERTATION**

**PATTERNS OF GROWTH DOMINANCE AND  
NEIGHBORHOOD EFFECTS IN EUCALYPTUS PLANTATIONS AND  
TROPICAL FORESTS**

**Submitted by**

**Doi The Bui**

**Department of Forest, Rangeland, and Watershed Stewardship**

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DOI BUI ENTITLED PATTERN OF GROWTH DOMINANCE AND NEIGHBORHOOD EFFECTS IN EUCALYTUS PLANTATIONS AND TROPICAL NATURAL FORESTS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

**Committee on Graduate Work**

[Redacted signature area]

[Redacted signature area]

**Adviser**

**Co-Adviser (if applicable)**

[Redacted signature area]

## ABSTRACT OF DISSERTATION

### PATTERNS OF GROWTH DOMINANCE AND NEIGHBORHOOD EFFECTS IN EUCALYPTUS PLANTATIONS AND TROPICAL FORESTS

Forest stands have a broad range of tree sizes, even when all trees develop as a single cohort. Differences in size might result from different rates of resource uptake or resource use efficiency. Dominant trees often account for the majority of increment, but non-dominant trees can contribute a major part of stand growth in some cases. Pattern of growth dominance may provide predictive insight into the growth of trees and forest. My dissertation contains three chapters to explore growth dominance patterns of *Eucalyptus* plantations in Hawaii and Brazil, and natural tropical forests in Panama.

Chapter 1: Growth dominance was assessed in young plantations of *Eucalyptus saligna* under different treatments of planting density and fertilization. I found that effects of density treatment on stand growth declined over time, while those of fertilization increased in ways that accentuated changes of stand development. The strong growth dominance pattern was exhibited under all treatments. The growth dominance positively increased over age. High density increased growth dominance, but high fertilizer had little effect on it. The growth dominance increased slightly as stand biomass and the variation in tree sizes increased.

Chapter 2: The 70-year-old plantations were used to explore the pattern of growth dominance. The growth of trees was still influenced strongly by neighbors. The interaction with neighbors explained 52% of the variation in focal tree in Hawaii, and 32% in Brazil. The accumulated stem biomass was high in old plantations, yet growth dominance by large trees remained strong or moderate; “reverse pattern” was not supported.

Chapter 3: Pattern of growth dominance in natural tropical forests was characterized in Panama. The “reverse pattern” was exhibited as expected. Tree growth increased with tree size, but the contribution of large trees to stand growth was lower than their proportional contribution to stand biomass. The reverse growth dominance was stronger in old tropical forests than the 20-year-old one recovered from clear-cutting. Growth dominance pattern did not change in two decades.

Doi The Bui  
Department of Forest, Rangeland, and Watershed Stewardship  
Colorado State University  
Fort Collins, CO 80523  
Fall 2008

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## INTRODUCTION

Forest development leads to changing competitive environments for each tree, with some trees increasing dominance over others (Oliver and Larson 1996, Franklin et al. 2002, Long et al. 2004, Binkley et al. 2006). Forest stands have a broad range of tree sizes, even when all trees develop as a single cohort, in even-aged stands. Differences in size might result from different rates of resource uptake or efficiency of resource use, leading to differences in tree growth rates. Larger, dominant trees often account for the majority of increment in a stand. However, smaller or non-dominant trees can contribute a major part of stand growth in some cases. Patterns of growth dominance through stand development may provide predictive insight into the growth of trees and forest. Conceptually, a four-phase model for stand development was proposed by Binkley (2004), with forests progressing from little or no dominance early in stand development to strong dominance when larger trees account for a disproportionately large amount of total stand growth. In late stages of stand development, dominant trees may decrease to the point where smaller trees account for most of stand growth. Some phases of this model have been tested in young plantations (Binkley et al. 2002, 2003, 2004), and in natural temperate forests (Binkley et al. 2006). However, patterns of growth dominance and its change over time are lacking in old plantations, mixed species stands, and natural forests in the Tropics. Moreover, changes of growth dominance under varied silvicultural treatments in young plantations remain unknown.

In stand development, two common patterns have been observed: (1) trees differentiate into various classes, including dominant, co-dominant, intermediate and

suppressed (Oliver and Larson 1996); and (2) there is an increase in stand production at early stage, followed by a peak at the canopy closure, and then a decline at late stage of stand development (Ryan et al. 2004). The decline in annual production of wood after canopy closure is very common, but may not be universal. These patterns relate to tree competition for resources (Archibold 1995), that some trees may capture more resources (especially light) than the others, and use them more efficiently, leading to the difference in tree sizes (Binkley et al. 2004). There is a trade-off between competing for light and competing for nutrients (Tilman 1988). In theory, this could reduce leaf area index (LAI) in nutrient-poor settings. Where nutrients are in short supply, trees invest more in roots (Leigh 1999). Many studies have shown the empirical evidence for the peak and decline of forest productivity (Assmann 1970, Ryan et al. 1997, 2004).

The current structure of a stand has been shaped by the historical and environmental processes related to the spatial patterning (Moeur 1993, Pretzsch 1997, Youngblood et al. 2004) and development of individual trees. Stand structure changes over time as a result of the invisible inter- and intra-specific interactions of trees. At a given age, a stand exposes its pattern of development as a result of interacting processes inside (Binkley 2004). In turn, the current arrangement of trees (a component of stand structure) influences stand development and production through controlling individual tree growth and competition (Boyden 2005). The range of tree sizes and spacing is greater in older stands, continuing to influence tree growth. Are competitive interactions between trees strong at the old stands? How do they influence the variability in tree growth?

My dissertation explores patterns of growth dominance at young and old *Eucalyptus* plantations in Hawaii and Brazil, and at tropical natural forests in Panama. Chapter 1

explores response of growth dominance to silvicultural treatments in young plantations of *Eucalyptus saligna* near Pepeekeo, Hawaii. Chapter 2 looks at the spatial, neighborhood effects on individual tree growth, testing for a predicted pattern of “reverse” growth dominance pattern in 70-year-old monoculture plantations in Hawaii and Brazil. Chapter 3 explores the pattern of growth dominance in tropical natural forests in Panama to see if patterns in forests with large, old trees differ between monocultures and diverse native forests.

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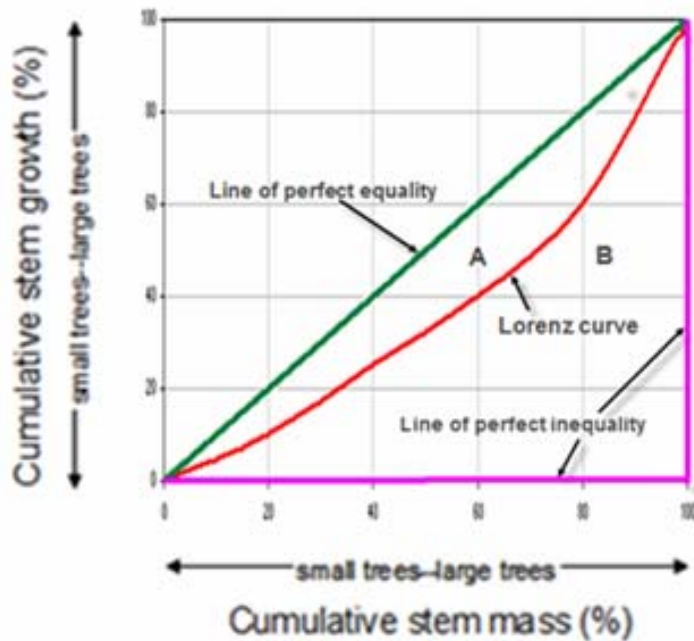
## **IMPLICATION OF GROWTH DOMINANCE PATTERN**

Growth dominance is dominance in increment (a quantitative increase in size in a specified time interval due to growth) of a tree or a group of trees compared to other trees or groups within a stand. Growth dominance pattern is a pattern of cumulative distribution of stem growth (increment) as a function of cumulative stem biomass (Binkley 2004). Growth dominance pattern reflects the productivity of a portion of trees in a stand. The pattern may change over time depending on the growth and resource use efficiency of forest trees.

The Lorenz curve and Gini coefficient were applied to characterize growth dominance pattern and calculate growth dominance coefficient at stand level. The Lorenz curve is a graphical representation of the cumulative distribution function, often used to show income distribution. The percentage of households is plotted on the X axis (ranked from lowest to highest), with the corresponding cumulative incomes on the Y axis (Model 1). It can also be used to show distribution of assets. The Gini coefficient is a measure of statistical dispersion applied to the Lorenz curve, most prominently used as a measure of inequality of income distribution or inequality of wealth distribution. It is defined as a ratio, in which the numerator is the area between the Lorenz curve of the distribution and the uniform distribution line (line of perfect equality, i.e. 1:1 line, Model 1), and the denominator is the area under the 1:1 line. The Gini coefficient is between 0 and 1. It would be 0 when all observations line up along the 1:1 line (all trees show growth proportional to size), and a maximum approaching 1.0 (all trees has 0 growth except for one). The Gini index is the Gini coefficient expressed as a percentage, and is

equal to the Gini coefficient multiplied by 100 (an approach to calculation of Gini coefficients in Appendix by Satoshi M. 2003).

To apply this approach in ecological study, trees were ranked from smallest to largest in size (biomass) within a stand, and put on X axis by percentage. The percentage of total stand growth (increment) contributed by each tree was placed cumulatively on the Y axis, with the same tree order as on the X axis (Binkley 2004). A stand has a “strong growth dominance” if the curve falls far below the 1:1 line with a strongly positive growth dominance coefficient.

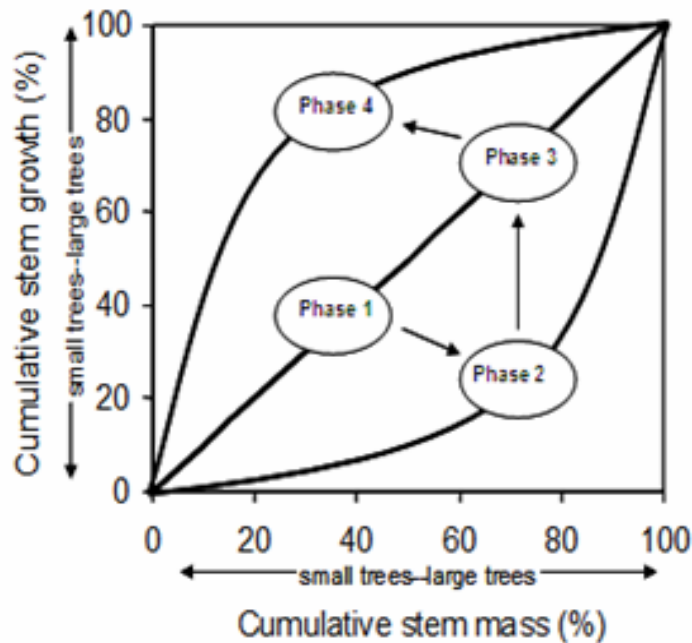


Model 1. Lorenz curve, line of perfect equality (1:1 line) and line of perfect inequality

The classic use of Lorenz curve and Gini coefficient for economic distributions cannot be above the 1:1 line, because the X axis is simply a ranked sort of observations. However, using the cumulative distribution of tree mass on the X axis allows the growth dominance curve to rise above 1:1 line, leading to negative growth dominance

coefficient. A stand has strong “reverse” growth dominance if the curve lies far above the 1:1 line, with a big negative growth dominance coefficient.

Pattern of growth dominance for a given stand may be one of the four phases (Model 2) proposed by Binkley (2004).



Model 2: Conceptual model of four phases of growth dominance in stand development (Binkley, 2004). Cumulative stem biomass for the stand is plotted on the X axis, with trees ranked from smallest to largest. Cumulative stem growth (production) is plotted on Y axis, with the same tree ranking. Phase 1 (no or little dominance) where trees express similar contributions to stand growth as well as stand mass (equality). Phase 2 is a period of strong growth dominance, where larger trees account for a disproportionately large amount of total stand growth (inequality). Growth dominance declines during phase 3 as growth of the larger trees slows. Phase 4 shows “reverse growth dominance” when the growth of larger trees is less than their proportional contribution to total stand biomass.

## CHAPTER 1

### RESPONSE OF GROWTH DOMINANCE TO SILVICULTURAL TREATMENTS IN YOUNG PLANTATIONS OF *EUCALYPTUS SALIGNA*

#### Abstract

I used existing datasets from 18 interior plots of the experimental plantation of *Eucalyptus saligna* established in May 1994 near Pepekeo, Hawaii to test the impacts of planting density and fertility treatments on growth dominance pattern. Effects of density treatment on stand growth decreased over age, while the effects of fertilizer increased in ways that accentuated changes of stand development and growth dominance. The expectation of strong growth dominance in the young plantation was strongly supported by giving positive growth dominance coefficients. Growth dominance was stronger in the high density treatment at all ages, but very variable with the fertility treatments. Growth dominance coefficient increased over age, from 0.30 at age 3 to 0.36 at age 6, and 0.45 at age 8 and 10 in the high-density treatment; and from 0.11 at age 3 to 0.16 at age 6, and 0.24 at age 8 and 10 in the low-density treatment. Growth dominance slightly increased over increased stand biomass and variation in tree sizes under all treatments and at all ages. Future work is needed to explore changes of growth dominance patterns for older plantations, and responses of growth dominance to other treatments as well.

*Keywords: stand growth; growth dominance; competition; forest plantation; Eucalyptus saligna*



## **1.1. Introduction**

Forest growth and development are important attributes determining the structure of a forest (Oliver and Larson 1996). In turn, stand structure is a key factor influencing the growth, function and disturbance regimes of forests (Boyden 2005). Changes in forest structure affect processes such as photosynthesis and respiration (Waring and Schlesinger 1985; Coops et al. 2001) and tree growth (O'Hara 1988, 1989; Smith and Long 1989; Arbaugh and Peterson 1993), related to variation in the amount and distribution of leaf area. Changes in structure also influence suitability for wildlife (Hunter 1990, Morrison 1992), and composition of under-story communities (Latham 1998).

Stand development leads to changing competitive environments for each tree, with some trees increasing dominance over others (Oliver and Larson 1996, Franklin et al. 2002, Long et al. 2004). Larger trees (i.e., dominant trees in size) are typically expected to obtain a larger portion of site resources than smaller trees in stand, and growth rates (both absolute and relative) typically differ among size classes. The relationship between stand growth and dominance can be represented by a pattern of cumulative distribution of stem increment as a function of cumulative stem mass (Binkley 2004). A specific pattern of growth dominance may be shown in a stand at a certain age, and accounts for stand development at that age.

Stand growth dominance changes over time (Binkley 2004) and closely relates to current increment of all trees. The growth of dominant trees continues to increase in a

stand, even after the growth for the whole stand has declined (Assmann 1970). However, the growth of non-dominant trees may be a cornerstone for growth dominance pattern.

Some recent studies showed the different patterns of growth dominance, such as a “strong dominance” pattern for young plantations of *Eucalyptus saligna* (Binkley et al. 2002, 2003, 2004), and a “reverse dominance” pattern for the natural forests of the Rocky Mountains, USA (Binkley et al. 2006). These studies also mentioned the interaction of tree dominance and stand production through stand development. A hypothesis was proposed that changes in the growth of trees and stands resulted from regular changes in dominance and resource-use efficiency by dominant and non-dominant trees (Binkley 2004). From these studies, changes in growth dominance in particular and forest dynamics in general have been explored. However, growth dominance and its changes in plantation stands under different silvicultural treatments remain unknown.

Growth dominance patterns are expected to differ among forest type, through stand age (Binkley et al. 2006), and in response to silvicultural treatments. Growth rates of dominant trees would increase under greater tree spacing and higher resource availability because of less competition. Supply of fertilizers is a practice to meet the ability of fast-growing trees to achieve extremely high rates of production (Nambiar and Brown 1997). Rapid growth of dominant trees should have a positive feedback, leading to greater resource acquisition (relative to non-dominant trees) and further increases in growth rates (Binkley 2004). Therefore, this chapter was developed to test a hypothesis that growth dominance would be stronger under higher density and better nutrient supply (high fertilization) in young stands of *Eucalyptus saligna*. In addition, growth dominance

would be expected to increase over stand age, then declining as growth rates diminish. Binkley (2004) showed the onset of dominance at two years in a monoculture of *Eucalyptus saligna* in Hawaii, increased dominance through the age 10 years, then a relaxation of dominance by the age of 20. However, patterns of tree or species dominance and changes in stand structure are the results of complex interactions, but not the result of obligatory laws (Oliver and Larson 1996). Therefore, our ability to make general inferences will depend on accumulating a body of evidence of patterns of growth dominance.

The objectives of the chapter were to elucidate the impact of silvicultural treatments on stand growth and growth dominance in young plantations, testing the hypothesis of positive associations between stand growth rates and growth dominance in response to spacing, fertilization, and stand age. The homogeneity, rapid growth, and early canopy closure of *Eucalyptus saligna*, resulted in widespread, short-rotation plantations throughout the Tropics, with more than 15 million ha (Neilson 2000, FAO 2007). Improvements in intensive silviculture have provided tremendous improvements in stand growth rates over the past 30 years (Stape 2002a). Improved understanding of relationships between stand growth and growth dominance is useful for further enhancing and sustaining plantation productivity.

## **1.2. Materials and method**

### ***Study site description***

An experimental plantation of *Eucalyptus saligna* was established near Pepeekeo, Hawaii in May 1994. This plantation experiment was funded by grants DEB93-06356

and DEB97-08521 from the National Science Foundation (Photo 1). It is located at 19°50'28.1 N and 155°07'28.3 W, about 13 km northeast of Hilo. The 4-ha plantation was at 350 m elevation, with a mean annual temperature of 21°C and average annual rainfall of 4,000 mm (Binkley et al. 1992). Rainfall is distributed uniformly through the year, but the winter months tend to be wetter and cloudier, and have shorter daylight periods. The slope is modest (<5%) and the soils are over 2 m deep, acidic (pH 5–6 in water), thixotropic, isothermic Typic Hydrudands in the Kaiwiki series (Binkley and Resh 1999). Previous land use included 80 years of sugarcane agriculture. In 1993, the last sugarcane crop was harvested about one year before the planting of *Eucalyptus* seedlings. The site was fallow for nine months, plowed in February of 1994 to turn under the developing vegetation (mostly C<sub>4</sub> grasses), sprayed two months later with glyphosate herbicide (Roundup, Monsanto Company Agricultural Products, St. Louis, Missouri, USA).



Photo 1. Aerial view of the 30 x 30 m plots at 18 months old. Closed-canopy plots were planted at 1 x 1 m spacing (high-density); more open plots were planted at 3 x 3 m spacing (low-density). A gully/buffer strip winds through the middle of the plantation. Photo credit: R. S. Senock from Ryan et al. (2004)

The *Eucalyptus saligna* seedlings were planted in May of 1994 after six months in a greenhouse from a single, open-pollinated seed stock. This site was previously used to test hypotheses about causes of age-related decline in growth rates (see Binkley et al. 2002, Giardina et al. 2002, Ryan et al. 2004).

### ***Experimental design***

The plantation for this study contained 18 30 x 30 m plots. 18 interior subplots (nine 10 x 10 m, and nine 15 x 15 m) were set up using a 2 x 3 factorial combination of tree spacing (i.e. planting density) and fertility treatments in a randomized complete block design (RCB). The experiment was designed with two levels of tree spacing (1 × 1 m or 3 x 3 m) equal to 10000 trees/ha (“high density,” HD) or 1111 trees/ha (“low density,” LD) at planting, and three levels of fertilization (“control,” CT; “high fertilization,” HF; or “restore fertilization,” RF), organized in three randomized blocks. The three fertilization regimes were designed to test the role of changes in nutrient limitation over time for the previous study. The control treatment received modest fertilization at the time of planting and at 6 months old, and the HF treatment was fertilized heavily several times each year to remove any possible nutrient limitation (Ryan et al. 2004). The RF treatment was treated like the control treatment until age 3 years when fertilization rates matched those of the HF treatment in April of 1998.

### ***Growth measurements***

Diameter at 1.37 m height of all stems in the interior subplots was first recorded in January 1995, 7 months after planting. Measurements of diameter were repeated at every 2 - 3 months until 79 months, then repeated at every one or two years. The last

measurement was in July 2004. I used data measured at ages 14, 24, 36, 49, 60, 72, 96 and 122 months (equivalent to 1, 2, 3, 4, 5, 6, 8 and 10 years old, respectively) for this analysis. All these data were inherited from the previous studies conducted in this experimental forest (Ryan et al. 1997, 2004; Binkley et al. 2002, Giardina et al. 2002).

### ***Aboveground woody biomass (AGB<sub>w</sub>) estimation***

AGB<sub>w</sub> (including boles, bark, and branches) was estimated using the available allometric equation of aboveground woody biomass (in kg) and diameter at breast height (dbh, in cm):  $AGB_w = 0.0662*(dbh)^{2.50}$ , with SEE = 1.16 kg,  $r^2 = 0.99$ ,  $P < 0.001$ ,  $n = 57$  (Ryan et al. 2004). Trees used to develop this equation were randomly sampled from the 10-m buffer area of each plot, periodically throughout the study. Allometry did not differ among treatments or over time (Ryan et al. 2004).

Woody biomass current annual increment (CAI) was calculated as follow:  $CAI = \text{woody biomass of current year} - \text{woody biomass of previous year}$ . I assumed that a tree would have “no increment” if its diameter at the current measurement was smaller than that at the previous one.

### ***Statistical analysis***

The random assignment of treatments to plots made these analyses appropriate for RCB. Diameters of trees of each subplot were repeatedly measured. Multiple measurements on the same experimental unit were not independent. They would be correlated. This experiment was two-factor-repeated-measures design, in which tree spacing and fertility were two factors, and stand age was repeated measure. Stand growth and growth dominance coefficient were assessed with a randomized-block, repeated

measures ANOVA, using data from year 3 to 6 (the period 1 with one-year interval) because canopy closure for the LD treatment occurred in year 2 (Ryan et al. 2004), RF treatment was applied at year 3, and one of the LD-HF plots was harvested in 1999 for another study (Binkley et al. 2002); and data from year 6 to 10 (the period 2 with two-year interval). Two periods were analyzed using two density treatments (HD and LD) and three fertility treatments (CT, HF, and RF). ANOVA was accomplished using SAS Proc Mixed with “REML” estimation method, which can accommodate missing cells, and Proc GLM using Tukey’s HSD with a  $P < 0.05$  for a Type I error (SAS version 9.0 SAS Institute Inc., Cary, NC. 1999)

### **1.3. Results**

#### **1.3.1. Stand growth**

At the investigation in July 1995 (14 months after planting), the plots with  $3 \times 3$  m spacing (LD) had on average 1175 stems/ha, compared to 9444 stems/ha on average of the plots with  $1 \times 1$  m spacing (HD). The density declined at a rate of -12% per year in the HD plots and -3% per year in the LD plots, respectively (Fig. 1.1). Increased competition between trees was the main reason for declined density, especially after canopy closure. Density of some LD plots at ages 1 to 3 years was greater than the initial planting density (1111 trees/ha) due to “sprouting” of *Eucalyptus saligna*. There were more than one stem from a tree planted.

Aboveground biomass of the young *Eucalyptus* plantation increased rapidly over age, especially in the LD treatment (Figs 1.4 and 1.10A). Until age 6 years, aboveground

woody biomass was lower in the LD treatment than the HD treatment, but did not differ at age 8 (~134 Mg/ha), then was greater in the LD at age 10 (Fig. 1.10A).

Stand growth rate changed strongly over time and fertility treatment at two periods of stand development ( $P < 0.001$ , Table 1.1), and with tree spacing at the period 2 ( $P = 0.002$ ), but not with tree spacing at the period 1 ( $P = 0.43$ ). Stand growth under all treatments decreased rapidly over time until age 5 years, and slightly increased at age 6 years, then declined again at age 8 years, finally balanced at age 10 years (Fig. 1.2).

Interaction of tree density and fertility treatments exhibited significantly different effects on stand growth at the period 1 ( $P < 0.001$ ), but not at the period 2 ( $P = 0.11$ ). However, this interaction did not differ with stand age at both periods (Table 1.1).

At year 2, the combination of HD-HF treatment lead to the highest growth of 33.4 Mg ha<sup>-1</sup>yr<sup>-1</sup> (Fig. 1.3), significantly different from the growth of other combinations ( $P < .01$ ), while the combination of LD-CT treatment showed the smallest growth (19.6 Mg ha<sup>-1</sup>yr<sup>-1</sup>). At year 5, two years after fertilizing in the RF plots, stand growth was significantly different. The LD-RF combination had the highest growth (23.4 Mg ha<sup>-1</sup>yr<sup>-1</sup>), while HD-CT combination showed the lowest (Fig. 1.3).

### **1.3.2. Growth dominance**

The density treatment strongly affected growth dominance in two periods, while fertility treatment was significant at only the period 2 ( $P < 0.004$ , Table 1.1), several years after applying fertilizers. Growth dominance changed strongly with stand age (Fig. 1.10 B), especially in the period 1 ( $P < 0.001$ , Table 1.1). Density and fertility treatments showed strong interactions in the period 1 ( $P < 0.01$ ), but not at period 2 ( $P = 0.12$ ). The



interaction of density  $\times$  age and fertility  $\times$  age were not significant at any period, while the density  $\times$  fertility  $\times$  age interaction was significant at period 1 with  $P = 0.01$  (Table 1.1). Therefore, it would be appropriate to assess 6 combinations of density and fertility treatments rather than looking at separate treatment of density or fertility.

When two factors (density and fertility) were analyzed in the last year of each period, the density treatment exhibited strong effects on growth dominance at all ages, from 3 to 10 ( $P < 0.001$ ; Table 1.2), while fertility treatment did not until age 8 ( $P = 0.04$ ), and age 10 ( $P = 0.05$ ). Density and fertility interaction was not significant at ages, except at age 4 and 5. Therefore, I assessed growth dominance of 6 combinations of density and fertility treatments in these two ages (Fig. 1.5) in order to test the response of growth dominance to these treatments.

Response of growth dominance to two silvicultural treatments at each age was variable. At age 3, density treatment affected growth dominance while fertility treatment did not. Growth dominance coefficients averaged 0.30 (SD: 0.05) in the HD treatment, significantly different from 0.10 (SD: 0.03) in the LD treatment (Fig. 1.4). At year 6, the coefficients increased compared to those in year 3 in both treatments ( $0.36 \pm 0.05$  and  $0.16 \pm 0.07$  in the HD and LD treatments, respectively). Fertility treatment still did not exhibit the different effect on growth dominance (Fig. 1.6). At year 8, the effect of density was still strong ( $P = 0.01$ ), and effect of fertility started to increase. Positively great coefficients of all combinations at age 8 indicated that growth dominance remained strong under all silvicultural treatments.

Growth dominance also responded to silvicultural treatments when the two-year interval was applied (period 2). The effects of density and fertility treatment were

significant, but the interaction was not ( $P = 0.12$ ; Table 1.1). At year 10, growth dominance coefficient of the HD plots was significantly higher than that of the LD plots ( $0.45 \pm 0.14$  versus  $0.24 \pm 0.07$ ). Besides, the control treatment caused greatest growth dominance at this age (0.63 at the HD-CT treatment), significantly different from the HF and the RF treatments. Both density and fertility treatment had significant effects on the growth dominance at age 10 (Table 1.2 and Fig. 1.4). However, the growth dominance at age 10 did not differ from that at age 8 in each combination, indicating a relaxation of growth dominance in coming years.

Growth dominance coefficient changes not just over age, but also in relation to stand biomass and variation in tree size. In two density treatments, growth dominance coefficient increased linearly with coefficients of variation in tree sizes (Fig. 1.9). The variation was greater in the HD treatment than in the LD treatment. Growth dominance increased slowly with increased stand biomass as well with  $r^2 = 0.11$ ,  $P = 0.015$  for the HD treatment, and  $r^2 = 0.14$ ,  $P = 0.007$  for the LD treatment, respectively (Fig. 1.10 C).

## **1.4. Discussion**

### **1.4.1. Response of stand growth to the planting density treatment**

The naturally decreased density or self-thinning is a universal process in stand development. Tree leaf area reaches a maximum sooner in the higher density stands (Ryan et al. 2004), resulting in the higher mortality. In this analysis, initial planting density played a substantial role in changing stand structure and growth over a span of 10 years of the *Eucalyptus saligna* plantations. In stands with smaller growing space (the HD treatment) the intense competition was exhibited, resulted in greater decrease in

density, especially after the canopy closure (Fig. 1.1). Therefore, stand growth changed strongly in relation to planting density.

In first two years, density treatment was the crucial reason for a different increase of stand growth, ramping up by 50 to 100% each year, peaking in year 3 (except the combination of the HD-CT; Fig. 1.2). The growth rate of plots did not completely follow the universal pattern as presented by Ryan et al. (1997) because they were applied with the restore fertilization regime, by which some of plots received more fertilizer since age 3. In general, the growth pattern was the same with two density treatment under the same fertility treatment. The stand growth increased and reached a peak after 3 years growing, followed by a decline of -32% at age 4 years and about -6% at age 5 years, then slightly increased at year 6 before a gradual decline to the age of 10 years at most stands (Fig. 1.2). In the 20<sup>th</sup> century, the decline in growth in old stands was explained by a changing balance between photosynthesis and respiration (Yoda et al., 1965; Whittaker and Woodwell, 1967). However, an experiment at Pepeekeo demonstrated that respiration was not responsible (Ryan et al. 2004), decreased GPP was the answer. The decline related to changes in resource use efficiency of dominant trees and non-dominant trees (Binkley 2004).

#### **1.4.2. Response of stand growth to the fertility treatment**

Fertilizers are always expected to improve tree and stand growth, and forest productivity. Stand growth might peak earlier and decline more rapidly on higher quality sites (Beck 1971; Ryan et al. 1997). After age 2 years, the fertility exhibited the strong effect on stand growth, and especially manifested with the HF and RF treatments versus

the control treatment. Under high fertilizers, trees might capture more nutrients and reach the leaf area maximum sooner, resulting in increased stand growth. The stands under the HF and control treatment reached the peak of stand growth at age 3 years, while those under the RF treatment did at age 6 years due to the late fertility application. However, after this age, stand growth rate declined more rapidly in the HF and RF treatments than in the control treatment even though the HF and RF plots were more productive.

#### **1.4.3. Response of growth dominance to the planting density treatment**

Growth dominance was strongly influenced by initial planting density through all periods of the study. Stand density was one of the determinants for canopy closure in forest plantations of the fast-growing *Eucalyptus saligna*. It was only 1.5-2.0 years for the HD plots, and 2.0-2.5 years for the LD plots to close their canopy (Ryan et al. 2004), leading to the increased competition in the early periods of forest development. The competition accounted for clear differentiation and changes in growth dominance over age, related to the tree stem growth, biomass accumulation and the resource use efficiency by dominant and non-dominant trees (Binkley 2004). The same-species trees growing on the same site would intensify competition because of their similarity (Boyden et al. 2008). The spacing between trees greatly influenced tree sizes and growth, and the differentiation in tree sizes.

The dominant trees might capture and use resources more efficiently than the non-dominant and suppressed trees, and accounted for more of the stem growth than of the stem mass. As a result, growth dominance coefficients of the HD plots were significantly higher than those of the LD plots. Under low density, dominance was weaker, especially

prior to the peak in stem increment (near the time of canopy closure; Ryan et al. 1997), and efficiency of resource use of dominant trees and other trees was high (Binkley et al. 2002). Significant differences in effects of density treatment on growth dominance at early period would claim the key factor for changes in stand development patterns.

The expected phase 2, strong growth dominance, developed in all stand from age 3 to 10 years. In most cases, although accounting for a small percentage of stand stem mass, the largest trees (so-called dominant trees in size) contributed a large percentage of stand growth. In particular, the largest 20% of trees accounted for from 40-50% of the stem growth in HD plots from year 4 to year 10, while the smallest 20% contributed only 3-5% of stand growth, representing very strong growth dominance (Fig 1.6). In the LD plots, the largest 20% of trees accounted for only 22-30% of the stand stem growth, and the smallest 20% contributed 8-10% of stand growth, showing the lower growth dominance. These results support my hypothesis that growth dominance would be stronger with higher density. Trees had to compete more intensely in higher density condition, resulting in less growth of suppressed trees. For example, at age 3 years, when stand growth peaked, the cumulative distribution curve of the stand growth was below that of the stand mass, confirming the strong growth dominance at the plantation, especially in the HD treatment (Fig 1.7). Under the HD treatment and at age 3 years, the largest 20% of trees accounted for about 50% of the total stand stem mass, but contributed up to 70% of stand growth. In the LD plots, the largest 20% of trees accounted for 40% of the stand mass, but contributed only 45% of stand increment (Fig. 1.7). At ages 4 to 10 years, the patterns of growth dominance was still strong (Fig. 1.6) but slightly different in percentage of stand mass and growth that the 20% largest of trees

accounted for when the growth dominance increased over time. However, from age 4 to 6, growth dominance did not change much in both pattern and value (Fig. 1.6).

#### **1.4.4. Response of growth dominance to the fertility treatment**

Growth dominance did not differ between fertility treatments at the period 1 ( $P = 0.78$ ), but varied greatly in the period 2 ( $P = 0.004$ , Fig 1.8B). In the previous analyses, fertilization strongly affected the stand biomass and growth because nutrients would be necessary for tree growth and biomass accumulation. However, the response of growth dominance to fertilization was different. Growth dominance was influenced by tree differentiation and efficiency of resource use of the dominant and non-dominant trees (Binkley 2004) within a stand. The fertility treatment had not significantly affected until age 6 because of late effects of fertilizers on this measure; in other words, effect of fertilizers on growth dominance was slow to develop. This result did not support my hypothesis that growth dominance would be stronger with better nutrient supply. In contrary, growth dominance was weaker in the HF and RF treatments at age 8 and 10 than that in the control (Fig 1.8B). The combination of fertility and planting density treatments did not show the interactive effects in the two periods. However, there were exceptions at ages 4 and 5 when growth dominance coefficients were significantly different, in which the HD-HF combination had the highest growth dominance coefficient at age 4, but the HD-RF was highest in age 5. In the same fertility treatment, stands under the HD treatment always had greater growth dominance coefficients than did those under the LD treatment, supporting the hypothesis that the greater the planting density, the stronger the growth dominance.

The expected strong growth dominance pattern was apparently shown in young *Eucalyptus saligna* stands under all spacing and fertility treatments at all ages, suggesting that dominant trees continued growing stronger than non-dominant trees in these periods.

#### **1.4.5. Response of growth dominance to stand age, biomass, and tree differentiation**

Fig. 1.8 exhibits that growth dominance increased over age under both density and fertility treatments from age 3, when stand growth started declining (Ryan et al. 2004). From this age, efficiency of resource use of non-dominant trees declined, lowering total stand stem production. The increase in growth dominance was demonstrated when the dominance curves dropped farther off the 1:1 line from year 3 to year 8, indicating increasingly strong growth dominance over time (Fig 1.6). However, growth dominance trended to relax at age 10 when there was no difference in value of growth dominance coefficients of age 8 and 10 ( $P = 0.36$ ). Future studies of growth dominance patterns should be developed in the longer time to have the answer for this trend.

The growth dominance coefficients correlated strongly with stand age. Under both treatments, the logarithmic lines depicted well the relationship of growth dominance coefficients and stand age (Fig 1.8) with very high  $r^2$ . Growth dominance coefficient increased from age 3 to age 8 and relax at age 10 in both HD and LD treatments. Growth dominance also increased over age in the control and HF treatments until age 8. The growth dominance coefficients increased more strongly over time in the early period, followed by a slighter increase or a decline in some LD plots in the last period that may be expected a relax pattern of growth dominance in the future. This increasing trend agreed with the previous study of Binkley et al. (2003) for a *Eucalyptus* monoculture,

and a *Facaltaria* monoculture in 20 years of stand development, for which a progressive domination of the stands was led by the largest trees.

Growth dominance coefficients and the coefficients of variations (CV) in tree sizes were moderately correlated. Universally, the stronger the tree differentiation, the greater the CV can be seen. In my study, growth dominance coefficients increased linearly as the CV of tree sizes increased (Fig. 1.9) for both density treatments. Great coefficients of variation showed the strong differentiation of trees in stand into dominant and subordinate trees (Binkley et al. 2002) that may be a driver of age-related decline in forest growth (Ryan et al. 1997). The relative declines in stand growth from age 3 to age 10 years are along with the pattern of within-stand dominance (Binkley et al. 2003). Growth dominance increased not only with variation in tree size, but also increased slightly with stand biomass (Fig. 1.10 C). This pattern was clearer in Eucalyptus monocultures in Chinchuck, Hawaii (Fig. 1.11 B, Binkley et al. 2003). Growth dominance highly correlated with stand mass by a linear line.

## **1.5. Conclusion**

The treatments planting density and fertility had strong effects on stand biomass and growth. Increased nutrient improved tree growth and demonstrated nutrient limitation in the *Eucalyptus saligna* plantations (Ryan et al. 2004). Fertilization increased growth, and as a result in dramatic increase of GPP (Giardina et al. 2003). Different densities strongly affected stand structure and growth. Time to close canopy would be shorter and competition be more intensive in the higher density plots. However, effects of density



treatment on stand growth decreased when over time, while the effects of fertilizer increased, resulting in changes of growth dominance and stand development.

The pattern of growth dominance for the young stands of *Eucalyptus saligna* in the experimental forest near Pepeekeo, Hawaii was strong (phase 2) through my study, agreed with the conceptual model of Binkley (2004).

Planting density affected growth dominance until age 8 years, while fertility treatment did not exhibit the different effects on growth dominance before age 8 years. The interaction of these two treatments was strong only in some ages (ages 4 and 5), in which effect of fertility under high density treatment was the most apparent. At year 4, the HD-HF combination had greatest effect on stand domination when growth dominance coefficient was 0.42, but at year 5, the HD-RF combination showed the greatest effect with growth dominance coefficient of 0.47.

Growth dominance for *Eucalyptus saligna* plantations increased over age until age 8 years, but remained unclear for higher stand ages although a potential trend of relaxing or declining in growth dominance. The dominant trees in stands still contributed larger percentage of stand growth than that of stand mass. Dominant trees used resources more efficiently, even though total stand growth declined.

Growth dominance coefficients really increased with stand age and tree sizes, promising a predictable trend of growth dominance based on variation in tree size.

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Many thanks to the National Science Foundation (Michael Ryan and others) for allowing me to access the data from the experimental plantations of *Eucalyptus saligna* in Pepeekeo, Hawaii funded by grants NSF DEB93-06356 and NSF DEB97-08521.

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## Tables and figures for chapter 1

Table 1.1. ANOVA results for variables: stand growth and growth dominance coefficient at two periods in *Eucalyptus saligna* stands in Pepeekeo, Hawaii. Stand age was added as a repeated measure.

Source	Growth (CAI)				Growth dominance coefficients			
	Period 1 (3-6 yrs)		Period 2 (6-10 yrs)		Period 1 (3-6 yrs)		Period 2 (6-10 yrs)	
	DF	Pr > F	DF	Pr > F	DF	Pr > F	DF	Pr > F
Block	2	0.49	2	0.90	2	0.26	2	0.24
Spacing	1	0.43	1	0.002	1	<0.001	1	<0.001
Fertility	2	<0.001	2	<0.001	2	0.78	2	0.004
Spacing*fertility	2	<0.001	2	0.11	2	<0.001	2	0.12
Age	3	<0.001	2	<0.001	3	<0.001	2	0.01
Spacing*age	3	0.58	2	0.90	3	0.55	2	0.86
Fertility*age	6	<0.001	4	0.41	6	0.54	4	0.18
Spacing*fertility*age	6	0.33	4	0.96	6	0.01	4	0.07
Model	25	<0.001	19	<0.001	25	<0.001	19	<0.001
Error	45		27		45		27	
Total	70		46		70		46	

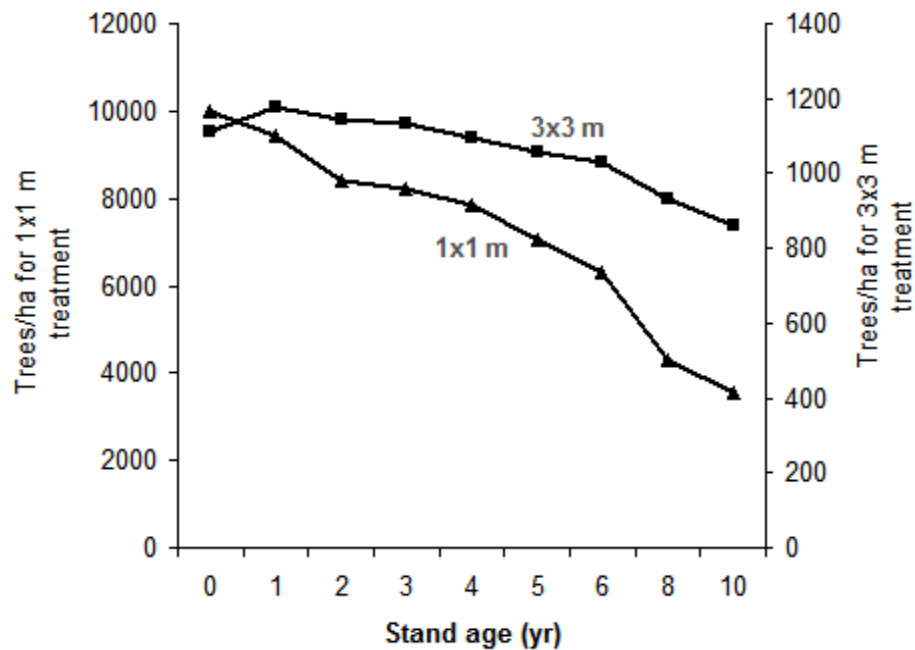


Fig 1.1. Density changes in the experimental plantations under the two initial spacing treatments in Pepeekeo Hawaii. The increased density at ages 1, 2 and 3 of 3x3 m spacing plots was due to more than one stem being grown from a tree.

Table 1.2. ANOVA for responses of stand growth and growth dominance coefficient (GDC) at the last year of each period (age 3 to 6 with an one-year interval, and age 6-10 with a two-year interval) in *Eucalyptus saligna* stands in Pepekeo, Hawaii. \*DF: degree of freedom

Age	Sources	DF	Growth	GDC	Age	Sources	DF	Growth	GDC
<b>3</b>	Model	5	< .014	0.001	<b>6</b>	Model	7	.02	0.01
	Error	6				Error	9		
	Total	11				Total	16		
	Block	2	0.16	0.27		Block	2	0.93	0.12
	Density	1	0.66	< .001		Density	1	0.18	< .001
	Fertility	1	< .001	0.96		Fertility	2	< .001	0.80
	Interaction	1	0.23	0.09		Interaction	2	0.34	0.09
<b>4</b>	Model	7	0.03	0.01	<b>8</b>	Model	7	0.02	< .015
	Error	10				Error	9		
	Total	17				Total	16		
	Block	2	0.55	0.39		Block	2	0.79	0.51
	Density	1	0.69	< .001		Density	1	0.07	< .01
	Fertility	2	0.01	0.65		Fertility	2	< .01	0.04
	Interaction	2	0.06	0.03		Interaction	2	0.76	0.11
<b>5</b>	Model	7	< .001	< .001	<b>10</b>	Model	7	0.08	0.03
	Error	10				Error	5		
	Total	17				Total	12		
	Block	2	0.88	0.79		Block	2	0.14	0.29
	Density	1	0.69	< .001		Density	1	0.06	< .001
	Fertility	2	< .001	0.06		Fertility	2	0.03	0.049
	Interaction	2	<u>0.04</u>	<u>&lt; .001</u>		Interaction	2	0.92	0.44

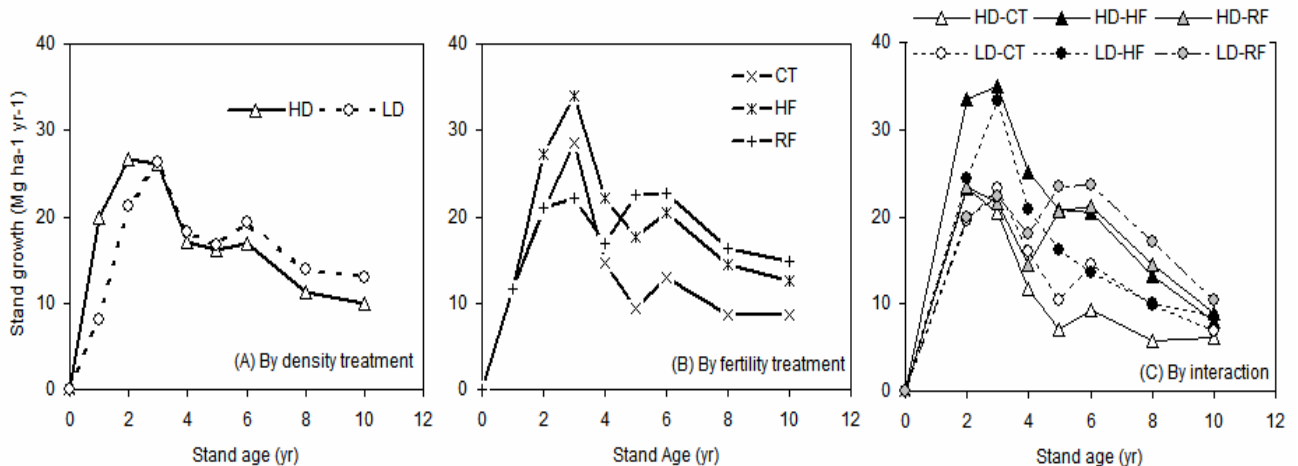


Fig 1.2. Current growth rate differed by fertility treatment but not by density treatment in stands of *Eucalyptus saligna* in Pepekeo, Hawaii (HD = 10000 trees/ha; LD = 1111 trees/ha; CT, Control; HF, High-Fertility; RF, Restore-Fertility)

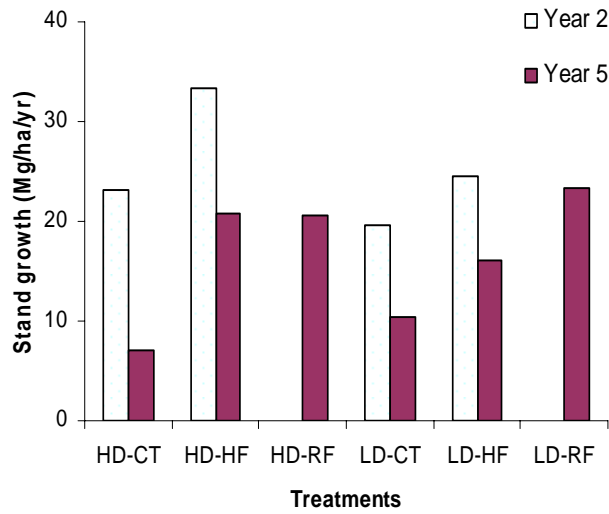


Fig 1.3. Stand growth for combination of density and fertility treatment at year 2 (blank bars) and year 5 (dense bars). HD, high density; LD, low density; HF., high fertility; RF, restore fertility; CT, control.

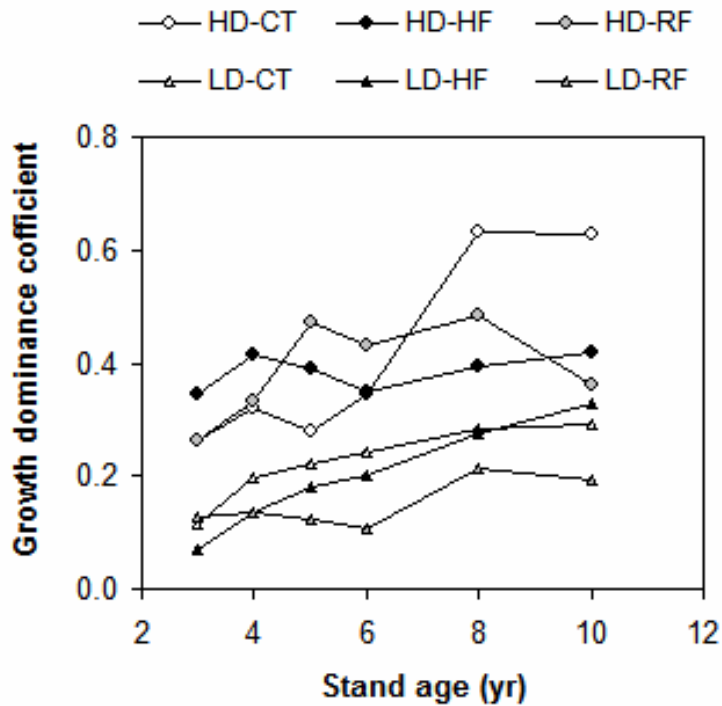


Fig 1.4. Growth dominance coefficients increased over time in most treatments from age 3 to 8 and trended to relax or decline at age 10 (HD, high density; LD, low density; HF., high fertility; RF, restore fertility; CT, control). Growth dominance was positive, and was stronger in the HD treatment than in the LD treatment, but did not differ with fertility at the period 1.



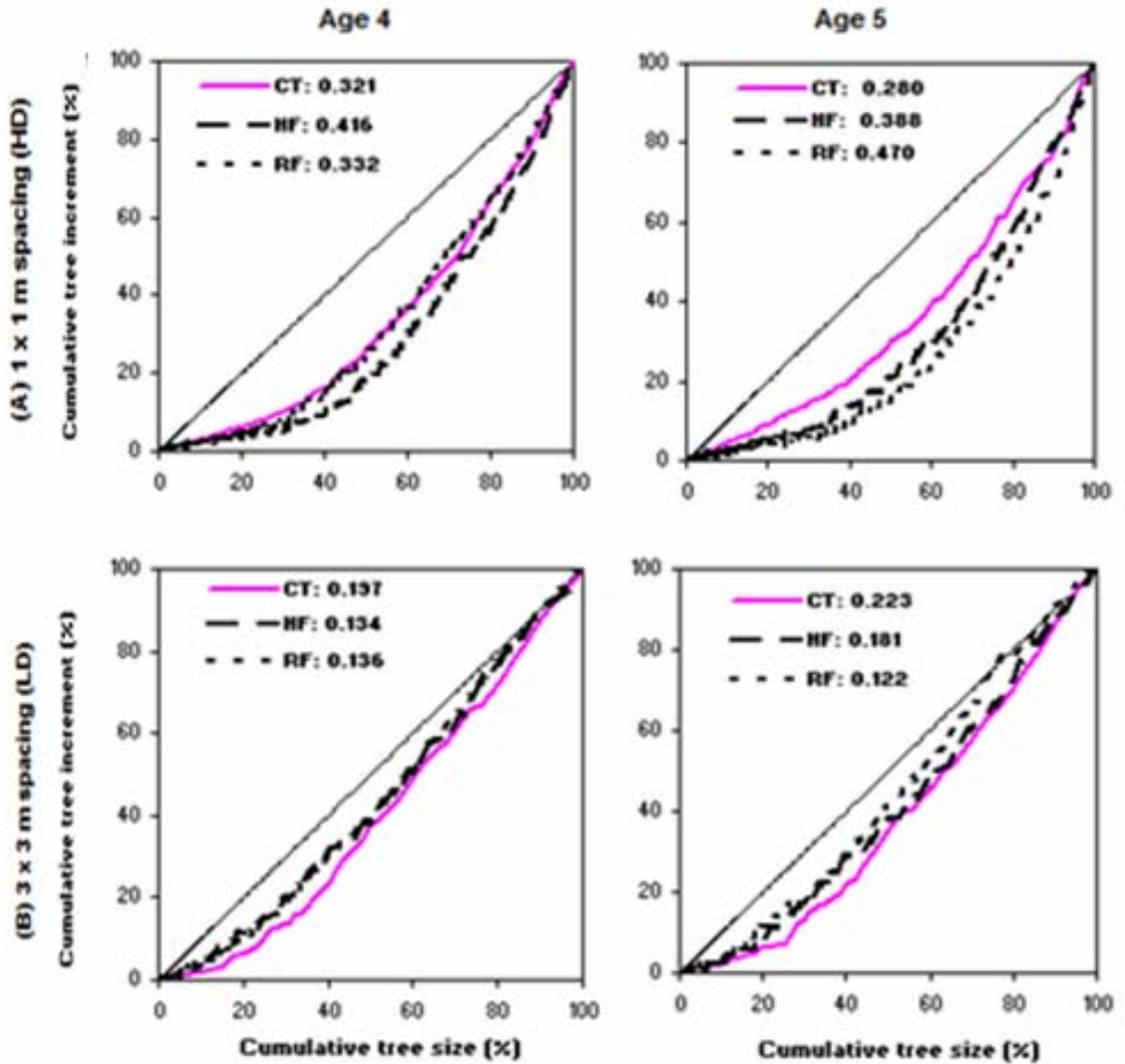


Fig 1.5. Growth dominance curves and coefficients for *Eucalyptus saligna* monocultures under the combination of density and fertility treatment at ages 4 and 5, exhibiting the effects of interaction. HD, high density; LD, low density; CT, control (solid line); HF, high fertility (dash line); RF, restore fertility (dotted line).

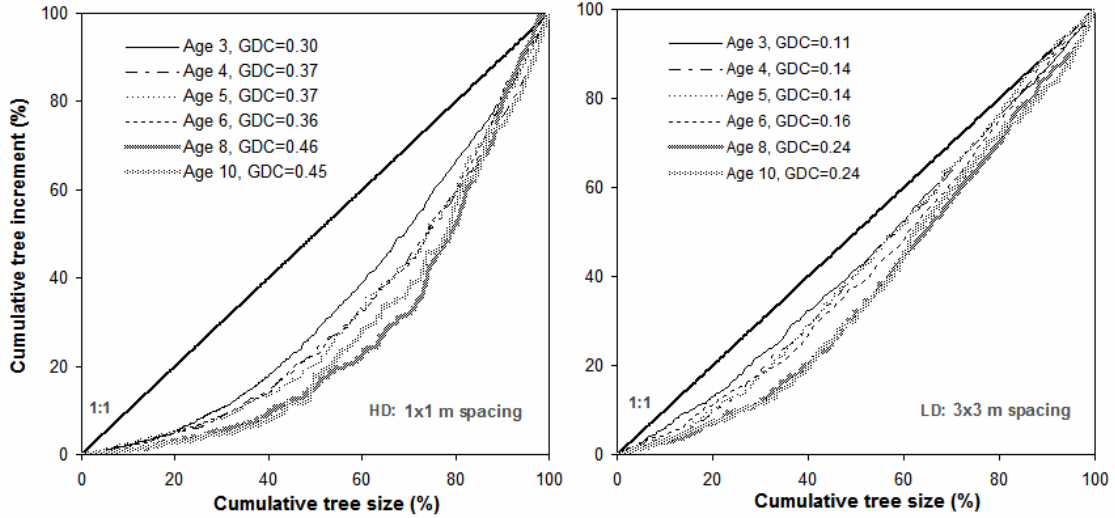


Fig 1.6. Relationship between woody biomass (trees ranked from smallest to largest) and current woody increment showing increased growth dominance in stand development. At age 10 years, the largest 20% of the trees of the HD plots contributed 45% of stand growth, compared with 27% for the LD plots; and the smallest 20% of the HD plots contributed only 3% of stand growth, compared with 7.5% for the LD plots.

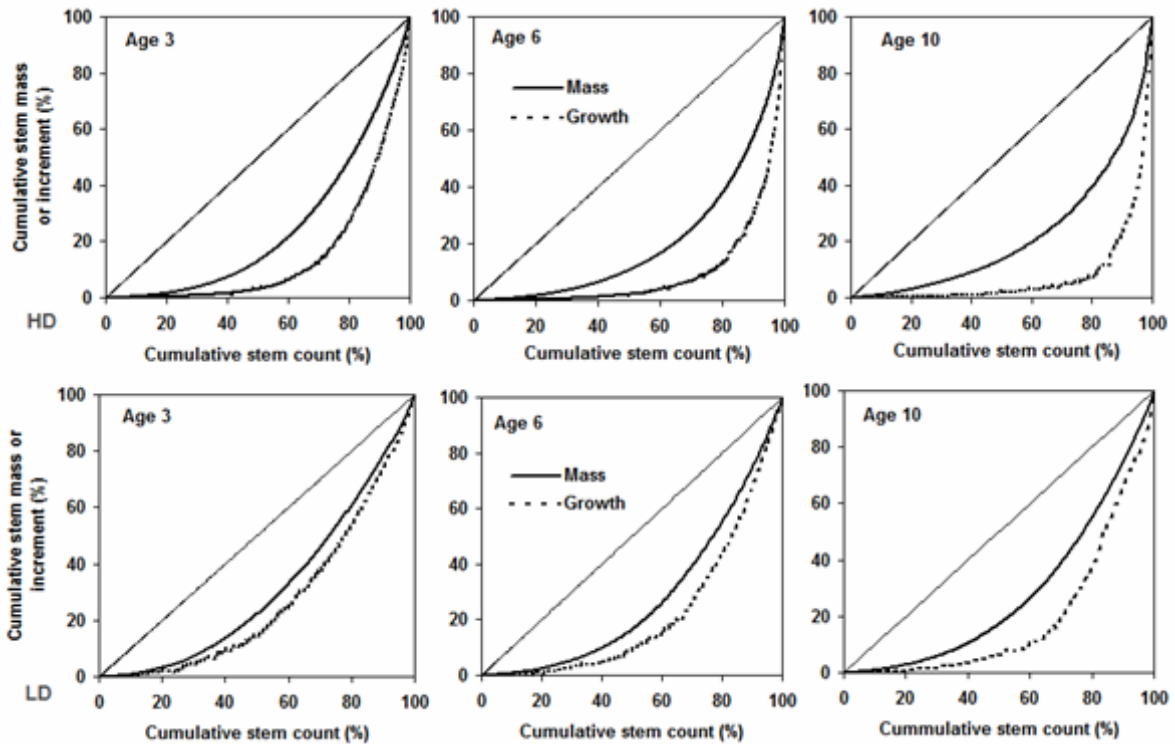


Fig 1.7. Cumulative distributions showing the percentage of trees accounting for the percentage of the total stand stem mass (solid lines) and the stand increment (dotted lines) in ages 3, 6 and 10 in the high density (HD) and low density (LD) treatments. The increment lines are below the biomass lines, exhibiting the strong growth dominance of stands.

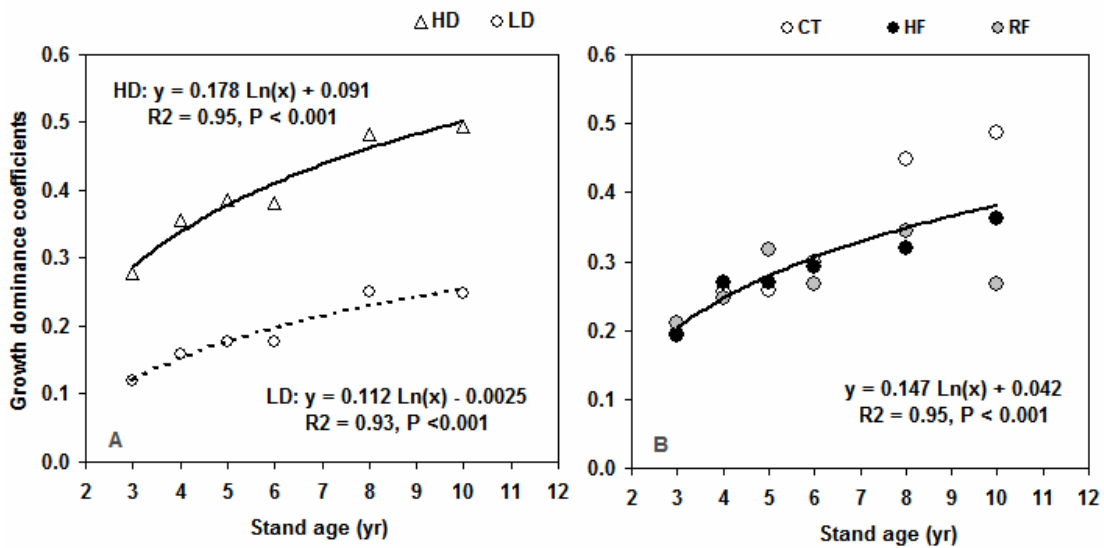


Fig 1.8. Growth dominance coefficients increased over time, and were significantly different with spacing treatment at all ages from 3 to 6, but not with fertility treatment until age 8. Growth dominance coefficients strongly correlated with stand age with a logarithmical line.

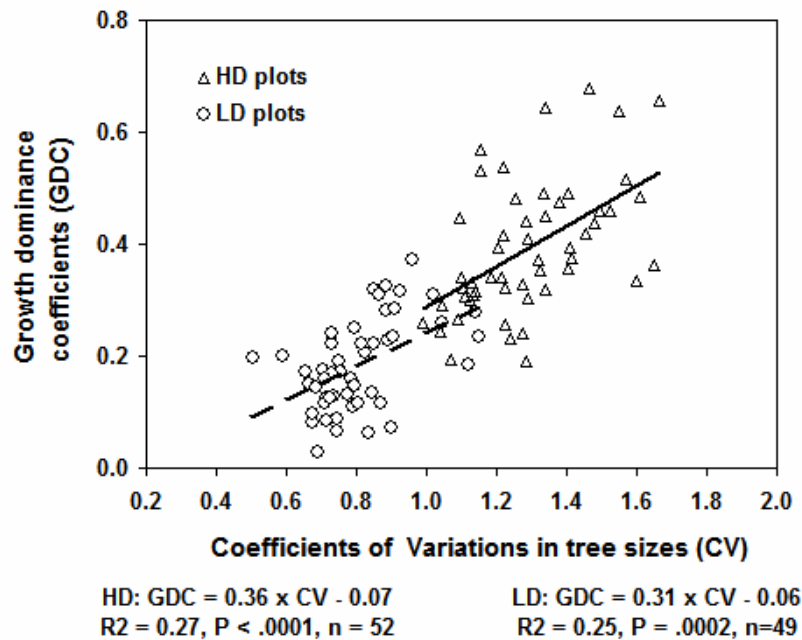


Fig 1.9. Correlation between growth dominance coefficients (G) and coefficients of variation in tree sizes (CV) for HD (triangles) and LD (diamonds) plots. CV of HD plots was greater on average than that of LD plots due to stronger competition among trees in very dense condition.

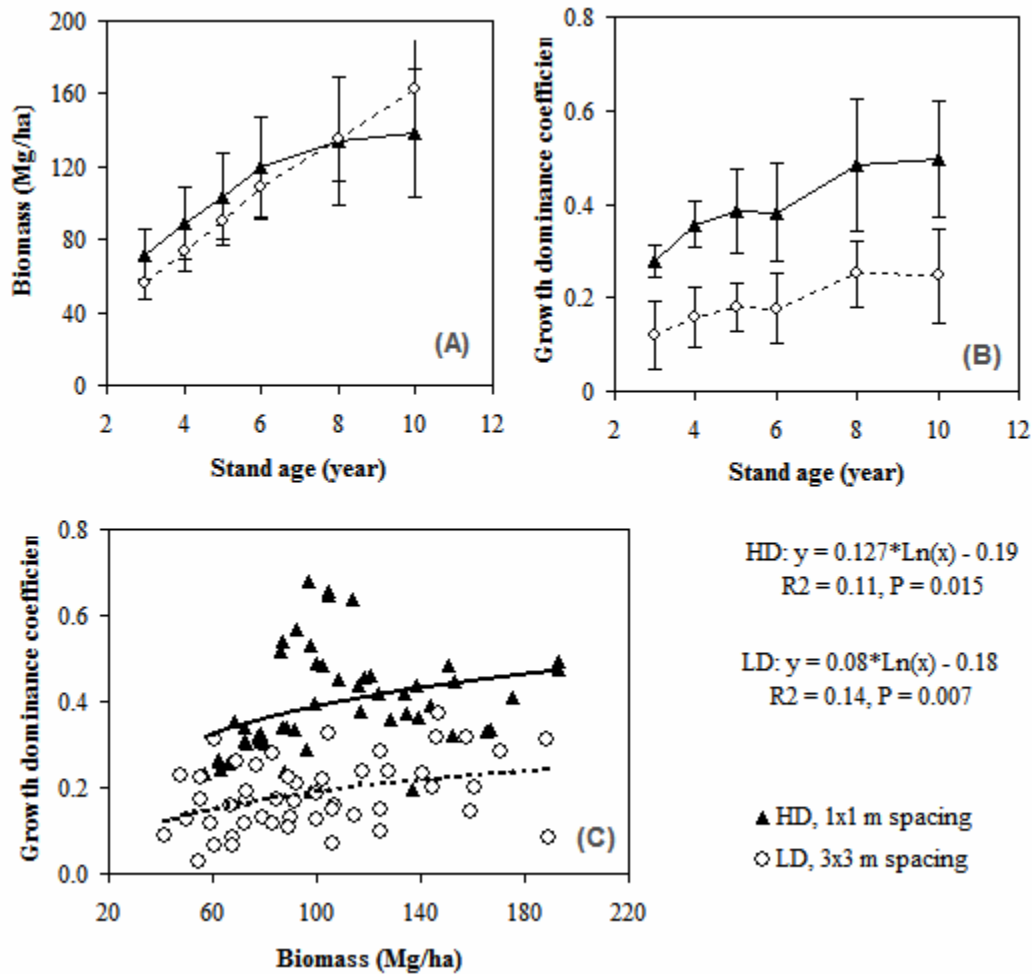


Fig 1.10. Growth dominance changed over age and biomass. Stand biomass in the HD treatment was greater than that in the LD treatment until age 7, but smaller from age 8 (A). Growth dominance had the same pattern in the HD and LD treatments. Both increased over stand age but relaxed at age 6. Growth dominance was stronger at the HD treatment at all ages (B). Growth dominance coefficient changed in relation to stand biomass (C) with logarithmical line.

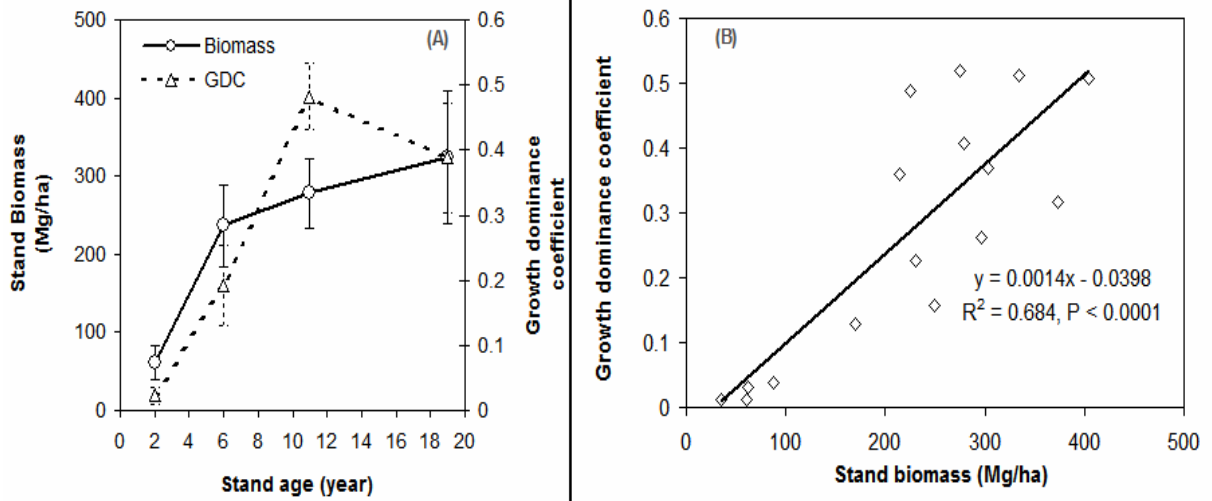


Fig 1.11. Relationship of growth dominance coefficient and stand age, and stand biomass of stands in Chinchuck, Hawaii (Binkley et al. 2003). Stand biomass increased over age from age 2 to 20 years; growth dominance increased strongly from age 2 to age 10 but declined at age 20 (A). Growth dominance had very good correlation with stand mass (B) with a linear line.

## CHAPTER 2

### NEIGHBORHOOD EFFECTS AND GROWTH DOMINANCE PATTERN OF OLD PLANTATIONS OF *EUCALYPTUS SALIGNA*

#### Abstract

I examined 70-year-old plantations of *Eucalyptus saligna* in Hawaii and Brazil to characterize competition between trees and patterns of growth dominance at the stand level. The growth of trees was strongly influenced by size and distance of neighboring trees; neighborhood interactions explained as much as 52% of the variation in focal tree growth in Hawaii, and 32% in Brazil. The higher growth rates in Hawaii were associated with higher stand densities, and taller trees with less taper than in Brazil. The accumulated stem biomass was very high in these plantations (609 Mg/ha in Hawaii, and 325 Mg/ha in Brazil), yet growth dominance by large trees remained moderate or strong; the expected pattern of reverse growth dominance did not apply.

*Keywords: neighborhood effects; growth dominance pattern; old plantations*

#### 2.1. Introduction

Forest structure changes over time and space, directly influencing tree growth and stand development, species diversity, wildlife habitat, and fire behavior (Hunter 1990, Morrison 1992, Latham 1998, Harrod et al. 1999, Ehle and Baker 2003, Waltz et al.

2003, Homyack et al. 2004, Youngblood et al. 2004). The current structure of a forest results from biological and ecological processes, typically characterized by attributes such as average tree size, density (Boyden et al. 2005a), tree size distribution, and stand age. Within a stand, the growth of a tree is influenced by many factors, especially competitive interactions with other trees (Stoll et al. 2002). Individuals of the same species compete more intensely with their neighbors because of the similarity in resource needs or physiological ecology (Argyres and Schmitt 1992, Boyden et al. 2005a), so competition in monoculture plantations may be stronger than in diverse natural forests (see next chapter). The relationship of focal and neighboring trees in terms of sizes and distances has been a central theme of studies on tree competition (Weiner 1984; Wagner and Radosevich 1998; Boyden et al. 2008). Nearest neighbor analyses can explore the dynamics of tree competition. Spatially explicit competition indexes have been developed to understand local variability in tree performance. However, this kind of research for forest plantations has been lacking, especially for the old plantations. Plant competition is usually “asymmetric” (Begon 1984) with larger individuals obtaining a disproportionate (for their relative size) share of the available resources (Weiner and Thomas 1986). The success of individual trees in stands depends on their abilities to obtain limiting resources and use them efficiently for growth (Binkley et al. 2004). Tree density has strong and predictable relationships with tree growth, as commonly modeled by the inverse density-yield relationships (Yoda et al. 1957, White and Harper 1970).

Stand growth dominance changes over time (Binkley 2004), as shifts in resource acquisition and use by individual trees shifts in relation to changes in tree sizes. The growth of dominant trees in a stand may continue to increase, even after the growth for

the whole stand has declined. The relationships between the sizes and current growth rates of trees within stands can show patterns of strong dominance (with the largest trees providing more than a proportional share of total stand growth), low dominance (where growth is proportional to size), or reverse growth dominance (where the largest trees account for smaller proportion of stand growth than of stand mass (Binkley et al. 2002, 2004, 2006; see Chapter 1). Some recent studies showed a “reverse” growth dominance pattern in forests of the Rocky Mountains (Binkley et al. 2006) or a “strong dominance” pattern for young plantations (Binkley et al. 2003a, 2004; Chapter 1). Some of these studies mentioned the interaction of tree dominance and stand production through stand development, but not the relationships between tree competitive intensity and growth dominance.

To explore these ideas, I used data from old plantations of *Eucalyptus saligna* in Hawaii (about 70 years old) and Brazil (66 years old). The strong competition intensity was tested for these old stands. A model to predict the growth rate of the old *Eucalyptus* trees based on asymmetric competition indexes related to neighbors’ size and distances from the focal tree was calibrated. I expected that growth rates of dominant trees in these old plantations would be slow enough that the pattern of growth dominance would be reversed with the largest trees accounting for less of the stand’s growth than of the stand’s biomass. I also examined how growth dominance might change through stand development by comparing my results in Hawaii with two previous studies with monocultures of *Eucalyptus saligna* from nearby sites (Pepeekeo up to 10 years of age (Chapter 1), and Chinchuck up to 20 years of age (Binkely et al. 2003).



## 2.2. Materials and method

### *Study site*

Plantations of *Eucalyptus saligna* were established in the 1930s (about 70 years before my measurements) on the former sugarcane fields in the Kalopa section of Hamakua Forest (Fig 2.1). A similar plantation was established near Itatinga in São Paulo, Brazil in 1940.

### *Sampling and data collection*

Three 0.25 ha (50 × 50m) plots were set up in Hawaii in January 2006, along with four plots in Brazil in June 2006. Tree density was 270 trees/ha in Hawaii and 112 trees/ha in Brazil (provided by Professor Jose Stape, ESALQ, University of Sao Paulo, Piracicaba). All live *Eucalyptus saligna* trees in each plot were stem-mapped.

Diameters at 1.35 m height ( $d$ ) of all trees in plots were measured in 2006 and 12 months later. Accurate, precise measurements were needed to determine annual increments, so we had two people working on each tree – one person making sure the tape was located correctly around the bole (marked with paint or staples), and one person reading the diameter. The precision of diameter measuring procedure was evaluated by remeasurement by another crew member; repeatability averaged about 0.05 cm.

The height ( $h$ ) of 32 representative trees was measured in Jan 2007 in Kalopa, Hawaii on three plots by using a clinometer. The height of 38 trees in Brazil was measured after felling as part of the development of a stem biomass equation.

### *Equations for characterizing biomass*

Tree heights were estimated from the relationship between height and diameter for 32 trees in Hawaii and 38 felled trees in Brazil (Fig 2.2) by equations:

$$h = 18.902 \cdot \log_e d - 25.959 \text{ for Hawaii plots} \quad (1)$$

$$h = 11.975 \cdot \log_e d - 20.103 \text{ for Brazil plots} \quad (2)$$

Woody stem biomass ( $M_w$ , kg dry mass) has been commonly presented by a function of tree diameter ( $d$ , cm), tree total height ( $h$ , m), and an expression of tree form ( $f$ ) in some cases (Clutter et al. 1983). However, I used the model  $M = a \times (d^2 h)^b$  to calculate the woody biomass for both sites with available datasets of 36 trees in Chinchuck, Hawaii and of 38 trees from the same stand (but not same plot) used near Itatinga in Sao Paulo, Brazil, as follows:

$$M_w, kg = 0.0105 \times (d^2 h)^{1.0302} \quad (3)$$

$$r^2 = 0.99, P < 0.001 \text{ for Hawaii,}$$

$$M_w, kg = 0.0278 \times (d^2 h)^{0.9727} \quad (4)$$

$$r^2 = 0.98, P < 0.001 \text{ for Brazil.}$$

The current density and tree sizes were different from Hawaii to Brazil. Differences in growth would need to be tested even though stand ages and environmental factors (soils and climate) are different. The independent sample t-test with a  $P = 0.05$  (SAS version 9.0 SAS Institute Inc., Cary, NC) was used.

### ***Neighborhood effects and focal tree growth***

I examined neighborhood effects around each focal tree by calculating neighborhood indexes ( $C_r$ ) in three ways: biomass within a radius (Index 1), symmetric distance-dependant (Index 2), and asymmetric competitive index (Index 3, 4, and 5 depending on

the values of exponent = 1, 2 and 3, respectively). Equations for neighborhood effects were as follows (after Boyden 2005):

+ Biomass index (Index 1): sum of biomass of all neighbors within a circle of radius  $r$ :

$$C_r = \sum_{i=1}^n B_i \quad (5)$$

+ Distance-dependent (Index 2): neighbor's impact decreases with the square of the distance from the focal tree (Weiner, 1984). In this model a tree's impact on a neighbor is still size-symmetric (Begon, 1984; Weiner et al., 1990):

$$C_r = \sum_{i=1}^n \frac{B_i}{r^2} \quad (6)$$

+ Asymmetric (Index 3, 4 and 5): these indexes are similar to Index 2 but included an additional scala, or size-ratio term to account for size-asymmetric competition. The size-ratio is similar to one developed by Bella (1971), and divides the biomass of the neighbor ( $B_i$ ) by that of the focal trees ( $B_j$ ) to create a scala that disproportionately increases or decreases the effect of that neighbor depending on its relative size. We tested three forms of this equation by changing the exponent ( $e$ ) on the size-ratio to 1, 2, or 3.

$$C_r = \sum_{i=1}^n \frac{B_i}{r^2} \left( \frac{B_i}{B_j} \right)^e \quad (7)$$

where  $i$  is the  $i$ th neighbor and  $n$  is the total number of neighbors within a given distance.

The effect of neighborhood size was evaluated by these five competition indexes at 6 neighborhood sizes (4m, 6m, 8m, 10m, 12m and 14m) for plots in both locations Hawaii

and Brazil. I developed and tested models of individual tree growth in relation with sizes and interactions of neighbors. Predictor variables were sizes of the focal and neighbor trees, and distances from the focal tree to neighbors. The best model was selected by using the information theoretic (Akaike's Information Criterion, AIC). A lower AIC value indicates stronger performance of a model (Burnham and Anderson, 1998).

### *Characterizing spatial patterns*

This study describes stem-mapping procedures for individual tree data collected from completely mapped plots. The statistics compare the observed cumulative distributions of distances between trees to a distance distribution for a point pattern generated by a random process. I used two different statistics, nearest neighbor analysis and *Ripley's K(d)* function in this study. These two statistics are powerful tools for describing and interpreting spatial patterns being developed for recent decades (Ripley 1981, Diggle 1983, and Moeur 1993).

Nearest Neighbor Analysis is a mathematical approach based on distance sampling with the assumption that the observed distance distribution conforms to a Poisson distribution, where the population is randomly distributed within an infinitively large area (Cottam et al. 1953). Clark and Evans' *nearest neighbor index* (1954) and *Pielou's index* of non-randomness (1959) were used in this study. Nearest neighbor analysis considers trees as point locations in a closed plane and tests whether a given point pattern departs from randomness toward clustering or regularity.

*Ripley's K(d)* Analysis is a second-order analysis designed to test randomness hypotheses based on the Poisson distribution, by examining the proportion of total

possible pairs of points in Euclidean space whose pair members are within a specified distance of each other (Reich and Davis 2003). The analysis is second-order because it is the variation rather than the mean of distance that is being studied (Getis and Franklin 1987). Spatial patterns in this study were analyzed using *Ripley's K* functions (Moeur, 1993). The  $K(d)$  function is the cumulative distribution function of distances ( $d$ ) from points (trees) in a domain  $A$  to other point in  $A$ . It estimates spatial dependence between points (trees) by considering the distances between all pairs of points in a mapped dataset. The  $K(d)$  function provides information on the scales and magnitude of spatial patterns (Fortin, 1994; Chen and Bradshaw, 1999) by looking at the variance in the distance between all possible pairs of points, instead of just the mean of the nearest neighbors as in a first order neighbor analysis. The  $K(d)$  function produces a cumulative distribution function that represents the expected number of points within a given distance ( $d$ ) of an individual point, and is weighted to correct for edge effects. The model can be used to test point data for departure from a spatially random pattern, as described by a Poisson process. Observed patterns differ from random at  $P = 0.05$  where the plot of  $L(d)$  falls outside the 95% confidence envelopes on Monte Carlo simulated Poisson process. Aggregated patterns are indicated by an  $L(d)$  line above the envelope, and regular pattern of tree distribution occurs where  $L(d)$  line falls below the envelope.

## **2.3. Results and discussion**

### **2.3.1. Stand growth**

Stand density and biomass of the *Eucalyptus saligna* plantations differed greatly from Hawaii to Brazil (Fig 2.3a). In Hawaii, tree density, average diameter (quadratic

mean), and height were 270 tree/ha, 53.5 cm and 46.6 m, respectively, compared with 112 tree/ha, 68.3 cm and 36.4 m for Brazil. Tree sizes ranged from 0.1 to 13.1 Mg/tree, with the stem biomass was 609 Mg/ha for stands in Hawaii (MAI  $\approx$  8 Mg ha<sup>-1</sup>yr<sup>-1</sup>), compared to 0.7 to 8.9 Mg/tree, and 325 Mg/ha for stands in Brazil (MAI  $\approx$  5 Mg ha<sup>-1</sup>yr<sup>-1</sup>). The average growth rate of individual trees was 22.8 kg tree<sup>-1</sup>yr<sup>-1</sup> in Hawaii, notably lower than the 53.2 kg tree<sup>-1</sup>yr<sup>-1</sup> in Brazil. However, the current stand growth (CAI) was approximately 6.0 Mg ha<sup>-1</sup>yr<sup>-1</sup> for both locations (Fig 2.3b), less than half that of the 10-year-old plantations in Pepekeo, Hawaii (see Chapter 1).

### 2.3.2. Spatial patterns and Neighborhood effects

Spatial pattern of tree locations in the *Eucalyptus saligna* stands apparently remained regular in distances of less than 3.5 m (in Hawaii, Fig 2.6b) or 5 m (in Brazil, Fig 2.6d), according to Ripley's  $K(d)$  method. The averaged distance between trees was greater 5.5 m in Hawaii, and 7.5 m in Brazil at the time when trees were investigated. Beyond these distances, trees were essentially randomly spaced after about seven decades to grow (Fig 2.6). Two methods *Nearest Neighbor Analysis* and *Pielou's index* showed that the averaged distances of samples were greater than the expected values, indicating that tree distribution tended toward regularity (Table 2.2). If the populations were randomly distributed, we would expect the average distance between points to be greater than the average distances of samples. This regular or random pattern of tree distribution would not influence the tree competition but the size and distance would really matter. The greater distances among trees may result in less competitive interaction.

The size and distance of trees strongly influenced the growth of individual trees, especially in Hawaii location where trees were substantially taller than in Brazil. The best model for competitive interaction used a 12-m radius (450 m<sup>2</sup>) in Hawaii, and an 8-m radius (200 m<sup>2</sup>) in Brazil. The average number of neighbors within a 12-m radius was 12 trees in Hawaii, and 4 trees in Brazil.

Large trees had a stronger competitive influence on small trees than the reverse, as the asymmetric competition indexes (Indexes 3a, 3b and 3c) outperformed the symmetric indexes (Indexes 1 and 2 in terms of biomass and distance-dependant, respectively) at all neighborhood sizes at both locations (Table 2.1). Particularly, symmetric indexes (Index 1 and Index 2) only explained < 20% of the variability in focal tree growth, while the best asymmetric indexes explained up to 52% (Hawaii, Index 3b) or 32% (Brazil, Index 3c; Fig 2.7). The value of exponents in the asymmetric index affected the model performance, especially at small neighborhood sizes. The greater the exponent in competition indexes (from 1 to 3), the better the model could explain the variability of focal tree growth at all radii. A given level of competition could be achieved through a number of combinations of neighbor numbers, size and distance compared to focal trees (Boyden, 2005). For example, increasing the logarithm of the competition index from 2 (which would be 5 trees of 1.7 Mg size within 12m) to 8 (about 11 trees of 2.1 Mg) decreased the predicted growth of focal trees by nearly 80% in Hawaii. The best models for tree growth related to the competition indexes may be used to explain partly variation in growth of the old *Eucalyptus* trees. This result supported my expectation of strong competition intensity that still occurred at age of 70 years at aboveground parts of stand.

### 2.3.3. Growth dominance

Growth dominance was stronger in Hawaii (GDC = 0.13) than in Brazil (GDC = -0.03, not differing from 0), but neither location showed the predicted pattern of reverse growth dominance (Fig. 2.5 b and d). In Hawaii plots, the cumulative distributions showed that the largest 20% of the trees accounted for about 50% of the total stand stem mass, but contributed up to 60% of the stand increment (Fig 2.5a). The largest 20% of trees in Brazil accounted for only 30% of both the total stand stem mass and stand increment (Fig 2.5c).

The expected phase 4 “reverse” dominance did not develop in either location. The dominant trees in Hawaii still contributed a very large proportion of stand growth, a pattern that leads to continued divergence of tree size distributions. The dominant trees grew proportionally for their size, which would sustain the current relative distribution of tree sizes into the future. Reverse growth dominance might develop in the future in these stands, but the hypothesis was refuted for age 70 years. Long-term datasets would be needed to test this.

Positive growth dominance in Hawaii plots could result from continued accelerating growth of the dominant trees relative to the non-dominant trees in terms of either resource acquisition or the efficiency of resource use (Binkley 2004). The pattern of growth dominance has not showed the sign for a growth relaxation in plantation stands in this age.

Growth dominance in plantations of *Eucalyptus saligna* changed substantially over time in the young plantations. Particularly, growth dominance increases with stand age in first 10 years at Pepeekeo (see Chapter 1), then weaken by age 20 at Chinchuck (Binkley



et al. 2003) when stem biomass reached to 240 Mg/ha, and CAI from 5 to 8 Mg ha<sup>-1</sup>yr<sup>-1</sup>. After seven decades growth dominance had weakened substantially at Kalopa, especially at Itatinga. Besides, the growth dominance pattern in Brazil plots was bearing a different story. In these stands, the efficiency of resource use of dominant and non-dominant trees might be not different in term of tree contribution to the stand growth. The growth curve for the smallest 20% was below the 1:1 line, but that of the largest 20% of trees was higher than the 1:1 line and the tree growth still increase over tree sizes (Fig 2.5d).

Variation in tree size might result in differences in growth dominance. In young plantations in Pepekeo, growth dominance increased over increased variation of tree sizes and stand age (see Chapter 1). The coefficient of variation was higher at Hawaii (0.94) than that at Brazil (0.25), consistent with the greater growth dominance in Hawaii (Fig 2.5 b and d). However, the coefficient of variation among plots did not correlate with growth dominance coefficients ( $r^2 = 0.12$ ,  $n = 7$  plots).

## 2.4. Conclusion

Competitive interaction was strongest within the 12 m radius in Hawaii location, and the 8m radius in Brazil. Neighbor interactions explained as much as 52% of the variation in focal tree growth in Hawaii, but only 32% in Brazil plots. Combination of sizes and distances of neighbors had large impact on tree growth of focal trees. The asymmetric competition indexes explained the variability of the focal tree growth better than the symmetric ones. The best models for predicting tree growth for the old *Eucalyptus* trees would be 3b at radius 12 m for Hawaii and 3c at radius 8 m for Brazil stands.

Plantations of *Eucalyptus saligna* at age of about 70 years did not show the expected pattern of reverse growth dominance as the larger trees continued to grow proportionally as well or better than smaller trees. This resulted in the positive growth dominance pattern in Hawaii, and weak (near zero) growth dominance in Brazil. Long-term and larger scale datasets are needed to determine whether monoculture plantations of *Eucalyptus* would ever show the pattern of reverse growth dominance.

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## Tables and Figures for chapter 2

Table 2.1. Performance of competition indexes for different ranges of neighborhood sizes. Correlation coefficients ( $r^2$ ) of the competitive influence of neighbors on focal tree growth were calculated using the model  $y = ax-b$  ( $a, b > 0$ ). Asymmetric indexes performed better this correlation and were used to predicted growth for the focal trees.

Location	Neighbor- hood sizes (m)	Index 1 (Biomass)	Index 2 (distance- dependent)	Index 3a (asymmetric1)	Index 3b (asymmetric2)	Index 3c (asymmetric3)
Hawaii	4	0.116	0.118	0.320	0.372	0.393
	6	0.056	0.084	0.319	0.377	0.400
	8	0.040	0.086	0.328	0.382	0.400
	10	0.096	0.136	0.420	0.460	0.472
	12	0.044 (301)*	0.176 (287)*	0.506 (237)*	<u>0.515 (235*)</u>	0.511 (236)*
	14	0.034	0.168	0.487	0.496	0.494
Brazil	4	0.051	0.009	0.090	0.143	0.170
	6	0.149	0.034	0.176	0.249	0.284
	8	0.147 (133)*	0.131 (134)*	0.261 (127)*	0.306 (124)*	<u>0.324 (123)*</u>
	10	0.001	0.024	0.102	0.146	0.167
	12	0.001	0.009	0.101	0.169	0.201
	14	0.004	0.018	0.133	0.205	0.236

\*In the parentheses was it the AIC values for the best model in each location.

Table 2.2. Nearest neighbor index by Clark & Evans and Pielou for plots at two research sites.  $\rho$ : density ( $n/A$ ),  $\bar{d}_E$ : expected mean distance between nearest neighbor (under CSR),  $\bar{d}$ : average distance between randomly selected plants to their nearest neighbor,  $R$ : Clark & Evans Nearest Neighbor Index, and P-value for testing null hypothesis of CSR (index=1)

Plot	Clark & Evans				Pielou's	
	$\rho$	$\bar{d}_E$	$\bar{d}$	$R$	P-value	P-value
HI1	0.036	2.62	3.20	1.22	0.0029	0.0066
HI2	0.022	3.40	4.22	1.24	0.0011	0.3239
HI3	0.023	3.31	4.50	1.36	< 0.0001	0.6520
BR1	0.017	3.81	5.37	1.40	0.0005	0.7345
BR2	0.009	5.21	6.90	1.32	0.0056	0.7135
BR3	0.010	5.00	7.32	1.46	< 0.0001	0.8352
BR4	0.008	5.45	7.96	1.46	< 0.0001	0.2368





Fig 2.1. Location of study where three plots were set up in Kalopa National Park, in Hilo, Hawaii (left), and near Itatinga, Sao Paulo, Brazil (right)

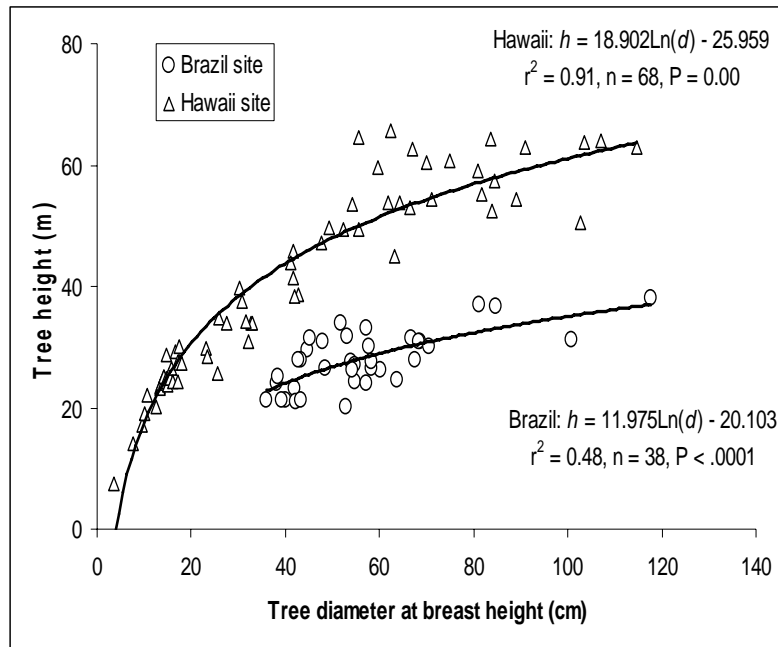


Fig 2.2. Relationship of tree height and diameter at breast height for two locations, Hawaii (triangles) and Brazil (rounds). The model in Hawaii was drawn from 36 trees in Chinchuck (data provided by D. Binkley) and 32 trees in Kalopa sites. The data from Brazil were obtained from 38 felled trees. Trees in Hawaii were about 80% taller for a given diameter than trees in Brazil. These equations are for trees with diameter  $\geq 5$ cm.

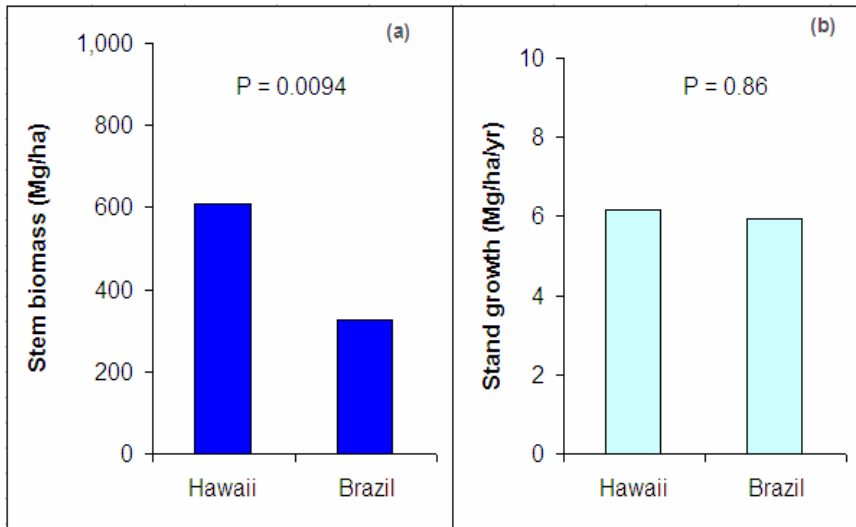


Fig 2.3. Stem biomass and stand growth for *Eucalyptus saligna* plantations in Hawaii and Brazil. Stem biomass was very different between two locations, but stand growth was almost the same.

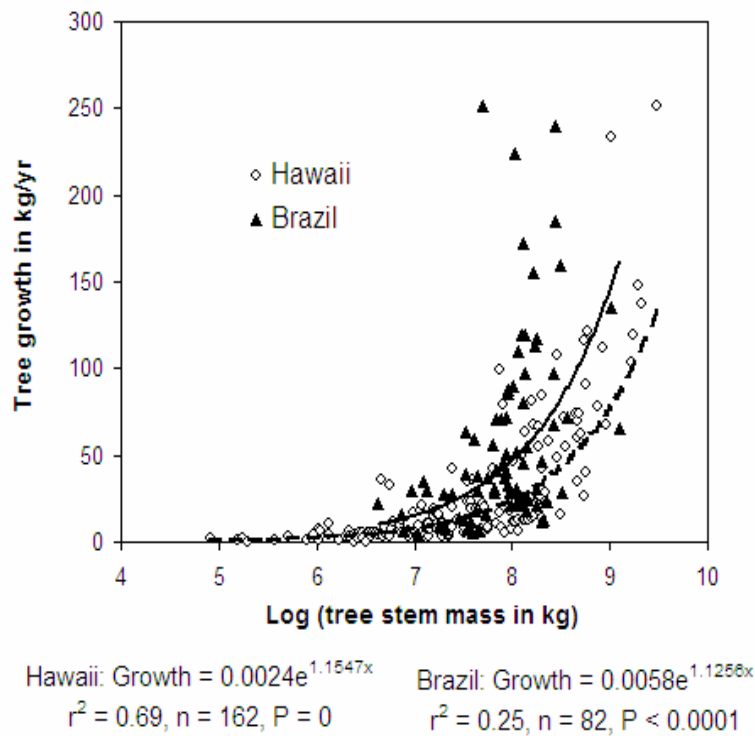


Fig 2.4. Relationship of tree stem growth and tree size for stands in Hawaii (circle) and Brazil (triangle). Trees used for the model had positive increment in between year 2006 and 2007. Growth rate was greater in Brazil plots than that in Hawaii for the same size trees; the lower density and smaller size of trees in Brazil allowed smaller trees to grow better than in Hawaii, where higher density and very large neighbors constrained the growth of small- and medium-size trees.

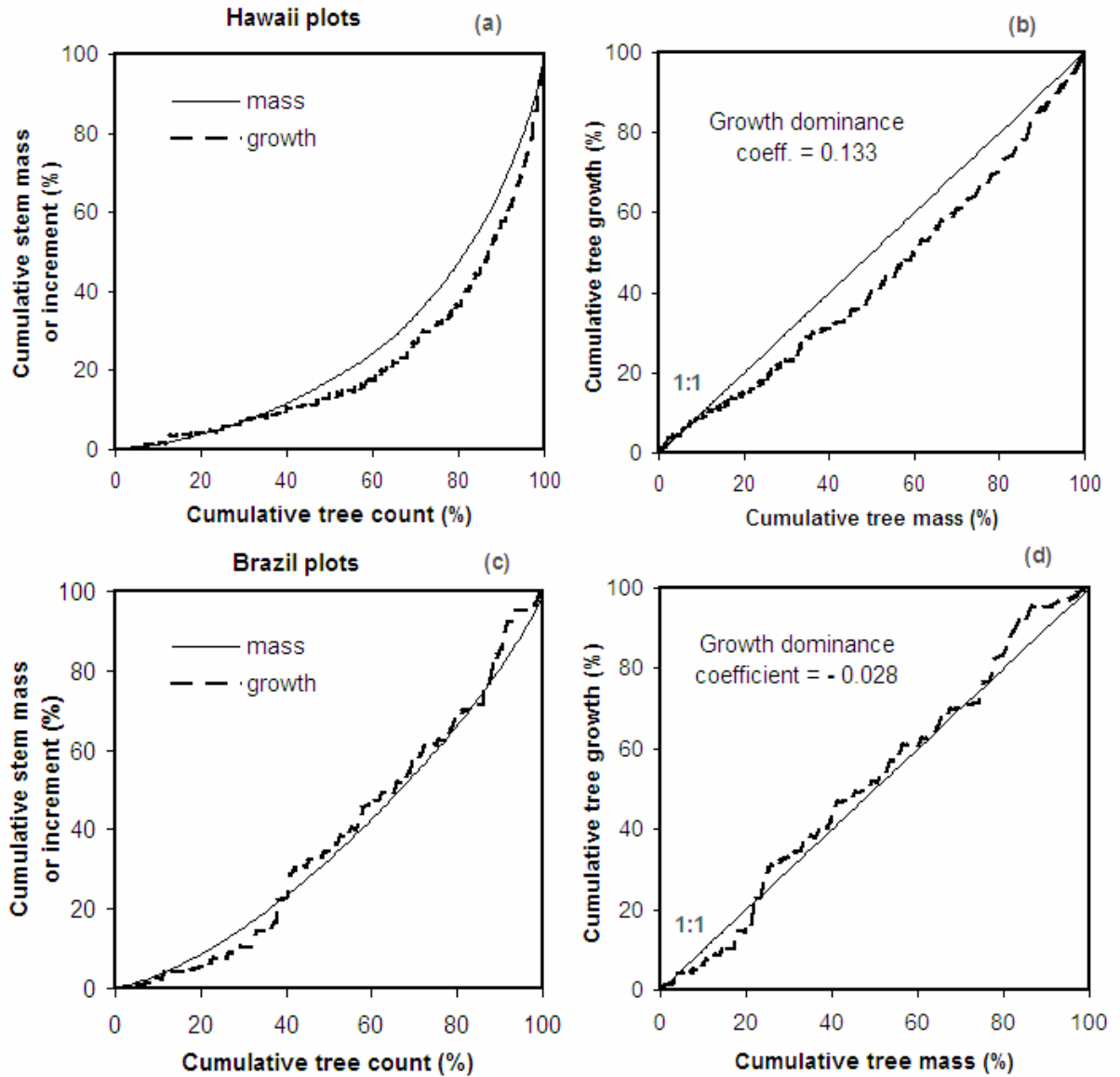


Fig 2.5. The cumulative distributions of tree mass and growth (increment) ranking from the smallest to the largest, and plotting the cumulative percent of the trees in Hawaii (a) and Brazil (c). Patterns of growth dominance for three 0.25-ha plots of old stands of *Eucalyptus* in Hawaii (b) and four 0.25 ha plots in Brazil (d).

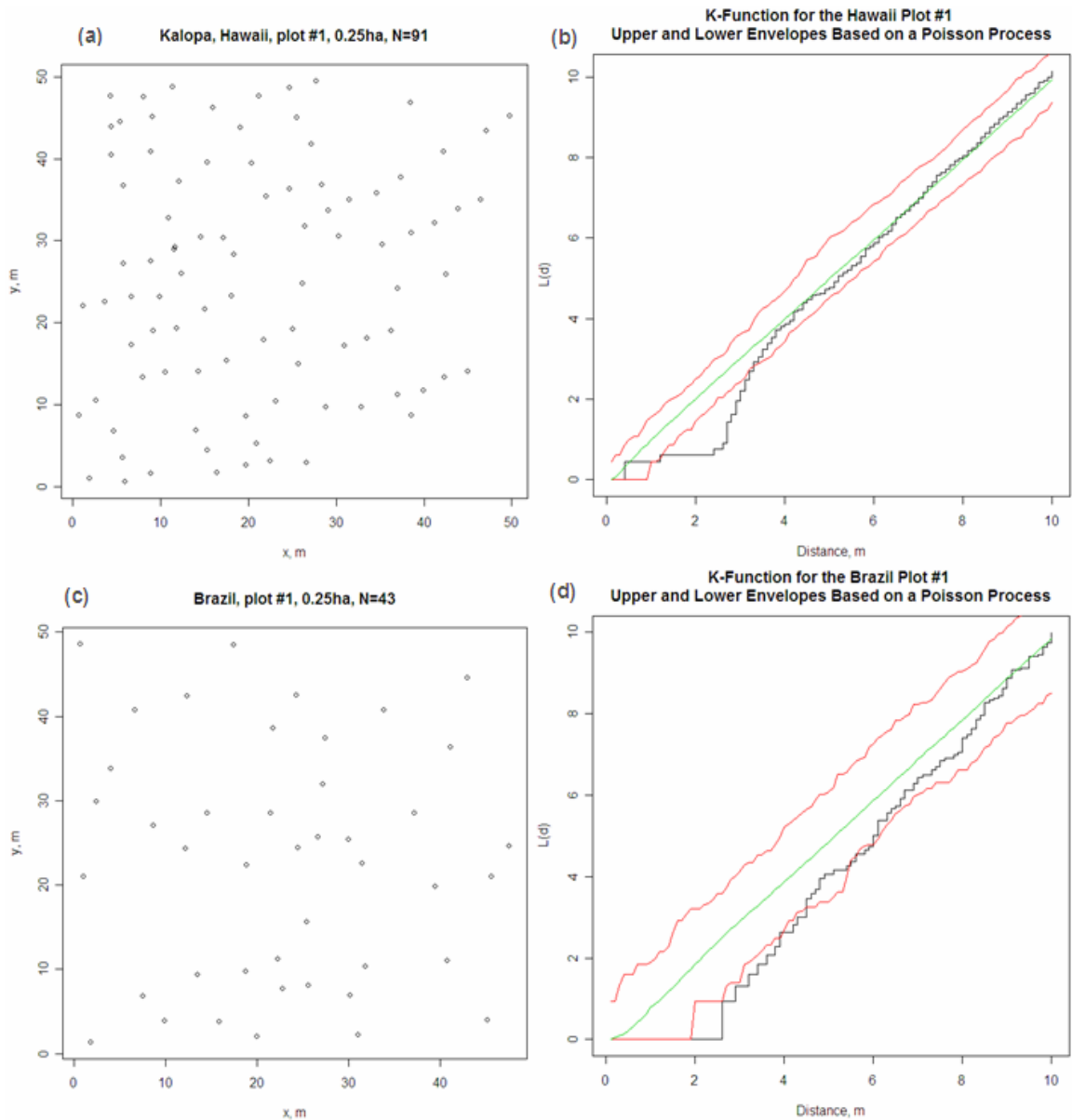


Fig 2.6. Stem-mapped and  $K(d)$  functions for the representative plots in Hawaii (a and b) and Brazil (c and d). Tree density in Hawaii was as double as in Brazil. Regular patterns remained at distance  $< 3$  m, as expected after about 70 years growing.

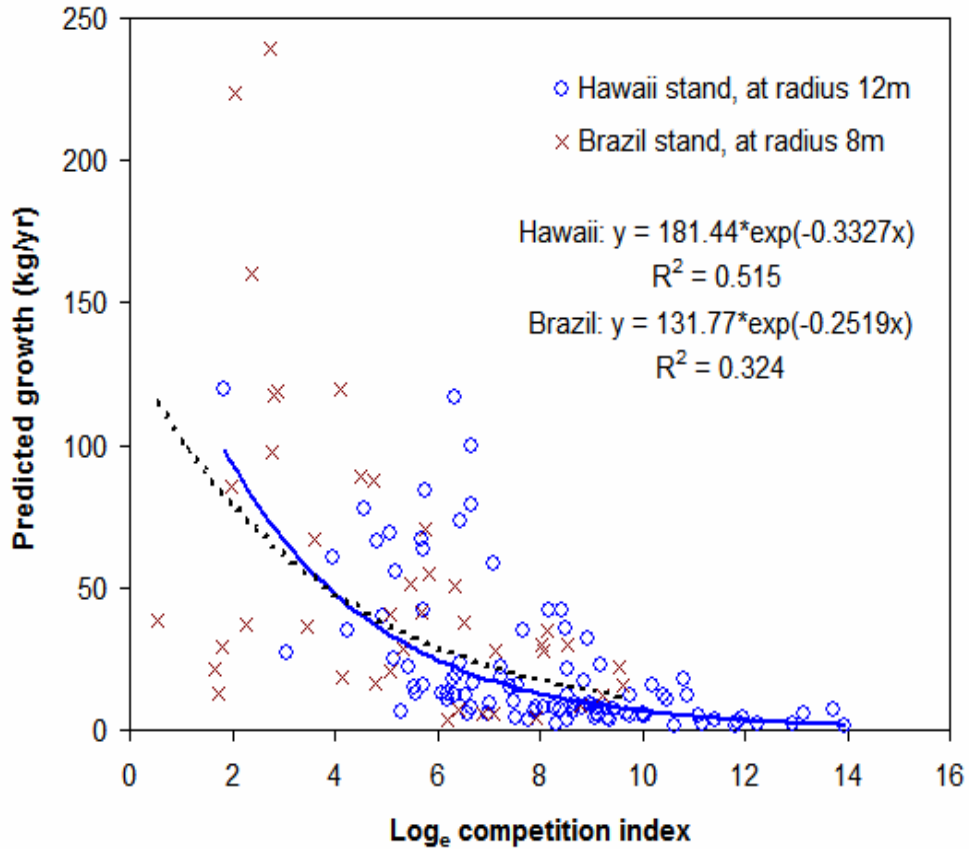


Fig 2.7. Growth of focal trees was influenced by competition when the best model was used at 12 m radius in Hawaii (solid line) and at 8 m radius in Brazil (dash line). The competition from neighbors appeared to have similar effects on focal-tree growth at both locations.

## CHAPTER 3

### **GROWTH DOMINANCE PATTERNS IN THREE TROPICAL FORESTS**

#### **Abstract**

I used the existing datasets from The Center for Tropical Forest Science to investigate the growth dominance patterns of three different tropical forests in Panama. The “reverse” dominance pattern occurred as expected in most forests in Panama with negative growth dominance coefficients. The reverse growth dominance of the Barro Colorado Island (BCI) forest was significantly stronger than the forests in Cocoli and Fort Sherman. About 76% of the growth of individual trees  $\geq 6$ cm diameter was explained by tree size. The 20% largest trees accounted for 8% (BCI) to 18% (Fort Sherman) of stand growth. Growth dominance patterns did not change much over two decades in BCI. The reverse growth dominance pattern was found in old forest, but the near-zero growth dominance was in the 20-year-old post-cutting forest in Fort Sherman.

*Keywords: growth dominance pattern and coefficients, tropical forest, Panama*

### 3.1. Introduction

Forest structure is a key factor in the growth and function of forests (Boyden 2005). The current structure has been shaped by the historical and environmental processes related to the spatial patterning (Moeur 1993, Pretzsch 1997, Youngblood et al. 2004) and development of trees. Structure and development of a forest are closely related. The structure of diverse forests changes over time, as a result of invisible intra- and inter-specific interactions of trees. The development of forests over time leads to changing competitive environments for each tree, with some trees increasing dominance over others (Oliver and Larson, 1996; Franklin et al., 2002; Long et al., 2004, cited by Binkley et al., 2006). Forest development has recently been represented by patterns of growth dominance, in terms of individual trees' contribution to stand biomass and growth.

Growth dominance patterns have recently been studied in forest plantations and temperate forests with composition of only few species. Dominance can be represented as frequency diagrams for stem sizes and growth (Binkley et al., 2006). Patterns of strong growth dominance were apparent in young plantations of *Eucalyptus* and *Facaltaria* monoculture, or mixed from 2 to 20 years old (Binkley et al. 2003), in the *Eucalyptus saligna* plantations from 1 to 10 years old, and under different silvicultural treatments (see Chapter 1). Old conifer forests in the Rocky Mountains showed the reverse growth dominance, where the larger trees contributed less to total stand growth than to stand biomass (Binkley et al. 2003, 2006). Patterns of growth dominance have not been examined for natural tropical forests.

Tropical forests have the greatest biodiversity of terrestrial ecosystems. Many lowland forests contain more than 100 species among trees of 10 cm or over in diameter at breast height on 1 ha, and in some more than 200 species may be found (Turner 2001). Species richness rises very rapidly with area or number of individuals sampled in a forest and plots of 5 ha or more may be required to sample local diversity adequately (Turner 2001). The tropical forests hold large stores of carbon and play a major role in the global carbon cycle (Dixon et al. 1994; Phillips & Gentry 1994; Houghton et al. 2001). Their importance has attracted a great deal of experimental and theoretical attention (Malhi et al. 1999; Malhi & Grace 2000), and several recent advances have led to a variety of estimates of carbon stocks and fluxes (Malhi et al. 1998; Clark et al. 2001b; Gurney et al. 2002). Recent studies on structure and growth, regeneration, biodiversity, or spatial patterns of the tropical forests have been also represented, but not on growth dominance patterns. A classic ecological theory states that species can only co-exist (assuming equilibrium assumptions apply) if the levels of inter-specific competition remain low enough to prevent competitive exclusion of some members of the community (Turner 2001). Natural tropical forests commonly have a smaller number of large trees compared to a great deal of smaller trees. The contribution of large and small trees to total stand growth depend on the balance of resource acquisition and efficiency of resource use by individual trees. Growth dominance patterns are also expected to change over time and vary over type of tropical forests.

Objectives of this chapter are to explore the pattern of reverse growth dominance in three different tropical forests in Panama; to compare growth dominance of old tropical



forest and a young one that recovered from clear cutting; and to investigate the change of growth dominance over time in the tropical forest.

## **3.2. Materials and method**

### *Study site and data*

I used the available datasets from the previous studies related to structure, growth, and ecology of tropical forests to determine patterns of growth dominance for these forests. The units of observations for this study were 1-ha subplots from within three permanent plots in Panama (Fig 4.1): the 50 ha Barro Colorado Island (BCI), the 6 ha Fort Sherman forest, and the 4 ha Cocoli plot.

The BCI plot was established in 1981 in a moist lowland forest. Rainfall averaged  $2640 \pm 460$  mm year<sup>-1</sup> for the period 1929-2001, with a 4-month dry season between January and April (Condit et al. 2001). Mean humidity is 78%, and daily maximum and minimum temperatures are 30.8°C and 23.4°C (1971-2001 average). The forest is partly deciduous, with about 10% of canopy leaves dropped at the peak of the dry season (Condit et al. 2001). Censuses have been carried out in 1981-1983, 1985, 1990, 1995, 2000, and 2005 (Hubbell & Foster 1983, 1986; Condit 1995, 1998; Condit *et al.* 1995; Leigh 1999). All free-standing woody stems  $\geq 10$  mm in trunk diameter were mapped, tagged, and identified between 1981 and 1983 (Croat 1978; D'Arcy 1987, Condit *et al.* 1996). The census was repeated in 1985 and every 5 years thereafter until 2005. Over 350,000 individual trees of over 300 species have been investigated over 25 years. The trunk diameter was measured to the nearest millimeter at 1.30 m above ground or above buttresses. If a trunk was swollen at 1.30 m, the measurement was taken 20 mm lower

(Condit 1995, p. 50). Points of measure (POM) were painted on buttressed stems during 1990–2000. Multi-stemmed, broken and re-sprouting trees were recorded and handled separately in growth analyses. Measurement problems were handled during each census by checking field sheets for consistency and by re-measuring problematic trees. A subsample of 1715 trees was re-measured to assess independently the quality of diameter data. About 96% of the data had a relative error of less than 10%. For a more detailed description of the field methodology, the reader is referred to Condit (1998). Sites for datasets are available to access on the websites <http://ctfs.si.edu/datasets/>.

The Cocoli plot was set up at a dry, semi-deciduous forest on the Pacific side, west of the Panama Canal, on a hillside near the Cocoli River. This site receives approximately 1950 mm of rainfall per year. The plot was 4 ha, L-shaped with a 300 x 100 m rectangle and a 100 x 100 m square set to the right side of the southernmost hectare. This secondary mature forest is estimated to be about 80-120 years old. The Cocoli plot has been investigated 3 times: 1994, 1997, and 1998. All free-standing woody plants with stem diameter 1 cm or above at breast height were tagged, measured, mapped, and identified to species.

The Fort Sherman plot is located in tropical moist forest on the Caribbean side of the Panama Canal, on a hilltop south of the Chagres River. This site receives approximately 2850 mm of annual rainfall. The plot is 6 ha in the form of a 400 x 100 m rectangle plus 140 x 140 m square contiguous to the left side of the southernmost hectare. A canopy research crane belonging to the Smithsonian Tropical Research Institute is found in the center of this 140 x 140 m square. The northernmost hectare of this plot was found in young forest approximately 20 years old. The Fort Sherman plot has been censused 3

times: 1996, late 1997 to early 1998, and 1999. All free-standing woody plants with stem diameter 1 cm or above at breast height were tagged, measured, mapped, and identified to species.

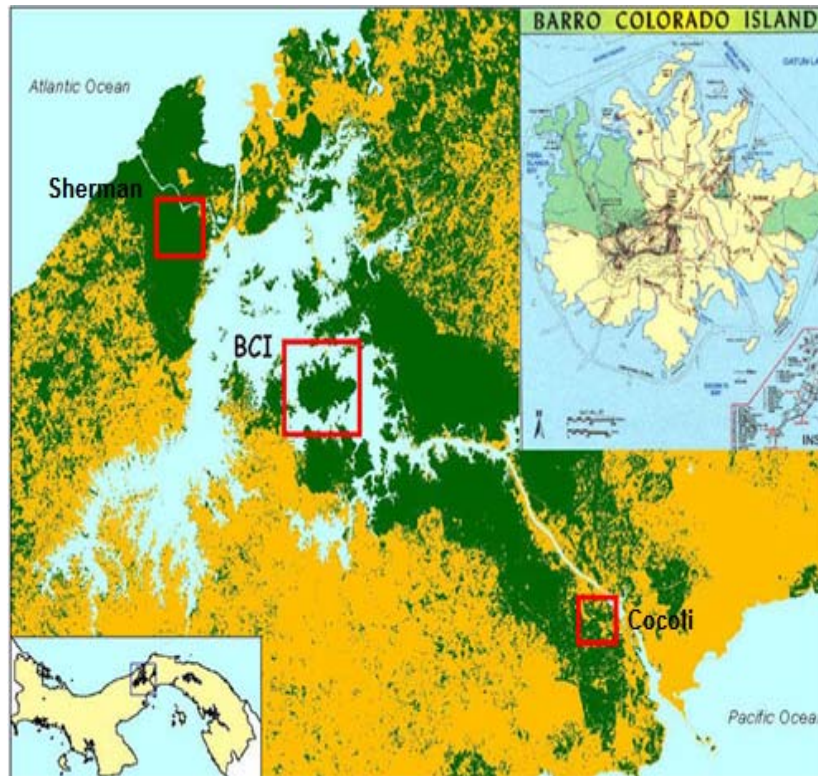


Figure 3.1: Study sites in Panama. From left top down: 6-ha Fort Sherman; 50-ha Barro Colorado Island (BCI); and 4-ha Cocoli plots.

I randomly selected four 1-ha subplots from the 50-ha BCI plot, using a written program of FOXPRO. For the 4-ha Cocoli plot, I simply divided it into four 1-ha subplots. For the 6-ha Fort Sherman plot, I selected three 1-ha subplots from the area of rectangle, along with one 1-ha subplot at the square to the left side of southernmost that were over 200 years old. I also used one 1-ha subplot with the age of 20 years old after a clear-cutting for the Fort Sherman plot to examine how growth dominance might differ

with forest age. These data were used to characterize the forest structures and test the hypothesis of “reverse growth dominance” pattern.

### ***Aboveground biomass (AGB) estimation***

To estimate the above-ground biomass (AGB) in these sites, I used the available biomass regression equations as in Table 3.1. These equations were examined and selected by Chave et al. (2003) as they had the highest mean correlation with the other methods. I assumed that all trees  $\leq 1$  cm diameter had the same wood specific gravity ( $0.54 \text{ g cm}^{-3}$ ). This average is lower than the mean reported by Brown (1997) for tropical America ( $0.60 \text{ g cm}^{-3}$ , averaged over 470 species) (Chave et al. 2003).

### ***Growth dominance patterns***

Stand growth can be illustrated in a variety of ways (Binkley 2004), such as frequency distributions, relationship of growth of each tree and its size, cumulative distribution of stand stem growth with tree sizes. The cumulative distribution can be analyzed by applying a modified version of a Gini coefficient. To calculate the growth dominance coefficient, all living trees during two successive censuses were used. Recruits would be counted in if they were alive until next census. Trees with negative growth were assumed having no increment. Therefore, the above-ground biomass change ( $\Delta\text{AGB}$ ) between two successive censuses was summation of increment of trees that were alive or current increment during an interval.

The interval for exploring growth dominance patterns was different between study plots. For subplots of Cocoli and Fort Sherman sites, I used only one interval of three years (1994-1997 for Cocoli and 1996-1999 for Fort Sherman plot). For those of BCI, I used the 3-year interval for the period 1982-1985, then the 5-year intervals for the period of 1985-2005. The use of two intervals at BCI allowed me to test for changes in growth dominance within the same plots over two decades.

### *Statistical analysis*

Forest biomass and growth of subplots in the same locations; and the forest growth and growth dominance coefficients of three locations were compared and analyzed using the independent sample t-test with a  $P = 0.05$  (SAS version 9.0 SAS Institute Inc., Cary, NC).

## **3.3. Results and discussion**

### **3.3.1. Forest growth**

The Cocoli forest had highest AGB with 314 Mg/ha in 1994, and growth rate of 9.3 Mg/ha/year at the period of 1994-1997. These measures for the Fort Sherman and the BCI forests were 221 Mg/ha in 1996 and 7.7 Mg/ha/year (1996-1999); and 260 Mg/ha and 8.2 Mg/ha/yr (1995-2000) calculated from 4 sampled subplots in each location (Table 3.2). The values of AGB were close to the average of tropical forests. Many broadleaf forests have an above-ground standing crop near 300 Mg dry matter per ha, most of which is wood (Leigh 1999). Chave et al. (2003) estimated that the BCI forest held 274 Mg ha<sup>-1</sup> of AGB, (including lianas in 2000; and the stand-level AGB increment

was  $7.05 \pm 0.32 \text{ Mg ha}^{-1}\text{yr}^{-1}$  in the period 1985-90, very close to the value average for the subset of BCI plots used in my analysis.

The BCI and Fort Sherman forests had twice as many trees as the Cololi forest (Table 3.2). Mortality rates during the intervals I examined were similar (between -3.2 and -3.4%/year) among the three locations somewhat higher than the average rate of -2%/yr since 1985 that Leigh (1999) reported. The mortality in the BCI and Fort Sherman forests was greater than the recruits. In mature forest on BCI, death rate of trees  $\geq 20 \text{ cm dbh}$  was nearly independent of size class (Chave et al. 2003).

Basal area of all trees  $\geq 10 \text{ cm dbh}$  was  $30 \text{ m}^2 \text{ ha}^{-1}$  (standard deviation among 1 ha plots within location of about 2.0) for all three forests (not including the 20 year-old post-cutting stand in Fort Sherman), which is a typical value for tropical forests (Dawkins 1959). The dry, semi-deciduous Cocoli forest had highest BA ( $31.25 \text{ m}^2 \text{ ha}^{-1}$ ) even though its density was lowest, indicating that more trees at higher diameter classes were found in this forest. The moist lowland forest at BCI has BA of  $28 \text{ m}^2 \text{ ha}^{-1}$  in 2000, very close to result of Leigh et al. (1990). Trees  $\geq 10 \text{ cm dbh}$  comprised of less than 15% in tree numbers, but counted for more than 85% in BA, This structure might influence patterns of growth dominance.

For these tropical forests, trees  $< 6 \text{ cm dbh}$  accounted for from 70-75% in number but only 1.0-3.5% in total biomass. The growth of individual trees was highly correlated to the tree size ( $r^2 = 0.76$ , Fig 3.2a). An average 1 Mg tree would have an increment of 25 kg/year, compared with 200 kg/year for an average 10 Mg tree. The 10-fold difference in size was greater than difference in growth rates, indicating a situation of reverse growth

dominance. Forest growth declined by about 1/3 ( $P < 0.05$ ) from 1985 to 2005 in the BCI forest (Table 3.2b), for unknown reasons.

### **3.3.2. Growth dominance pattern**

#### ***Growth dominance pattern in three different forests***

The growth dominance coefficients for Cocoli, Fort Sherman and BCI forest for all trees  $\geq 1$  cm dbh were -0.05 (S.D. 0.13) (mean not different from 0), -0.10 (S.D. 0.11), and -0.31 (S.D. 0.10), and all the growth dominance curves were above the 1:1 line (Fig 3.3 a). Therefore, the expected pattern of reverse growth dominance was found in Fort Sherman and BCI forests in Panama as the analytical approach of Binkley et al. (2006) was found (Fig 3.3). The Cocoli forest did not completely show this pattern because the growth dominance coefficient did not differ from 0. However, the largest trees accounted for proportionally less of the increment than of the mass in these three forests. 20% largest trees accounted for only from 8% (the BCI) to 18% (the Fort Sherman) stand growth. There was the imbalance between mass and increment (Fig 3.3c) that resulted in reverse pattern of growth dominance.

The reverse growth dominance of the moist lowland forest in BCI was significantly stronger than of the dry, semi-deciduous forest in Cocoli or the tropical moist forest on the Caribbean side in Fort Sherman ( $P = 0.02$ ). There was no difference in growth dominance between the Cocoli and Fort Sherman forest ( $P = 0.54$ ) in terms of growth dominance coefficient, but the pattern was different.

The reverse growth dominance of these three forests was stronger when considering only trees  $\geq 6$ cm dbh, with growth dominance coefficients falling to -0.29; -0.22 and -0.41 for Cocoli, Fort Sherman, and BCI forest, respectively (Fig 3.3b).

The pattern of reverse growth dominance was also found in some forests of the Rocky Mountains, USA (Binkley et al. 2006), even though they were comprised of one or few species. This pattern was attributed the result of growth acceleration of the non-dominant trees, and growth decline of dominant trees, or a combination of both. This suggested that any kind of forests could develop the reverse pattern when smaller trees dominated larger trees in growth compared to biomass.

Tree differentiation in tropical forests is apparently different from that in the monocultures because of the species diversity. There might be more sub-dominant trees in tropical forests because some shade-tolerant species would be found under the main forest crown. However, shade-tolerant usually does not mean that shade makes growth faster – just that trees do not die because of low light intensity. The natural tropical forests have relatively similar LAI (between 6 and 8) because so little light reaches the forest floor that additional leaves could not pay for themselves (Leigh 1999). However, there is a trade-off between competing for light and competing for nutrients (Tilman 1988). In theory, this could reduce LAI in nutrient-poor settings. Where nutrients are in short supply, trees invest more in roots (Leigh 1999). However, the information on whether these forests suffer from nutrient limitation is lacking. The explanation for the pattern of reverse growth dominance related to the efficiency of resource use in these forests is needed in the future studies.



### *Growth dominance pattern in young and old stands in the Fort Sherman forest*

The reverse dominance was apparently exhibited in the old forest in Fort Sherman with a growth dominance coefficient of -0.11, compared with -0.02 (not different from 0) of the 20-year-old, post-harvest forest (Fig 3.4). In the younger forest, growth of the larger trees balanced the growth of the smaller trees, resulting in the pattern of “no growth dominance”.

### *Changes in growth dominance over time in the moist lowland forest of BCI*

Growth dominance in plantations and temperate forests changes over time (Binkley et al. 2003, 2006; and Chapter 1 of this dissertation), but unknown in tropical forests. To investigate the change of growth dominance, I used datasets from 5 censuses with an interval of 5 years (from 1985 to 2005) in the BCI big plot.

In my study, the trend of growth dominance change was not clear when growth dominance coefficients for 4 continuous periods did not change much (Fig 3.5) in the old forest at BCI. In value, the growth dominance coefficient was greatest negative at period 1985-90 (-0.39), then declined to -0.31 at the following period (1990-95), and a little increased at the last two periods (-0.32 and -0.34). The growth dominance coefficients at three last periods were not significantly different, and it was difficult to recognize the difference of growth dominance curves in these periods (Fig 3.5). This result indicates that the pattern of growth dominance of the BCI changed little during 20 years (1985 - 2005), even though forest growth declined by about 1/3 (Fig. 3.2).

### 3.4. Conclusion

The expected phase 4 “reverse” dominance was exhibited in most forests in Panama, and at all periods of study in the BCI forest. Tree growth increased with tree size, but the contribution of large trees to stand growth was lower than their proportional contribution to stand biomass. Growth dominance patterns did not change over time in two decades in the BCI forest. The old forest had stronger reverse growth dominance than the 20-year-old post-cutting forest in Fort Sherman. The future investigation and more censuses in other tropical forests may be needed for conclusions about growth dominance pattern and its change in tropical forests.

### Acknowledgements

I thank the Center for Tropical Forest Science for allowing me to use the existing data. Special thanks to Bao Tran who developed the code in FOXPRO language to randomly select 1-ha sub-plot from the big plots.

### Tables and figures for chapter 3

Table 3.1. Regression equations for total above-ground biomass in the Panama forests. The first equation was applied only to trees  $\geq 10$  cm diameter (measured at 1.30 above ground - dbh); the second to trees  $1 \text{ cm} < \text{dbh} < 10 \text{ cm}$ ; and the third to trees with  $\text{dbh} \leq 1 \text{ cm}$ .  $p$  is the oven-dry wood specific gravity (in  $\text{g cm}^{-3}$ ),  $p^*$  is the mean wood specific gravity of the plot ( $0.54 \text{ g cm}^{-3}$ ). AGB is the above ground biomass (in  $\text{kg tree}^{-1}$ ) (Chave et al. 2003)

<i>Method</i>	<i>Regression equation</i>	<i>Sample size</i>	<i>d.b.h.</i>	<i>Location</i>	<i>Reference</i>
1	$\text{AGB} = \exp[-2.00 + 2.42 \ln(D)]$	378	$\geq 10 \text{ cm}$	Pantropical	Chave et al. (2001)
2	$\text{AGB} = \exp[-0.37 + 0.333 \ln(D) + 0.933 \ln(D)^2 - 0.122 \ln(D)^3]$	316	$> 1 \text{ cm}$	Brazil	Chambers et al. (2001)
3	$\text{AGB} = p/p^* \exp[-1.839 + 2.116 \ln(D)]$	66	$\leq 1 \text{ cm}$	SE Mexico	Hughes et al. (1999)

Table 3.2. Change in density and AGB in Panama forests

Forest	Period	N/ha (start-end)*	AGB (Mg/ha) (start-end)	Mortality (trees/ha)	Recruitment (trees/ha)	BA of trees $\geq$ 10cm dbh ( $\text{m}^2 \text{ha}^{-1}$ ) (start-end)	Growth (Mg/ha/yr)
Cocoli	1994-97	2045-2163	314-341	195 (3.2%/yr)	313	29.7-31.9	9.3
Ft Sherman	1996-99	4540-4400	221-241	445 (3.3%/yr)	305	24.2-26.9	7.7
BCI	1995-00	4862-4378	260-286	833 (3.4%/yr)	349	25.3-28.0	8.2

\*Density and AGB at the start and the end of period of study. AGB increment was real increment, the recruitment was excluded in calculation.

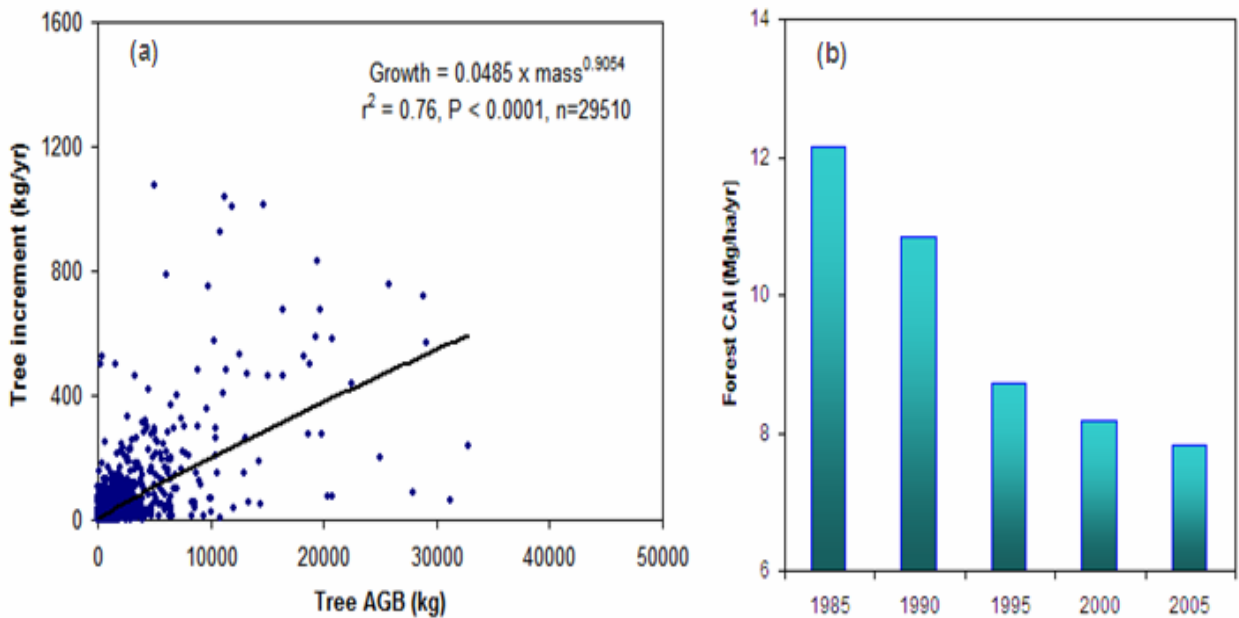


Fig 3.2. (a) Relationship between individual tree increment and tree size for forests in Panama. The variation in tree size was great, but larger trees grew faster on average than smaller trees. (b) Forest growth in the BCI plot decreased over time. The forest growth was calculated by multiplying the individual tree growth by forest density of the last year of each period.

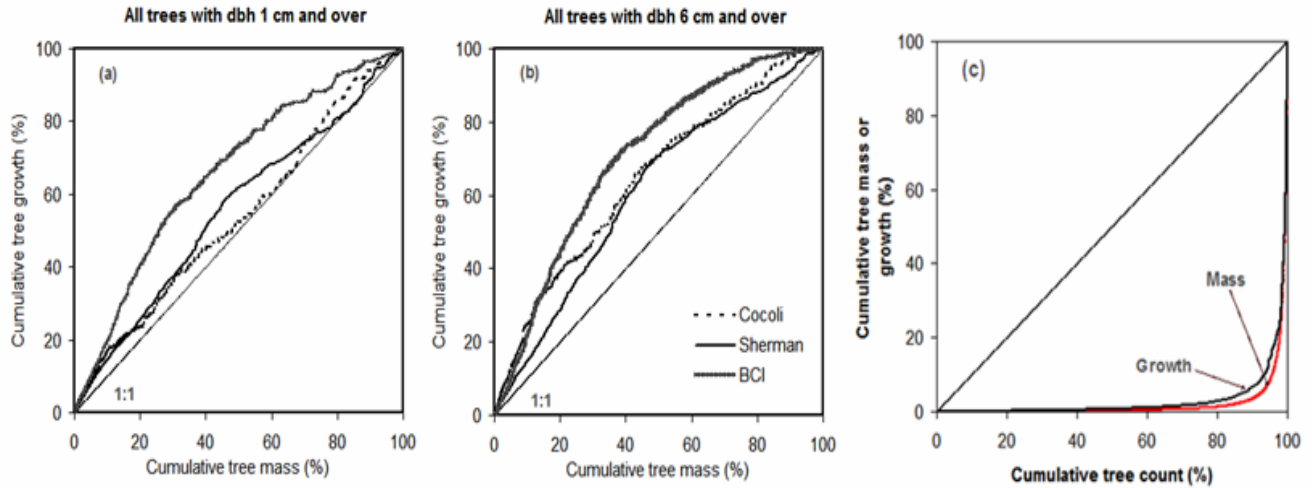


Fig 3.3. The growth dominance pattern for three forests in Panama for all trees  $\geq 1$  cm (a) and  $\geq 6$  cm (b). The growth dominance coefficients of BCI forest differed from those of Cocoli and Fort Sherman forests. A cumulative distribution of stand mass and growth (c)

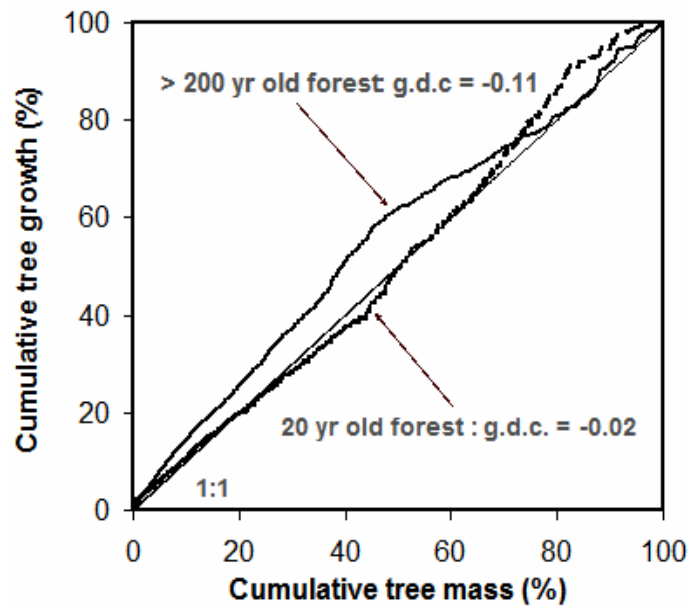


Fig 3.4. Growth dominance coefficients for the 200-yr-old (solid line) and 20-yr-old forest (dash line) in Fort Sherman. There was only one 1-ha subplot analyzed in 20-yr-old forest. It had been recovered for about 20 years after clear cutting.

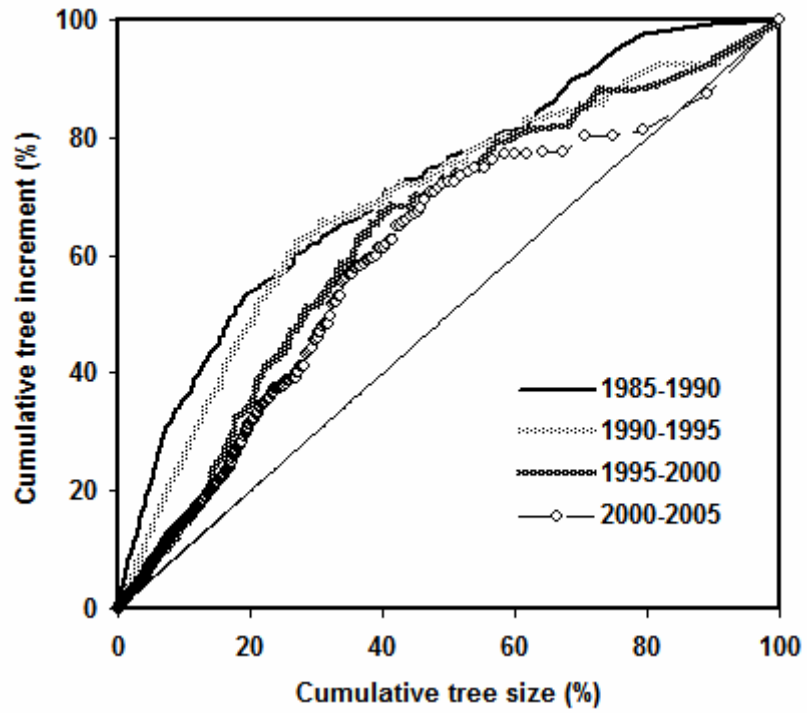


Fig 3.5. Illustration of growth dominance changes for the BCI plot of lowland tropical forest in Panama. Reverse growth dominance pattern was shown but there was no significant difference between periods of the study.

## CHAPTER 4

### SYNTHESIS

Growth dominance patterns changed strongly over time and silvicultural treatments in young plantations (see Chapter 1), and in temperate natural forests in Rocky Mountains (Binkley et al. 2006). However, change of growth dominance over time was not clear in the tropical natural forests in only two decades (Chapter 3).

Growth dominance pattern in young plantation of my study agreed strongly with that of the previous study conducted by Binkley et al. (2003) in Chinchuck, Hawaii, in which growth dominance increased strongly from little at age 2 to strong at age 6 and stronger at age 10. However, the growth dominance declined at age 20 (Fig 4.1) as stands exhibited a relaxation in growth dominance.

I expected a reverse growth dominance pattern in the 70-year-old *Eucalyptus* plantations near Kalopa, Hawaii and Itatinga, Brazil. However, the dominant trees at these stands are still growing faster than the non-dominant trees, resulting in a positive growth dominance pattern in Hawaii and a very weak growth dominance in Brazil. A similar application occurred in the Cascade Head experimental forest (Binkley 2004) when the strong growth dominance patterns were found in forests aged from 74 to 104, and a weak growth dominance pattern at the 147-year-old forest, indicating that the trend of declining growth dominance in these forests after 100 years growing (Fig 4.2). Reverse growth dominance is expected to develop more in mixed species stands than in

monocultures. However, we wouldn't have answers. Future works should be needed to explore the processes (physiology/ecology) behind growth dominance.

We expected that reverse growth dominance would develop more in the old natural forests. This was supported in the study at the temperate forests by Binkley et al. (2006), when reverse patterns were found at the Rocky Mountains forests (Fig. 4.3 A). I also found the “reverse” pattern of growth dominance in some different tropical natural forests in Panama (Fig 4.3 B) in chapter 3 to claim the hypothesis.

The analyzing patterns of stand growth dominance may lead to useful insights to understand forest dynamics from the level of trees to stands, across decades of stand development.

#### Figures for chapter 4

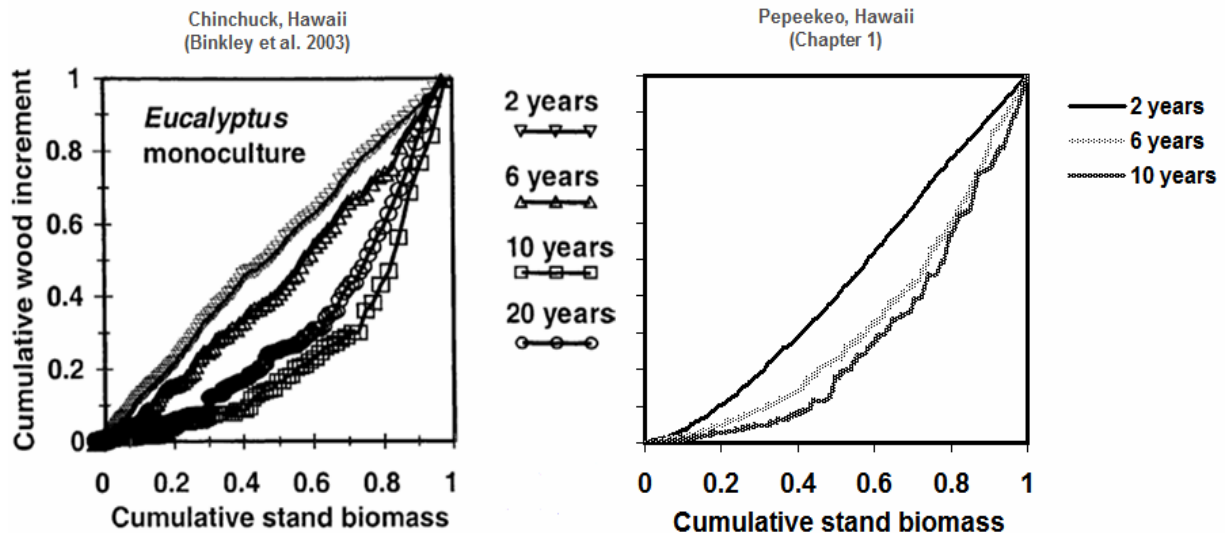


Fig. 4.1. Comparison of growth dominance changes over age in two *Eucalyptus* monocultures in Chinchuck (left) and Pepeekeo (right), Hawaii. Growth dominance increased from the little one at age 2 to the strong one at age 6 and 10 years. Growth dominance declined at age 20 in Chinchuck (Binkley et al. 2003).

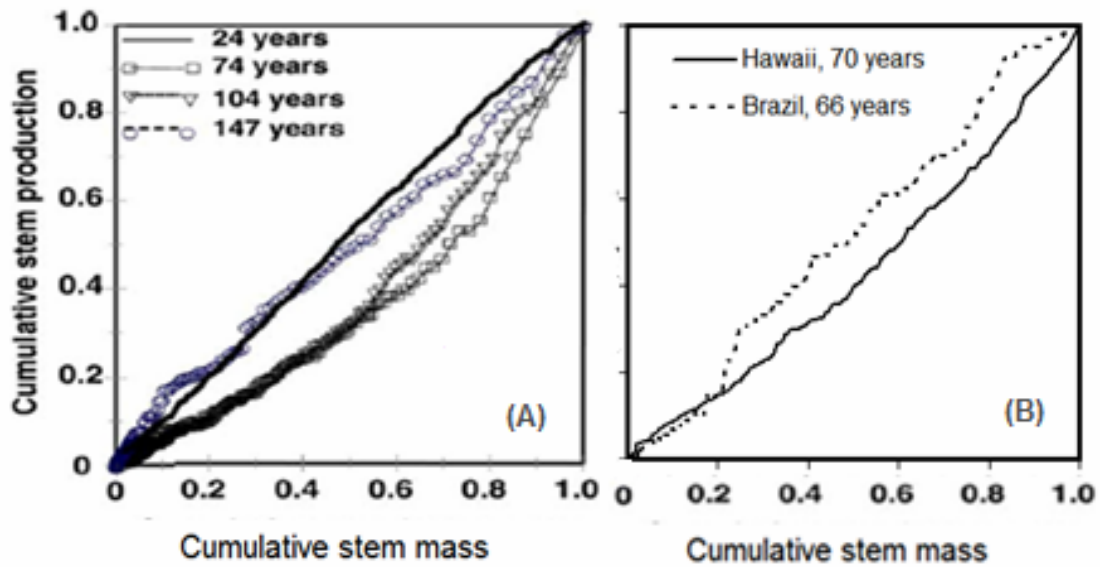


Fig. 4.2. Comparison of growth dominance patterns in the Cascade Head experimental forest (A) by Binkley et al. (2004), and *Eucalyptus saligna* plantations (chapter 2) at about 70 years old (B). The reverse growth dominance patterns have not found in these old forests, indicating that the dominant trees still grew strongly and accounted for the larger increment than the non-dominant trees.

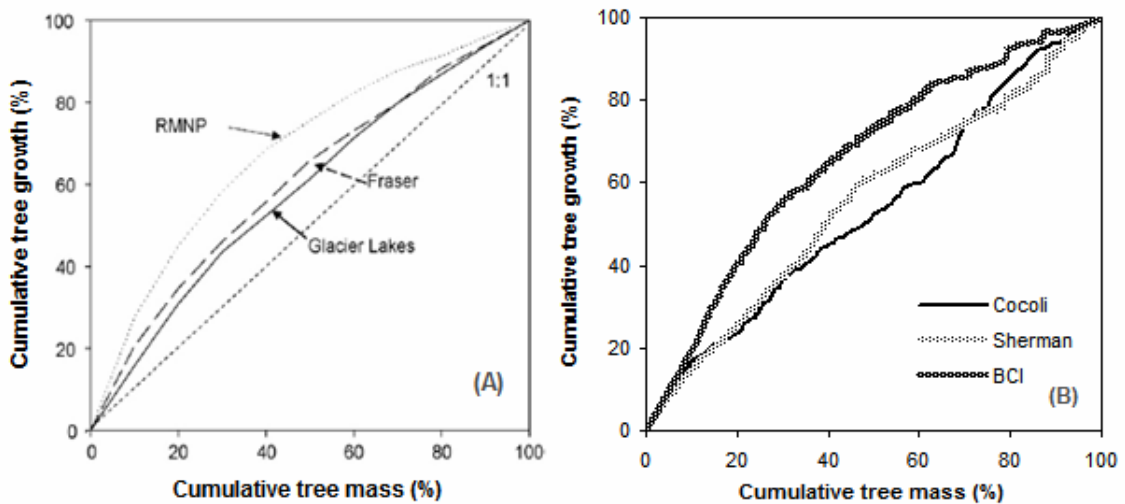


Fig 4.3. Comparison of growth dominance patterns in the Rocky Mountains forests (A) by Binkley et al. (2006) and in three tropical natural forests in Panama (B); reverse growth dominance patterns were found in these diverse forests.



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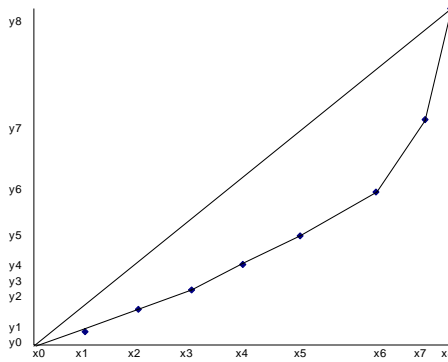
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## Appendix

### *Calculation of Gini coefficient (after Satoshi Miyamura 2003)*

Suppose we have the cumulative relative frequencies of income ( $Y_i$ ) and households ( $X_i$ ),  $i = 1$  to  $n$ . Taking the cumulative percentage of income on the vertical axis and the proportion of households on the horizontal axis, we may plot the two cumulative frequencies to obtain the Lorenz curve.

Denoting the Gini coefficient by  $G$ , we have  $G = A/(A+B)$  (4a) which must be between 0 and 1. When there is total equality the Lorenz curve coincides with the 45° line (line 1:1), area  $A$  then disappears and  $G = 0$ . With total inequality (one household having all the income), area  $B$  disappears and  $G = 1$ .



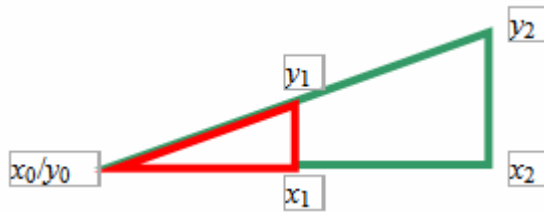
*Model 3:* Cumulative relative distribution of income ( $Y_i$ ) and household ( $X_i$ ) (a) and the Lorenz curve (b) with two separate areas for Gini coefficient calculation.

It is important to figure out the area  $B$ . This involves calculating the area for the triangles that can be drawn by joining the each plotted points, the cumulative frequency of households associated with it, and the point of origin.

To focus on the first triangle:



The area of this triangle can be calculated as  $[1/2*(x_1-x_0)*(y_1-y_0)]$ . The next triangle is below:



If we want the area of the second triangle it is  $[1/2*(x_2-x_0)*(y_2-y_0)]$ , but we have already calculated the first triangle. So the area we want in addition is:

$[1/2*(x_2-x_0)*(y_2-y_0)] - [1/2*(x_1-x_0)*(y_1-y_0)]$  or if we focus on the trapezoid, it is  $[1/2*(x_2-x_1)*(y_1+y_2)]$ .

In general, the G may be calculated from the following formula for area B:

$$B = \frac{1}{2} \{ (x_1 - x_0) \times (y_1 + y_0) + (x_2 - x_1) \times (y_2 + y_1) + \dots + (x_k - x_{k-1}) \times (y_k + y_{k-1}) \}, \text{ where } x_i$$

and  $y_i$  are the two cumulative relative frequencies on the X and Y axis, with  $x_0 = y_0 = 0$  and  $x_k = y_k = 1$ .

Alternatively, the Gini coefficient can be expressed as

$$G = \frac{A}{A+B} = \frac{A+B}{A+B} - \frac{B}{A+B} = 1 - \frac{B}{A+B} \quad (4b)$$

In case where  $x_k = y_k = 100$ , the area  $A + B = (100 \times 100)/2 = 5,000$ . Hence G

index now is  $G = 1 - \frac{B}{5,000} \quad (4c).$