ABSTRACT

RUBILAR, RAFAEL ALEJANDRO. **Biomass and nutrient accumulation comparison between successive loblolly pine rotations on the Upper Coastal Plain of Alabama**. (Under the direction of H. Lee Allen).

Upper Coastal Plain forest sites are characterized by highly weathered soils and intensive agricultural use. These conditions may predispose intensively managed sites to second rotation declines if managed carelessly. This study compared aboveground biomass and nutrient content changes between successive rotations of loblolly pine on the same site in the Upper Coastal Plain of Alabama and examined what first rotation factors were important in the biomass and nutrient accumulation in the second rotation. Individual tree biomass and nutrient content equations were compared for the first and second rotation. In addition, within tree nutrient concentration relationships were explored to evaluate their significance for whole tree nutrient content determinations.

Representative trees from the diameter distribution were destructively sampled from each rotation. Foliage, branch, stemwood, and stembark tissues, were separated, sampled, and analyzed for nutrient concentrations. Green-field and oven-dry weights were used to calculate nutrient contents. Regression equations for individual tree tissues biomass and nutrient contents as a function of tree diameter and height were fitted for each rotation. Stand biomass and nutrient contents were estimated by applying these equations to stand inventory data for each rotation. Forest floor biomass and nutrient contents were evaluated for both rotations. Soil samples obtained when the first rotation stand was harvested were used to characterize total N and available pools for other mineral soil nutrients.

Analyses of nutrient concentration relationships within the tree indicated that mobile nutrients concentrations of stemwood, bark, and branches decreased with distance from the top of the tree. Foliar nutrient concentrations and non-mobile nutrients for other tissues showed no patterns with tree height. Stemwood biomass regression equations were the same for the two rotations but nutrient content regressions differed. Foliage, branch, and bark biomass and nutrient content regressions also differed. Major differences between rotations were found for stemwood N and P; foliage, branch, and bark B concentrations, indicating reduced availability of these nutrients in the second rotation stand. Considering harvesting removals, micronutrient availability, especially B availability may be severely affected as a larger proportion of B, relative to other micronutrients was allocated to stemwood. Biomass and nutrient accumulation in the second rotation stand was highly correlated with soil exchangeable P at the end of the first rotation. The forest floor was a large C reservoir and a large nutrient sink for N, P, K, S Zn, and Cu.

BIOMASS AND NUTRIENT ACCUMULATION COMPARISON BETWEEN SUCCESSIVE LOBLOLLY PINE ROTATIONS ON THE UPPER COASTAL PLAIN OF ALABAMA

By

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DEDICATION

To my happy newborn son and my lovely wife, Dario and Claudia.

PERSONAL BIOGRAPHY

Rafael Alejandro Rubilar Pons was born in Santiago, Chile in 1969. His parents Norton Rubilar and Rosario Pons and two older sisters Gloria and Viviana composed his family. He completed his high school studies at the Instituto Nacional Jose Miguel Carrera, in Santiago. The spirit of this traditional school encouraged him to pursue his best in life and a love for his country. In 1988, he was accepted as a forest engineer student at the Facultad de Ciencias Forestales at the Universidad de Chile in Santiago. It was here that he met his future wife Claudia who has brought love and continuous challenges to his life in aspects not related with science. As an undergraduate, he participated in several student activities and organizations and soon realized his research and teaching vocation, working as a teaching assistant. In 1990, Rafael met his first mentor and friend Ph.D. Jorge Toro Vergara, with whom he worked until 2000. Jorge helped him to expand his knowledge of geology, soils, ecology, ecophysiology, and plant growth. In 1991, Rafael received the CORMA recognition of excellence as the highest ranked student in his class. In 1993, Rafael finished his studies, received his BS in Forest Sciences, and was offered a soils mapping position with Forestal Valdivia S.A. He moved to Valdivia, where it always rains, 800 km south of Santiago. In 1994, Dr. Toro offered him the soils mapping coordinator position with Bioforest S.A. In 1996, Bioforest S.A moved to Concepcion, 450 Km south of Santiago, and Rafael was hired as the leader of the Soils and Site Program. During this period, he had the unique opportunity to investigate Chilean forest soils and develop a program of site-specific silviculture for radiata pine and eucalyptus plantations. During this experience, he developed a strong passion for forest soils, ecology, and physiology. He also had the opportunity to meet several outstanding

researchers in site productivity and fast-growing forest plantations including Stanley Gessel, Sadanandan Nambiar, Lee Allen, Richard Waring, John Turner, Marcia Lambert and Joe Landsberg. Several of them encouraged him to pursue graduate studies and provided wonderful insights on research topics concerning sustained productivity of forest plantations. In 1998, he received his degree in Forest Engineering with maximum distinction upon completing his BS thesis. He also received the Faculty of Forest Science award as the best student in the class and had the honor of making the graduation speech. In July 2000, Rafael received a Fulbright scholarship, married Claudia, and was accepted as a graduate student at North Carolina State University. He moved to Raleigh, finished his MS coursework in one and one-half years, and was accepted as a Ph.D. student at NC State University, where he continues his scientific development. His second and third mentors, Lee Allen and Dan Kelting have provided balanced and invaluable guidance on scientific and professional duties. In August 2002, Dario Ariel, Rafael's and Claudia's first son came to this world bringing a new feeling of love and happiness to their lives. For non-academic activities, Rafael and Claudia have traveled across Chile, enjoying the sounds of nature, the landscape, and new people, and fulfilling a depth sense of life.

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I want to express my gratitude to the Fulbright scholarship program for opening the doors for a new life and understanding about the world; to the members of my committee, Lee Allen and Dan Kelting who provided advise during of development of this work; to several NC State University people who helped me, especially Denise Pauliac, lab manager for the Forestry Department, Heather Morrell, lab assistant, Mr. William Bryan, Superintendent Hodges Wood Products Laboratory, and Paula Zanker, Field and Lab Research Manager. I appreciate the efforts of International Paper personnel who provided field assistance during our biomass assessment and were very cooperative in providing all types of information.

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CHAPTER 1

Comparison of Biomass and Nutrient Content Equations for Loblolly Pine Successive Rotations at an Upper Coastal Plain Site.

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ABSTRACT

Biomass and nutrient content equations, used for several research comparative objectives, are assumed site- specific. This study compared first and second rotation biomass and nutrient equations between successive loblolly pine plantations on an upper Coastal Plain Site on Alabama. In addition, nutrient concentration relationships with crown position for the second rotation stand were explored in order to evaluate their significance for biomass studies determinations. Representative trees from the diameter distribution of the stand were sampled destructively on each rotation. Tissues were separated into foliage, branch, stemwood, and stembark and analyzed for nutrient concentration and dry weight. Distance from the top of the tree was recorded for all tissues of the selected second rotation trees and plotted against nutrient concentrations. Regression equations for individual tree tissues biomass and nutrient content were fitted for each rotation and compared. Analyses of nutrient concentration relationships with crown position indicated that mobile nutrients concentrations of stemwood, bark, and branches decreased with distance from the top of the tree and height activity of the live crown. Foliar nutrient concentrations and non-mobile nutrients for other tissues show no patterns with tree height. Stemwood biomass regression equations are equivalent after two rotations but not nutrient contents. Foliage, branch, and bark biomass and nutrient content regressions differ. Major differences between rotations were in stemwood N and P; and foliage, branch and bark B concentrations, which suggested reduced availability of these nutrients for the second rotation stand.

INTRODUCTION

Biomass equations have been developed to estimate aboveground dry matter and nutrient content accumulation of loblolly pine for a wide range of objectives, including: comparisons of harvesting and site preparation treatments (Tew et al, 1986), thinning and stand density (Wells, 1975; Harms and Langdon, 1976; Urrego, 1993), fertilization (Albaugh et al., 1998), genotypes (Pope, 1979; Pope and Graney, 1979), site and soil factors (Nemeth and Davey, 1974; Ku and Burton, 1973; Smith et al, 1963), and primary productivity and nutrient cycling (Kinerson, 1977; Wells and Jorgensen,1975; Switzer, 1966, 1972). Although, results from these studies indicate that equation parameters may significantly differ between sites, silvicultural treatments, and genotypes, a single set biomass and nutrient content equations is typically developed due to practical and economical considerations. The underlying assumption of similarity of biomass equations is likely, under similar stand density conditions (Harms and Langdon, 1976). However, nutrient content equations are likely to be site specific (Van Lear et al., 1984).

This study compares biomass and nutrient content equations developed from trees sampled from first and second rotation plantations on the same site, as part of a study to assess differences in the biomass and nutrient accumulation between rotations of loblolly pine. Specifically, we evaluated nutrient concentration relationships with crown position, and compared coefficients of biomass and nutrient equations between rotations.

MATERIALS AND METHODS

Location of the study

The study was established in 1980 as a part of a larger study examining the long-term effects of management practices on site productivity in the Southeastern USA (Tew et al, 1986). The site is located on a Smithdale soil on gentle slopes (<5%) of the Upper Coastal Plain in Butler County, Alabama, approximately 20 km southeast from the town of Greenville, AL. These soils consist of thick layers of loamy sediments on narrow ridgetops and side slopes of the uplands. Annual rainfall averages 1473 mm (1960 to 2000), and is evenly distributed during the year. Average monthly temperatures range from a minimum value of 11.9ºC to a maximum value of 25ºC, with an annual mean of 18.5ºC (NOAA, 2000)

Stand Characteristics

The first rotation stand was a loblolly pine plantation of unknown genetic material established in 1960 on a recently abandoned old-field. Site index (base age 25) was estimated as 23.8 m using the Clutter and Lenhart (1968) equation. When the pine plantation was harvested at 22 years it had 695 trees ha^{-1}, an average diameter of 21 cm (DBH), a height of 19.2 m (H), a basal area of 26.4 m^2 ha^{-1}, and a volume of 271 m^3 ha^{-1}. Hardwood basal area averaged 0.7 m^2 ha^{-1}, with 0.4 m^2 ha^{-1} represented by sweetgum (*Liquidambar styraciflua* L.). Slash pine (*Pinus elliotti*) was present on a few plots and averaged 5.7 m^2 ha^{-1}. The dominant understory species was wax myrtle (*Myrica cerifera* L.) with 1.6 m^2 ha^{-1}. The first rotation stand had been thinned at age 17 but no records exist of the removals.

The second rotation was established in 1982 following clearfelling of the previous stand. After harvesting, previous established plots were used to impose a factorial design testing five combinations of harvest method and site preparation (main plots), and two cultural treatments (sub plots). The plantation was established in January 1983 with two seedlings per planting spot at a 2 x 3 m spacing. After planting, plots with the high cultural treatment received an herbicides treatments during May 1983 and 1984 (0.29 L ha^{-1} Oust and 2.33 L ha^{-1} Velpar-L), and an insecticide treatment during March 1984 (FURADAN at 1 g active/tree). In January 1985 double planted seedlings were cut where needed to provide just one seedling per planting spot, and a final herbicide treatment was applied on March 1985 (6% solution GARLON 4 in diesel applied to base of hardwoods).

Inventory measurements at age 17 year indicated a site index (base age 25) of 22.1 m using the equations of Clutter and Lenhart (1968). The stand averaged 1541 trees ha^{-1}, 16.4 cm DBH, 16.7 m total height, 34.1 m^2ha^{-1} basal area and 296 m^3ha^{-1} volume. Besides small vines and a few suppressed hardwoods, no significant non-pine vegetation was observed in the plots.

Biomass Sampling and Nutrient Analyses

Biomass sampling in the first rotation stand included fifteen trees representing the range of tree sizes present. For the stand, tree diameters ranged from 4.5 cm to 38.2 cm, and sampled trees averaged 21.9 cm and ranged from 8.4 to 35.6 cm. The heights ranged from 6.7 m to 25.0 m, and sampled trees averaged 18.7 m and ranged from 9.9 m to 22.8 m. First rotation biomass was sampled following the methods from Tew et al (1984).

Briefly, the sample tree was felled and divided into stem, branches > 2.54 cm, branches between 1.27 to 2.54 cm, branches < 1.27 cm, needles and cones. Stem discs were obtained from the bole every 3 m to the tip starting at 1.5 m. Green weight of each component was recorded in the field. Stem discs, and subsamples of foliage and branchwood from all branch sizes were obtained from each tree after a thorough mixing of each component. Each subsample was weighed green in the field, dried at 70ºC for 24 hours, and weighed dry. Field green weights were then adjusted to dry weight. Bark and wood wedge subsamples from each disc were obtained. Subsamples of each component were ground to pass 1 mm screen in a Wiley Mill grinder, and analyzed for nutrient concentrations.

Second rotation sampling included twelve trees representing the range of tree sizes present. For the stand, tree diameters ranged from 6.6 cm to 27.2 cm, and sampled trees averaged 16.5 cm and ranged from 9.1 to 26.4 cm. Height ranged from 9.4 m to 21.0 m, and sampled trees averaged 17.5 m and ranged from 15.1 m to 20.3 m. Trees were felled at the ground line and sample discs were obtained from the bole every 2 m to the tip starting at the stump. Green weights of sample discs and stem sections were recorded in the field. Stem discs and branch tissues were oven dried at 70ºC for moisture content determination. Bark and wood were separated from each disc and wood:bark ratios were calculated. Instead of using all branchwood and foliage material from each tree as was done in the first rotation, branch and foliage biomass was estimated using a two-stage approach. First, foliage and branchwood dry weights of individual branches were estimated using branch distance of insertion from the top of the tree (DFT) and diameter

(BD). Second, branch estimates were summed to provide a total tree estimate of branch and foliage biomass. Individual branch foliage and branchwood dry weights were estimated using live branches sampled to represent the BD and DFT distribution of all the branches (4 to 12 branches per tree). Foliage and branch tissues were separated in the field for each individual branch. Bark, wood wedge, and individual branch foliage and branchwood samples were ground to pass 1 mm screen in a Wiley Mill grinder, and analyzed for nutrient concentration. Average nutrient concentrations of tree components in the second rotation stand were obtained by dividing total nutrient content of each component by its dry weight in order to obtain weighted average values comparable to first rotation estimates.

Foliage, branch, and bark tissues for the first and second rotations were analyzed for nitrogen using a NC 2100 CHN auto-analyzer (CE, Instruments). Because of the low N concentrations in wood, N was obtained colorimetrically using a Lachat Rapid Flow Autoanalyzer (Lachat, 1986) after a wet semi-micro-Kjeldahl digestion (Bremner, 1961). In the case of P, K, Ca, Mg, sulfur (S), manganese (Mn), zinc (Zn), boron (B), and copper (Cu), a nitric acid wet digestion was applied using the method described by Jones and Case (1990) and concentrations were determined using an ICP-AES spectrophotometer.

In order to compare the repeatability of nutrient concentration determinations of archived samples, first rotation tissue samples were re-analyzed using second rotation procedures. Regression analyses indicated that Ca and Mg concentrations were the same, and N, P, and K were 3% lower, and 5% and 11% higher, respectively. These results indicated

small differences between old and new procedure concentration estimates, therefore, new concentrations were used, and additional S and micronutrient analyses of archived biomass samples were obtained.

Data Analyses

Data from the second rotation allowed for examination of the relationships between nutrient concentrations of stem, bark, branch, foliage, and wood:bark ratios, and the relative distance from the top of the tree (RDFT) and BD. These relationships were explored using graphical and regression analysis. In addition, average whole-tree tissue nutrient concentrations between rotations were tested using a t-test.

Because of differences in sampling procedures, estimation of tree biomass and nutrient content differed somewhat between rotations. First rotation dry weight and nutrient content were estimated using composite sample concentrations; subsample dry weights, and field green weights to estimate total biomass and nutrient content of each component. Second rotation estimations of whole tree foliage and branchwood dry weights and nutrient content were calculated by adding estimates generated by individual branch regression equations (Equations 1, 2 and 3).

[1] $$\text{Log } Y = (a + b^* \text{LOG}_{10}(BD) + c^*\text{LOG}_{10}(DFT))^*CF$$

[2] $$\text{Log } Y = (a + b^* \text{LOG}_{10}(BD) + c^*(DFT^2))^*CF$$

[3] $$\text{Log } Y = (a + b^* \text{LOG}_{10}(BD) + c^*\text{LOG}_{10}(BD^2DFT))^*CF$$

where Y is the dry weight or nutrient content in grams or milligrams per branch, BD in cm, DFT in m, CF is the correction factor for logarithmic transformation bias suggested by Baskerville (1972) with the form CF = exp (Mean Square Error/2), and a, b and c are coefficients of the model. Tree biomass and nutrient contents of stemwood and stembark were calculated by multiplying stem sections field green weights by average nutrient concentrations, the ratio of dry to field green weight, and wood:bark ratios of the corresponding top and bottom sample disc of each section.

Regression analysis was used to test differences between rotations in the intercept and slope parameters of the tree biomass and nutrient content equations. The full model, used to test for differences in slope between rotations, was of the form:

[4] $$LOG_{10}(Y)=a*ROT + b* LOG_{10} (DBH^2H) + c*(ROT* LOG_{10}(DBH^2H))$$

where Y is the biomass or nutrient content in grams or milligrams per tree, ROT is rotation number (0,1) as a dummy variable, and a, b, and c coefficients of the model. If no differences in slope were found, the interaction term was dropped and a reduced model was used to test for intercept differences between regression equations (Equation 5).

[5] $$LOG_{10}(Y)=a*ROT + b* LOG_{10} (DBH^2H)$$

If slopes or intercepts were different ($p<0.10$), independent regression equations were generated for first and second rotation stands using a simple model of the form:

[6] $LOG_{10}(Y)= a + b* LOG_{10} (DBH^2H)*CF$

where Y is the biomass or nutrient content in grams or milligrams per tree, DBH in cm, H in m, a, and b coefficients of the model and CF the correction factor. All the models tested were selected based on best fits, R^2 values, and residuals analyses. Statistical analyses were performed using SAS software (version 8.2, SAS Institute Inc., Cary, NC, 2000)

RESULTS

Tree Nutrient Concentrations

Macronutrient concentrations in the foliage for the first and second rotation stand were in the order N > K > Ca > P = S > Mg = Mn > Zn > B > Cu (Tables 1 and 2). Concentrations for branches, stemwood and stembark ranked N > Ca > K > Mg > S = P for both rotations, and showed the same micronutrient order as second rotation foliage. The highest concentrations for each element were found in foliage, except for Ca, which exhibited highest concentrations in bark. Stemwood had the lowest concentrations for all elements.

In general, second rotation tissue concentrations were equal to or lower than first rotation concentrations (Table 1 and 2). Concentrations in the second rotation were 65%, 62%, 57%, 31%, and 25% lower ($p<0.05$) for stemwood N, P, Cu, Mn and Ca, respectively. Foliage K, B and Ca concentrations were 31%, 24%, and 21% lower, and branch Ca, B

and N concentrations were 27%, 21%, and 17% lower, respectively. Stembark concentrations of the second rotation were 7% and 9% lower for K and Ca, respectively, and ranged from 60 to 100% lower for Mn, Zn, Cu, and B.

Second rotation branchwood and bark concentrations were significantly related ($p<0.01$) to RDFT for all nutrients except for branch Mn and bark Ca and B (Table 4, Figures 1-3). R^2 ranged from 0.27 to 0.79 for branch concentrations, and from 0.50 to 0.77 for bark concentrations. Generally, stem and bark concentrations declined sharply from top of the tree to the base of the live crown. Mn stemwood, branch Ca and Mn, and bark Ca and B concentrations showed the reverse trend (Figures 1-3). Curvilinear relationships with RDFT were found for stemwood S, Ca and wood:bark ratios (Figure 3b and 3c). Weak or no statistically significant relationships were found between foliar concentrations and BD or DFT.

Estimation of Whole Tree Biomass and Nutrient Content

First rotation individual branch biomass and nutrient content estimates could not be developed due to sampling protocol. In the second rotation, biomass and nutrient contents of foliage and branchwood for individual branches were significantly related to BD and DFT ($p<0.01$) with R^2 ranging from 0.65-0.75 for foliage, and 0.86-0.93 for branches (Table 5). Micronutrient models for branchwood and foliage showed better relationships with BD^2DFT as compared to DFT^2 (Table 6).

Inter-rotation Comparison of Biomass and Nutrient Content Equations

Final individual tree biomass and nutrient content equations for foliage, branch, stemwood, and stembark components of the first and second rotation stands are presented in Table 7. Coefficients of determination (R^2) for both rotations ranged from 0.85-0.94 for foliage, 0.86-0.93 for branches, 0.85-0.99 for stemwood, and 0.56-0.98 for stembark (Table 7). In general, R^2 values were higher for the second rotation equations, except for Ca and biomass stembark.

The slope parameters for whole tree foliage biomass and nutrient content regressions did not differ between rotations (Table 7, Figures 4a and 4c). However, significant lower regression intercepts were found for biomass, N, K, Mn, and B content and higher intercepts for P, Ca, Mg, S content in second rotation trees. Foliage Zn and Cu content equations did not differ between rotations (Table 7 and Figure 4b).

In contrast, the slope and intercept parameters for the branchwood biomass and nutrient content regressions differed significantly for most nutrients (Table 7, Figures 5a and 5b). In the second rotation, significantly lower branch biomass and nutrient contents were found for small tree sizes compared to the first rotation.

Stemwood biomass equations were the same for both rotations and, except for Mn, nutrient content regression equations showed no significant differences in slope (Table 7). Significantly, lower intercepts were found for second rotation N, P, K, Mn, and Zn stemwood nutrient contents indicating lower concentrations than the first rotation.

Conversely, higher intercepts were found for Ca and Cu in the second rotation. Content equations did not differ for Mg, S, and B (Table 7 and Figure 6b).

Bark biomass and nutrient content equations showed no significant differences in slopes, except for B. Similar to stemwood, significant second rotation lower intercepts were found for N, P, Mn, Zn, and Cu, and higher intercepts were found for biomass, Ca, S, and B bark nutrients. Equations did not differ for bark K and Mg (Table 7 and Figure 7).

DISCUSSION

Tree nutrient concentrations

Whole tree foliage nutrient concentrations were lower for the second rotation stand with N, P and B at medium to low levels (Allen, 1987), indicating potential nutritional limitations for these elements at this site. Considering the variation of foliage nutrient concentration within the crown (Wells and Metz, 1963; Zhang and Allen, 1996), our composite samples would have lower concentrations than samples obtained for routine foliage analysis (upper crown-first flush). However, our foliage nutrient concentrations showed no trend with DFT or RDFT. A single foliage cohort, and the late winter sampling when foliage have stable nutrient contents (Zhang and Allen, 1996), may explain the lack of trend in our analysis.

Nutrient concentrations and variation with stemwood, branch, and bark tissues are in agreement with previous macronutrient values reported by Pope (1979), Pehl et al.

(1984), and Urrego (1993). In addition, Shelton et al. (1984) reported nutrient concentration levels similar to our results, indicating that the relative importance of each nutrient depends on the age, ratio of living to dead cells, and function of each tissue.

The largest inter-rotational differences in macronutrient concentrations were found for stemwood N and P concentrations, with substantially lower values in the second rotation, suggesting that N and P availabilities at the site have declined (Tables 1 and 2). First rotation stemwood N and P concentrations were similar to high fertility sites values reported by Pope (1979) and Shelton (1984), for 11 and 20 year-old stands respectively. In contrast, the second rotation values were similar to a 34 year-old stand on a low fertility site reported by Urrego (1993). Micronutrient concentrations showed a major decrease in stembark, but only B decreased simultaneously in branchwood and foliage (Tables 1 and 2) emphasizing a potential decline in B availability. In fact, B deficiencies have been suggested as one of the potential nutrient limitations on intensive managed loblolly pine plantations (NCSFNC, 1992 Research Note No. 8)

Stembark nutrient concentration gradients with tree height were more important for mobile elements, and the patterns have been reported before by Larsen et al.(1976), Ku and Burton (1973), and Urrego (1993). In addition, Larsen et al. (1976) indicated that the increase of concentration with tree height observed for N in bark reflects the decrease in bark thickness with height and an increase in the amount of live phloem cells. This direct relationship has been reported by Smith et al. (1963) for N, and was extended to P and Mg by Urrego (1993). Our results support previous findings and suggest that this

relationship extends to K, Mn, Zn and Cu. Higher mobility of N, P, K, Mg nutrients in the phloem (Marschner, 1995) match with their relationship with tree height and the large gradients exhibited within live crown (11 to 14.2 m). Similar patterns were observed for Zn and Cu, nutrients with moderate within-plant mobility. As expected, Ca exhibited no relationship with tree height. Our results for bark Ca did not coincide with Urrego (1993), who found an increasing gradient for Ca with tree height. However, we observed an increased variability in Ca concentration at mid-height that was probably associated with the variability in wood:bark ratio (Figure 2c) as suggested by Larsen et al. (1976). Mn bark concentrations showed higher concentrations with tree height, indicating a less direct association with its low mobility. In the case of bark B concentration, a poor relationship with tree height was coincident with its relatively low mobility.

The changes in nutrient concentrations with tree height for stemwood, bark and branches emphasizes the need to sample at more than one height instead of using only samples from DBH in order to prevent underestimation of tree nutrient content. Our results suggest that average branchwood, stemwood, and stembark concentrations are obtained at a RDFT between 0.17-0.19 of H, 0.65-0.75 of H, and 0.7-0.8 of H respectively. Appropriate sampling points for a tree 20 m height would be 3.4 to 3.8 m from the top for branches, 5 to 7 m from the base for stemwood, and 4 to 6 m from the base for stembark (Figures 2 and 3).

Estimation of Whole Tree Biomass and Nutrient Content

Foliage regressions were weaker as compared to branchwood regressions (Table 4 and 5). This pattern could be expected because foliage is an ephemeral tissue, and concentrations should be less directly related with branch diameter, and more dependent on seasonal changes (King et al. 1999; Zhang and Allen, 1996; Satoo and Madgwick, 1982). In addition, DFT does not represent the real distance where foliage is located in the crown (Baldwin et al., 1997). An improved model might include branch length as suggested by Satoo and Madgwick (1982) and branch angle. In the case of branches, DFT represents the location of the branch insertion in the stem, showing a significant relationship with biomass and branch micronutrient content (Tables 4 and 5). Although, nutrient concentrations were significantly related to DFT, DFT was not significant in the branchwood macronutrient content equations. This suggests that changes in nutrient concentrations were less important than dry weight changes for branchwood macronutrient accumulations.

Biomass and Nutrient Content Equations Comparison

Our results indicate that stemwood biomass regressions for the two rotations did not differ, however small differences existed for foliage and bark, and greater differences for branchwood. These results agree with Naidu et al. (1998) who indicate that biomass regressions for components other than stemwood for loblolly pine are site specific. In addition, Van Lear et al. (1984), comparing his equations with those developed by Clark and Taras (1976), indicated that biomass regressions are less site specific than nutrient

content regression equations due the variability in nutrient concentrations from site to site.

Changes in the nutrient content regression intercepts for foliage may reflect declines in nutrient availability. In fact, lower N concentration in the second rotation may reflect a reduced nutrient availability condition that should reduce current levels of foliage biomass (Vose and Allen, 1988).

Differences in individual tree branchwood biomass may be attributed to differences in stand density (1500 vs. 695 trees ha^{-1}), and consequently crown size (Harms and Langdon, 1976). Since the first rotation stand had been thinned 5 years prior to sampling, the dominant trees left after thinning may apparently have had larger branches compared to similarly-sized suppressed trees of the second rotation (Naidu et al. 1998). Genetic differences (e.g. 1^{st} generation vs. 2^{nd} generation) between rotations may also have caused differences in branchwood. Previous research has demonstrated little genetic influence on the relative distribution of dry matter in loblolly pine plantations (Pope, 1979; Pope and Graney, 1979). However, changes in nutrient availability in the stages of development of the second rotation stand may account for branchwood differences (King et al., 1999; Jokela and Martin, 2000).

In contrast to branches, nutrient content regressions for other tissues were similar, except for stembark B and stemwood Mn content (different regression lines). In fact, differences in regression intercepts between rotations were mostly associated with differences in

tissue concentration than dry weight. Stemwood N and P, and stembark micronutrient contents showed the largest differences in regression line intercepts between rotations.

Differences in stemwood N and P contents between rotations indicated that twice as many nutrients were used in the first rotation to produce the same amount of stemwood biomass as compared with the second rotation (Table 7 and Figure 6). The large N and P stemwood accumulations in the first rotation may have been luxury consumption because of high soil N and P availability immediately following agricultural abandonment (Richter, 2000) or higher nutrient use efficiency of the planted genotype in the second rotation. However, these differences highlight the potential effects of N and P availability on future productivity and indicate a large variation in P accumulation between rotations.

Although differences in intercepts between rotations for stembark biomass regressions were significant, estimates for these regressions were similar from a practical standpoint (Figure 7a). For example, an hypothetical tree with 18 cm DBH and 17.5 m H (average of medium tree sizes between rotations), will have a difference of 2.6 kg of bark for a tree of 101 kg (less than 3%). The small differences between biomass equations were not surprising considering stembark thickness variation with tree diameter (Haygreen and Bowyer, 1989). Differences in macronutrient content intercepts were mainly explained by differences in biomass and secondly by differences in nutrient concentrations between rotations (Table 1 and 2). In fact, a slight higher nutrient concentration of bark Mg in the second rotation stand resulted in similar nutrient equations for both rotations (Figure 7b).

Independent rotation biomass and nutrient content equations for almost every component indicate the need to obtain rotation specific estimates for each component except stemwood biomass. These results extend previous research findings (Naidu, 1998; Van Lear et al., 1984) that nutrient content equations are site-specific, indicating that equations may be rotation specific. To illustrate this point, our respective first and second rotation stand equations indicate that an average inter-rotational tree (18.5 cm DBH and 17.5 m H) will accumulate 0.21 g vs. 0.10 g of N respectively. Considering similar stand densities, a 100kg ha^{-1} difference will be established between rotations estimates using rotation specific equations.

CONCLUSIONS

Mobile nutrients concentrations of stemwood, bark, and branches decreased with distance from the top of the tree and height activity of the live crown. Foliar nutrient concentrations and non-mobile nutrients for other tissues showed no patterns with tree height. Stemwood biomass regression equations were the same for the two rotations but not stemwood nutrient content regressions. Foliage, branchwood, and bark biomass and nutrient content regressions differed. Major differences between rotations were in stemwood N and P; foliage, branches and bark B concentrations, suggesting reduced availability of these nutrients in the second rotation.

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Table 1. Mean and standard deviations in parenthesis of nutrient concentrations by tree component for the 22 year-old loblolly pine first rotation stand (n=15).

Tree Component	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	---------- % ----------						------ ppm -------			
Foliage	1.075	0.139	0.538	0.177	0.101	0.110	466	21.3	11.9	3.2
	(0.065)	(0.028)	(0.101)	(0.021)	(0.011)	(0.011)	(94)	(3.6)	(1.6)	(0.3)
Branches	0.280	0.030	0.114	0.237	0.047	0.028	173	14.8	8.8	2.6
	(0.082)	(0.013)	(0.050)	(0.043)	(0.009)	(0.010)	(32)	(3.6)	(2.3)	(0.7)
Stembark	0.218	0.023	0.073	0.267	0.030	0.031	90	13.4	7.1	2.9
	(0.029)	(0.006)	(0.036)	(0.078)	(0.009)	(0.008)	(37)	(2.8)	(1.3)	(0.3)
Stemwood	0.139	0.013	0.073	0.079	0.026	0.010	143	6.3	2.9	0.8
	(0.039)	(0.003)	(0.012)	(0.026)	(0.005)	(0.004)	(9)	(1.0)	(0.6)	(0.3)

Table 2. Mean and standard deviations in parenthesis of nutrient concentrations by tree component for the 18 year-old loblolly pine second rotation stand (n=12).

Tree Component	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	---------- % ----------						------ ppm -------			
Foliage	0.971	0.110	0.374	0.141	0.103	0.112	394	22.4	9.1	3.4
	(0.214)	(0.026)	(0.078)	(0.033)	(0.026)	(0.028)	(17)	(2.9)	(0.6)	(0.4)
Branches	0.232	0.032	0.166	0.173	0.057	0.023	164	14.1	7.0	2.4
	(0.033)	(0.008)	(0.026)	(0.012)	(0.010)	(0.006)	(13)	(1.8)	(0.7)	(0.4)
Stembark	0.198	0.018	0.068	0.243	0.036	0.025	12	6.3	2.6	NA
	(0.021)	(0.005)	(0.019)	(0.074)	(0.009)	(0.003)	(3.4)	(0.7)	(0.3)	NA
Stemwood	0.049	0.005	0.062	0.059	0.025	0.009	99	5.4	2.9	1.3
	(0.004)	(0.001)	(0.007)	(0.007)	(0.001)	(0.002)	(41)	(1.4)	(0.8)	(0.2)

NA **Not available**

Table 3. Two tailed t-test p-values comparing first and second rotation nutrient concentrations.

Tree Component	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
Foliage	0.082	0.011	<0.001	<0.001	0.844	0.824	0.014	0.385	<0.001	0.210
Branches	0.001	0.337	<0.001	<0.001	0.002	0.032	0.131	0.382	<0.001	0.232
Stembark	0.082	0.032	<0.001	<0.001	0.029	0.039	<0.001	<0.001	<0.001	<0.001
Stemwood	<0.001	<0.001	0.002	0.038	0.210	0.605	<0.001	0.060	0.972	<0.001

Table 4.- Regression models, coefficients and statistics expressing the relationship between component nutrient concentration and RDFT. Model types A: Y = a + b*LOG10(RDFT), B: Y = a + b*RDFT, and C: Y = a + b*RDFT+c*RDFT2.

Tree Component	Nutrient	Units	Model Type	a	b	c	Coefficient of determination (R^2)	p-value Overall Model
Branches	**N**	**%**	**A**	0.0082^{ns}	-0.2978**	-	0.62	<0.001
	P	**%**	**A**	-0.0046*	-0.0491**	-	0.79	<0.001
	K	**%**	**A**	-0.0512**	-0.1557**	-	0.65	<0.001
	Ca	**%**	**B**	0.1337**	0.3730**	-	0.32	<0.001
	Mg	**%**	**A**	0.0132**	-0.0590**	-	0.59	<0.001
	S	**%**	**A**	-0.0037^{ns}	-0.0358**	-	0.64	<0.001
	Mn	**ppm**	**B**	137.556**	164.26*	-	0.03	0.081
	Zn	**ppm**	**A**	9.1708**	-6.9952**	-	0.32	<0.001
	B	**ppm**	**A**	5.3894**	-2.2291**	-	0.27	<0.001
	Cu	**ppm**	**A**	1.1906**	-1.6956**	-	0.39	<0.001
Stembark	**N**	**%**	**A**	0.1720**	-0.2068**	-	0.50	<0.001
	P	**%**	**A**	0.0116**	-0.0543**	-	0.74	<0.001
	K	**%**	**A**	0.0351**	-0.2489**	-	0.75	<0.001
	Ca	**%**	**B**	0.2876**	-0.0540^{ns}	-	0.02	0.206
	Mg	**%**	**A**	0.0190**	-0.1322**	-	0.77	<0.001
	S	**%**	**A**	0.0216**	-0.0280**	-	0.61	<0.001
	Mn	**ppm**	**A**	8.0518**	-32.4199**	-	0.72	<0.001
	Zn	**ppm**	**A**	5.4852**	-8.2533**	-	0.75	<0.001
	B	**ppm**	**B**	2.5889**	0.1430^{ns}	-	0.01	0.358
	Cu	**ppm**	**A**	NA	NA	-	NA	NA
Stemwood	**N**	**%**	**A**	0.0450**	-0.0344**	-	0.64	<0.001
	P	**%**	**A**	0.0044**	-0.0066**	-	0.52	<0.001
	K	**%**	**A**	0.0564**	-0.0401**	-	0.45	<0.001
	Ca	**%**	**C**	0.0562**	0.0848**	-0.0927**	0.40	<0.001
	Mg	**%**	**A**	0.0239**	-0.0096**	-	0.45	<0.001
	S	**%**	**C**	0.0114**	-0.0193**	0.0209**	0.43	<0.001
	Mn	**ppm**	**B**	0.0123**	-0.0029*	-	0.03	0.080
	Zn	**ppm**	**B**	0.0007**	-0.0002**	-	0.13	<0.001
	B	**ppm**	**B**	0.0006**	-0.0004**	-	0.14	<0.001
	Cu	**ppm**	**B**	0.0003**	-0.0002**	-	0.33	<0.001

RDFT relative distance from the top expressed by DFT/H .
** significant at p<0.1, * significant at p<0.05, ^{ns} not significant.
NA **Not available**

Table 5. Regression coefficients for estimating branch and foliage biomass using the model: Y = (((EXP(a + b*LOG10(BD+1) + c*LOG10(DFT+1))) –1) 10-3)*CF and macronutrient content using the model: Y = (((EXP(a + b*LOG10(BD+1) + c*DFT2)) –1) 10-3)*CF. All the estimations are in grams per branch for the 18 year-old loblolly pine second rotation stand.

Tree Component	Y (g)	A	b	C	CF Correction Factor	Coefficient of determination (r^2)
Foliage	**Biomass**	0.320**	4.302**	-0.958**	1.046	0.71
	N	1.121**	4.200**	-0.032**	1.048	0.71
	P	0.291**	3.922**	-0.028**	1.034	0.75
	K	0.723**	4.108**	-0.028**	1.045	0.72
	Ca	0.355**	4.041**	-0.030**	1.043	0.71
	S	0.306**	3.945**	-0.031**	1.039	0.72
	Mg	0.257**	4.005**	-0.033**	1.041	0.72
Branches	**Biomass**	-0.280**	4.416**	0.634**	1.016	0.93
	N	0.431**	4.487**	NA	1.018	0.91
	P	-0.132**	3.923**	NA	1.012	0.91
	K	0.318**	4.423**	NA	1.016	0.90
	Ca	0.013 ns	5.033**	NA	1.032	0.86
	S	-0.247**	3.869**	NA	1.014	0.89
	Mg	-0.066 ns	4.272**	NA	1.014	0.91

D branch diameter in cm, DFT distance from the top in m, CF correction factor, NA not applicable.
** **significant at p<0.1,** * **significant at p<0.05,** ns **not significant.**

Table 6. Regression coefficients for estimating foliage and branch micronutrient content in milligrams per branch for the 18 year-old loblolly pine second rotation stand. General Model: Y = (((EXP(a + b*LOG10(BD+1) + c*LOG10 (BD2DFT+1)) –1)*10-6)*CF

Tree Component	Nutrient (mg)	A	b	c	Correction Factor	Coefficient of determination (r^2)
Foliage	**Mn**	1.962**	7.695**	-1.156**	1.074	0.65
	Zn	0.872**	7.658**	-1.276**	1.055	0.67
	B	0.672**	6.357**	-0.861**	1.053	0.67
	Cu	0.268**	6.641**	-1.010*	1.044	0.69
Branches	**Mn**	2.309**	2.772**	0.692**	1.022	0.91
	Zn	1.495**	2.904**	0.438**	1.017	0.90
	B	1.142**	2.911**	0.474**	1.014	0.92
	Cu	0.745**	3.077**	0.349**	1.013	0.92

D branch diameter in cm, DFT distance from the top in m, CF correction factor.
** **significant at p<0.1,** * **significant at p<0.05,** ns **not significant.**

Table 7. Tree individual biomass and nutrient content regression equations comparison between the 18 year-old loblolly pine second rotation stand and the 22 year-old first rotation stand. Rotation effects on slope and intercepts. Tested models:

a) Full Model : $LOG_{10}(Y) = a*ROT + b*LOG_{10}(DBH^2H) + c*(ROT* LOG_{10}(DBH^2H))$,

b) Reduced Model: $LOG_{10}(Y) = a*ROT + b*LOG_{10}(DBH^2H)$.

Tree Component	Y	unit	Full Model Different Slopes p-value	R^2	Reduced Model Different Intercepts p-value	R^2
Foliage	**Biomass**	**g**	0.178	0.92	0.055	0.91
	N	**g**	0.980	0.90	0.010	0.90
	P	**g**	0.706	0.91	<0.01	0.91
	K	**g**	0.991	0.90	<0.01	0.90
	Ca	**g**	0.707	0.91	<0.01	0.91
	Mg	**g**	0.539	0.92	0.030	0.92
	S	**mg**	0.588	0.91	0.039	0.91
	Mn	**mg**	0.255	0.88	0.033	0.88
	Zn	**mg**	0.724	0.89	0.205	0.89
	B	**mg**	0.431	0.93	<0.01	0.93
	Cu	**mg**	0.660	0.90	0.143	0.90
Branches	**Biomass**	**g**	<0.01	0.92	0.010	0.89
	N	**g**	0.012	0.92	<0.01	0.90
	P	**g**	0.164	0.92	0.015	0.91
	K	**g**	0.034	0.92	0.411	0.90
	Ca	**g**	<0.01	0.92	<0.01	0.89
	Mg	**g**	0.021	0.92	0.024	0.90
	S	**mg**	0.081	0.91	<0.01	0.89
	Mn	**mg**	<0.01	0.91	<0.01	0.85
	Zn	**mg**	0.015	0.92	<0.01	0.90
	B	**mg**	0.032	0.91	<0.01	0.90
	Cu	**mg**	0.085	0.92	<0.01	0.91
Stemwood	**Biomass**	**g**	0.553	0.99	0.685	0.99
	N	**g**	0.844	0.96	<0.01	0.96
	P	**g**	0.981	0.97	<0.01	0.97
	K	**g**	0.856	0.97	<0.01	0.97
	Ca	**g**	0.680	0.97	<0.01	0.97
	Mg	**g**	0.720	0.98	0.172	0.98
	S	**mg**	0.198	0.91	0.777	0.91
	Mn	**mg**	0.028	0.94	<0.01	0.93
	Zn	**mg**	0.600	0.96	0.055	0.96
	B	**mg**	0.959	0.93	0.431	0.93
	Cu	**mg**	0.896	0.95	<0.01	0.95
Stembark	**Biomass**	**g**	0.190	0.98	<0.01	0.98
	N	**g**	0.856	0.97	<0.01	0.97
	P	**g**	0.144	0.95	<0.01	0.94
	K	**g**	0.528	0.90	0.166	0.90
	Ca	**g**	0.191	0.84	<0.01	0.84
	Mg	**g**	0.619	0.92	0.692	0.92
	S	**mg**	0.194	0.94	<0.01	0.94
	Mn	**mg**	0.433	0.96	<0.01	0.96
	Zn	**mg**	0.883	0.96	<0.01	0.96
	B	**mg**	0.035	0.97	<0.01	0.97
	Cu	**mg**	NA	NA	NA	NA

ROT rotation dummy variable, DBH diameter at breast height in cm, H height of the tree in m.

NA **Not available**

Table 8. Tree individual biomass and nutrient content regression equations for first and second rotation components. General Model : $LOG_{10}(Y) = a + b*LOG_{10}(DBH^2H)$

Tree Component	units	Y	a		b		CF Correction Factor		R^2 Coefficient of Determination	
			first	second	first	second	first	second	first	second
Foliage	**g**	**Biomass**	-0.997	-2.113	1.200	1.464	1.040	1.049	0.90	0.94
	g	**N**	-2.910	-3.085	1.185	1.180	1.056	1.012	0.88	0.93
	g	**P**	-3.956	-3.920	1.225	1.150	1.056	1.011	0.88	0.93
	g	**K**	-3.255	-3.560	1.195	1.197	1.064	1.012	0.87	0.93
	g	**Ca**	-3.875	-3.841	1.232	1.157	1.055	1.012	0.89	0.92
	g	**Mg**	-4.104	-3.849	1.228	1.121	1.040	1.012	0.92	0.92
	g	**S**	-4.054	-3.826	1.225	1.125	1.046	1.012	0.91	0.92
	mg	**Mn**	-1.317	-2.493	1.195	1.462	1.075	1.017	0.85	0.93
	mg	**Zn**	-2.783	-3.167	1.228	1.305	1.068	1.013	0.87	0.93
	mg	**B**	-3.030	-3.786	1.227	1.368	1.041	1.013	0.92	0.94
	mg	**Cu**	-3.492	-3.922	1.199	1.287	1.056	1.012	0.89	0.94
Branches	**g**	**Biomass**	-0.649	-3.558	1.258	1.976	1.048	1.040	0.91	0.92
	g	**N**	-3.059	-5.569	1.220	1.803	1.055	1.029	0.89	0.93
	g	**P**	-4.451	-5.799	1.319	1.628	1.060	1.023	0.90	0.93
	g	**K**	-3.861	-5.639	1.319	1.783	1.049	1.028	0.91	0.93
	g	**Ca**	-3.184	-6.421	1.234	2.003	1.056	1.038	0.89	0.92
	g	**Mg**	-3.943	-5.961	1.247	1.742	1.046	1.053	0.91	0.93
	g	**S**	-4.010	-5.923	1.205	1.622	1.071	1.022	0.86	0.93
	mg	**Mn**	-0.959	-4.721	1.146	2.080	1.055	1.044	0.88	0.92
	mg	**Zn**	-2.458	-4.756	1.251	1.796	1.048	1.031	0.91	0.92
	mg	**B**	-2.932	-5.248	1.316	1.847	1.066	1.033	0.89	0.92
	mg	**Cu**	-3.600	-5.349	1.345	1.746	1.062	1.028	0.90	0.93
Stemwood	**g**	**Biomass**	1.025	0.908	1.031	1.060	1.002	1.001	0.99	0.98
	g	**N**	-1.798	-2.334	1.017	1.043	1.025	1.002	0.92	0.98
	g	**P**	-2.937	-3.338	1.045	1.048	1.018	1.004	0.95	0.97
	g	**K**	-2.228	-2.260	1.060	1.044	1.009	1.006	0.97	0.96
	g	**Ca**	-2.011	-1.978	1.010	0.972	1.012	1.002	0.96	0.98
	g	**Mg**	-2.486	-2.624	1.012	1.039	1.007	1.002	0.97	0.98
	g	**S**	-2.995	-3.819	1.027	1.246	1.028	1.002	0.92	0.90
	mg	**Mn**	0.182	-1.231	1.030	1.363	1.000	1.040	0.99	0.85
	mg	**Zn**	-1.237	-1.528	1.045	1.103	1.005	1.018	0.98	0.89
	mg	**B**	-1.209	-1.222	0.949	0.942	1.009	1.023	0.96	0.82
	mg	**Cu**	-2.129	-1.872	1.049	1.035	1.016	1.003	0.95	0.97
Stembark	**g**	**Biomass**	1.192	1.372	0.771	0.695	1.003	1.003	0.98	0.95
	g	**N**	-1.470	-1.659	0.770	0.784	1.007	1.002	0.96	0.97
	g	**P**	-2.656	-3.453	0.825	0.991	1.014	1.007	0.93	0.95
	g	**K**	-2.499	-2.944	0.906	1.005	1.027	1.016	0.89	0.88
	g	**Ca**	-0.769	-0.274	0.609	0.423	1.018	1.017	0.85	0.56
	g	**Mg**	-2.807	-3.028	0.890	0.955	1.017	1.012	0.93	0.89
	g	**S**	-2.637	-2.279	0.851	0.713	1.014	1.004	0.94	0.93
	mg	**Mn**	0.963	-0.391	0.554	0.655	1.015	1.014	0.85	0.78
	mg	**Zn**	-0.492	-0.854	0.721	0.708	1.009	1.004	0.94	0.93
	mg	**B**	-1.161	-1.037	0.823	0.651	1.006	1.004	0.97	0.91
	mg	**Cu**	-1.195	-3.467	0.733	0.753	1.002	1.005	0.98	0.93

DBH diameter at breast height in cm, H height of the tree in m, NA not applicable.
NA Not available

Figure 1.- Branch nutrient concentration relationship with RDFT. a) P, the same pattern was shown for N, K, Mg, S, B, Zn and Cu concentration; b) Ca, a similar but not significant ($p<0.01$) pattern was shown for Mn concentration.

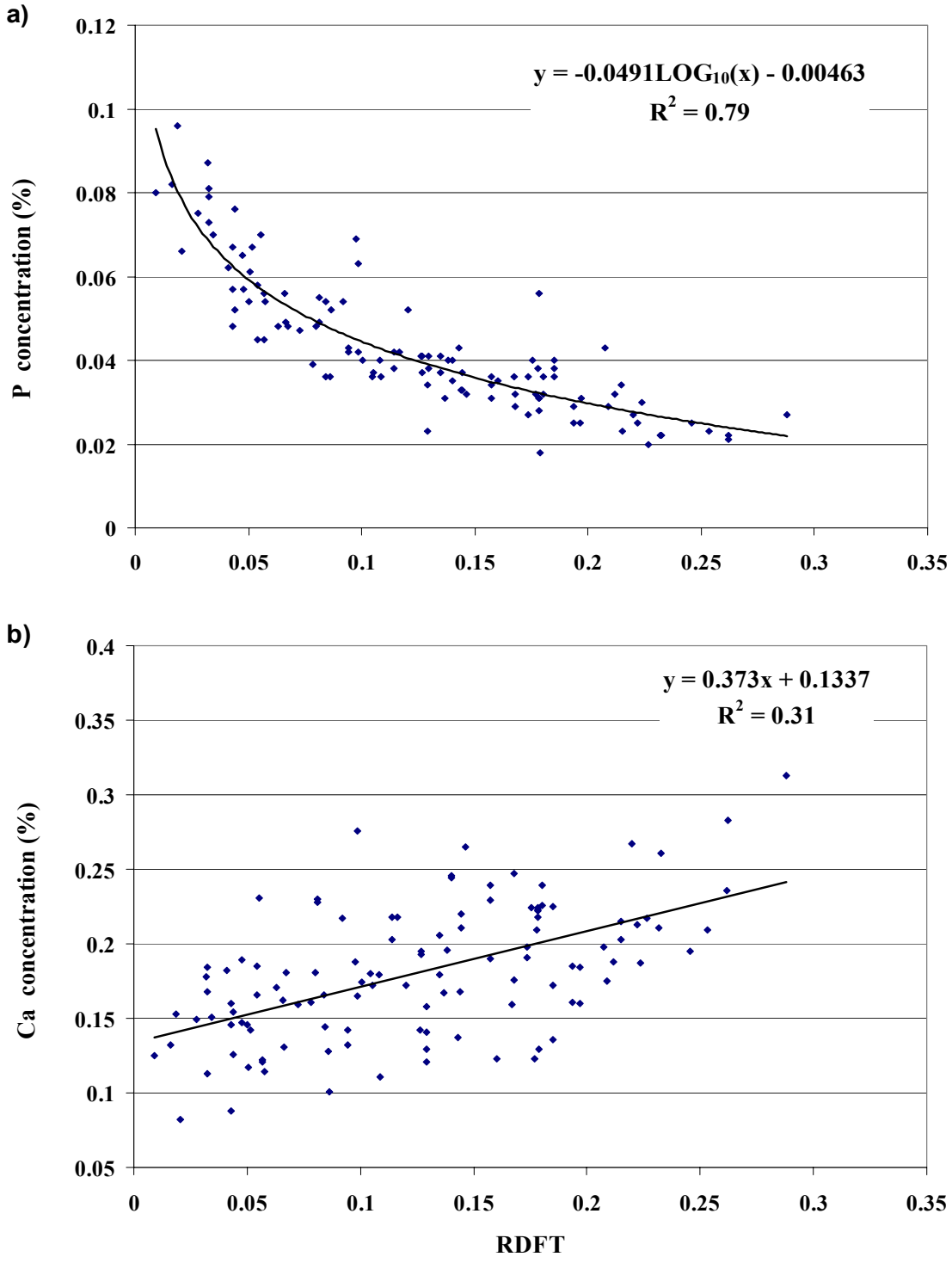


Figure 2.- Bark nutrient concentration relationships with RDFT. a) P, the same pattern was shown for N, K, Mg, S, Mn, and Zn concentration; b) B, the same pattern was shown for Ca concentration) Wood:bark ratios for disc samples obtained from each sampled tree.

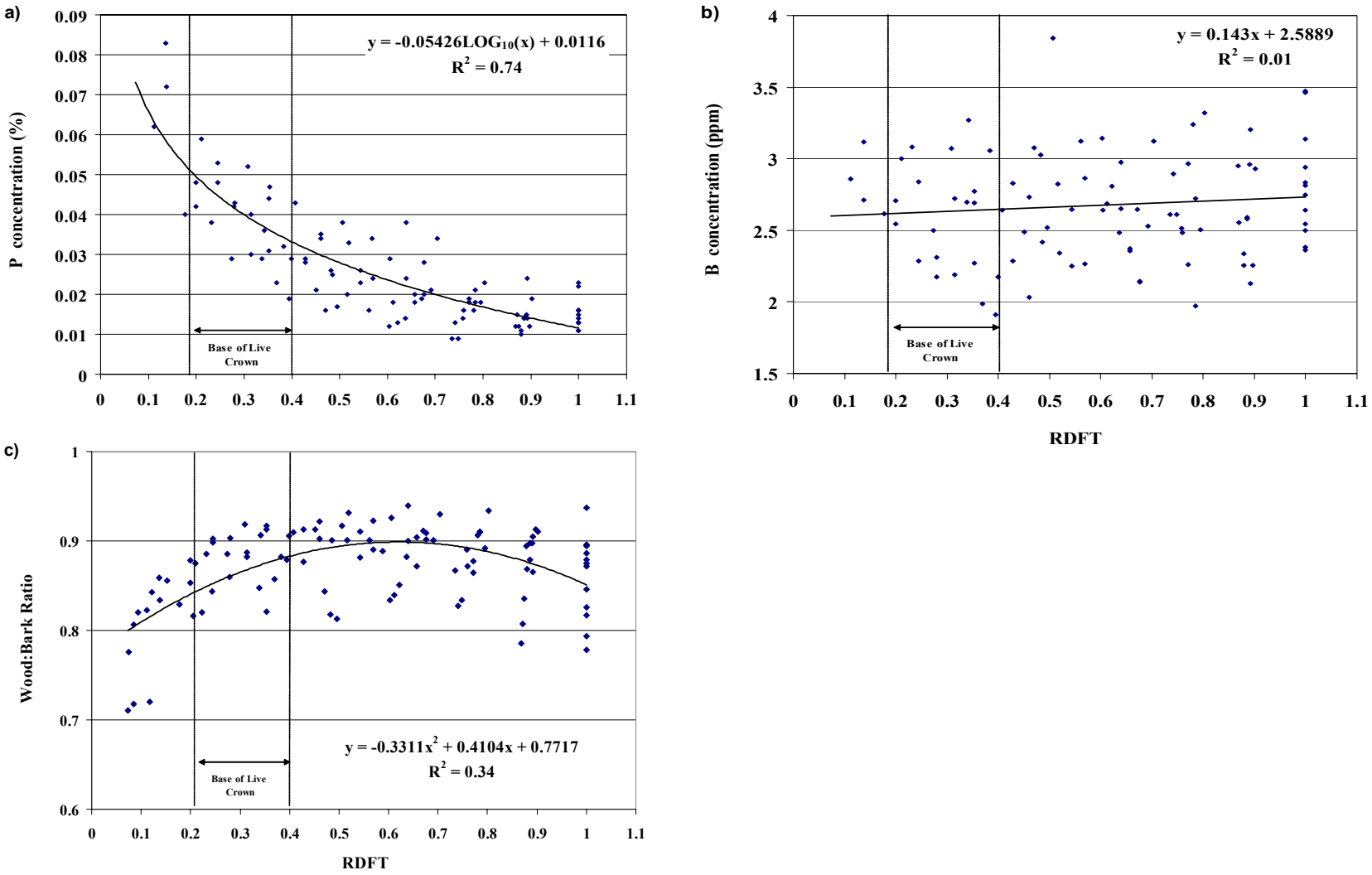


Figure 3.- Stem nutrient concentration relationship with RDFT. a) Nitrogen, and same pattern was shown for P, K, Mg; b) Ca; c) S; d) Cu and the same pattern was shown for Zn and B. Mn showed no change with DFT, graph not shown.

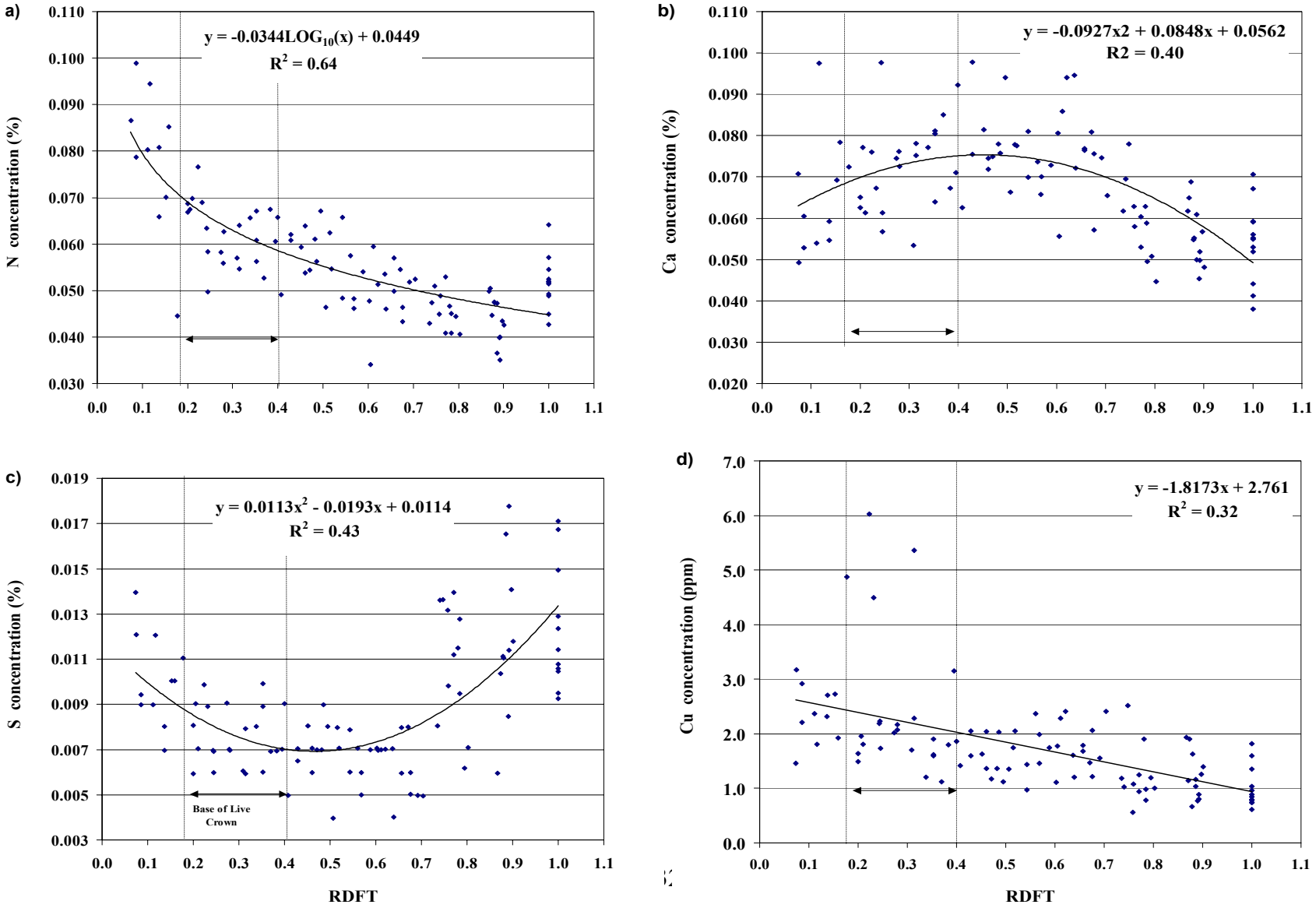
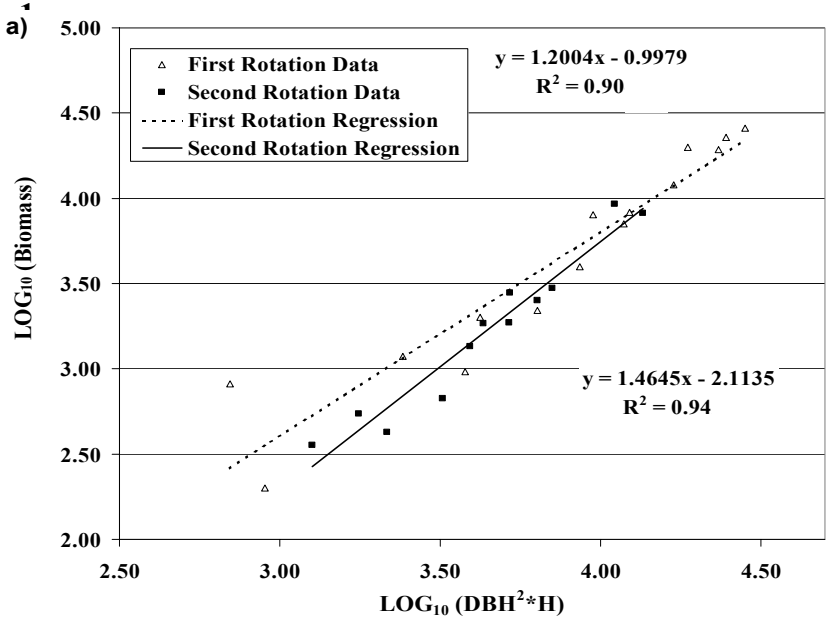
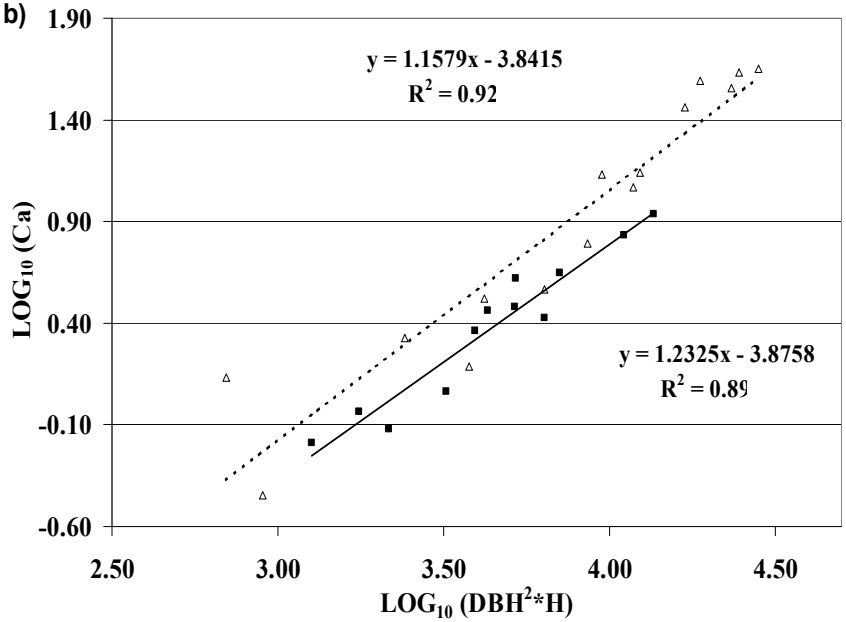


Figure 4.- Individual tree foliage regression equations comparison between rotations a) Biomass, and the same pattern was shown by Mg, S, Mn; b) Ca and the same pattern was shown by N, P, K and B; c) Zn, the same pattern was shown by Cu.





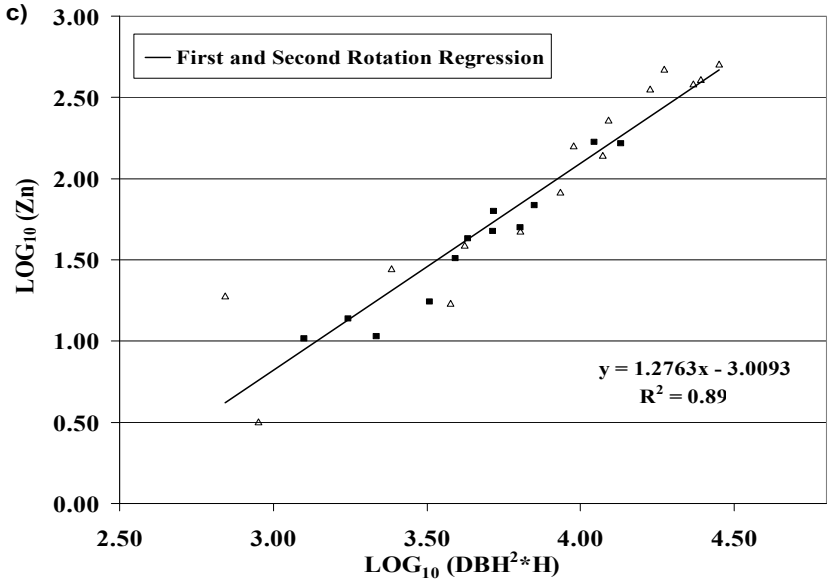


Figure 5.- Individual branch regression equations comparison between rotations a) Biomass, the same pattern was shown by N, Ca, Mg, S, Mn, Zn, B and Cu; b) P; c) K

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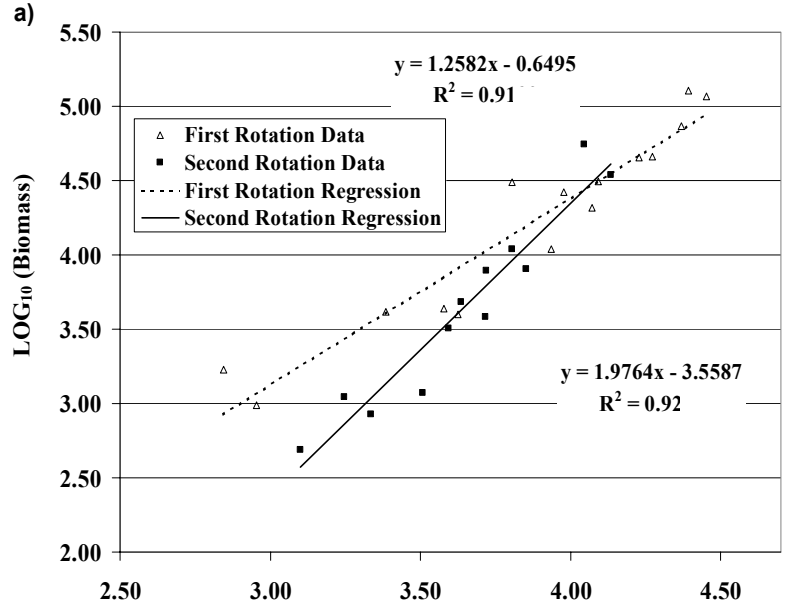

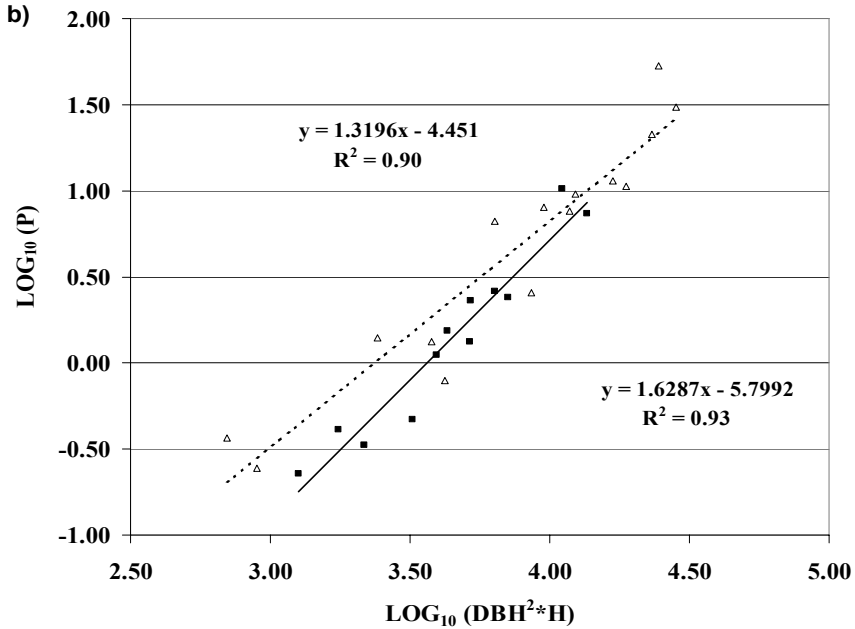

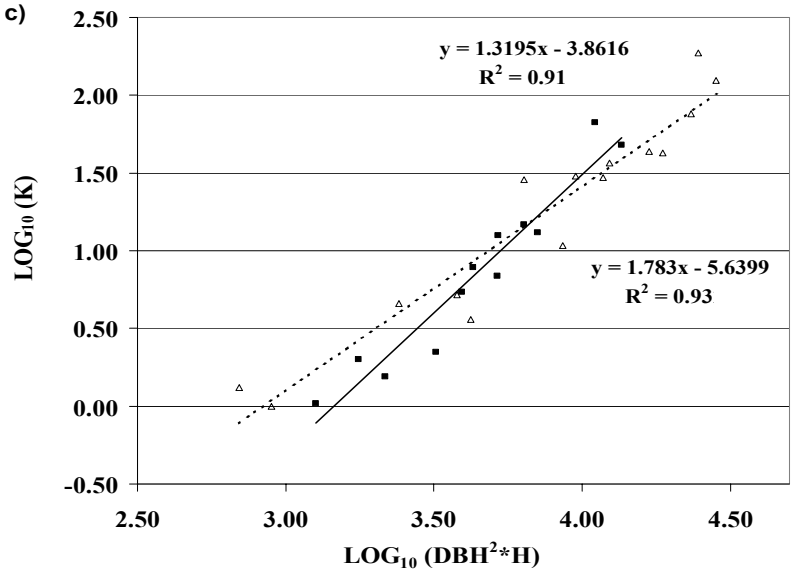

Figure 6.- Individual stem regression equations comparison between rotations a) Biomass, the same pattern was shown for Mg, S, Zn and B. b) P, the same pattern was shown by N, K, Ca, and Cu; c) Mn.

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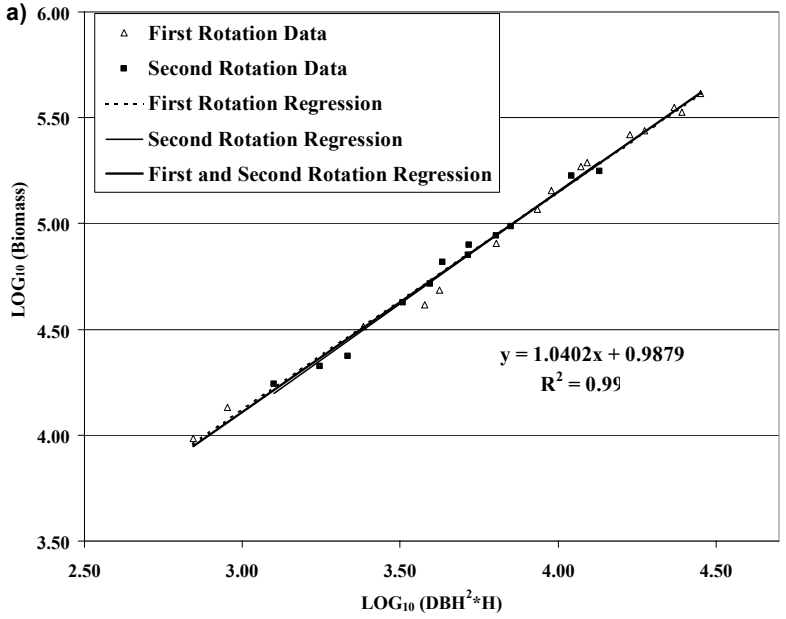
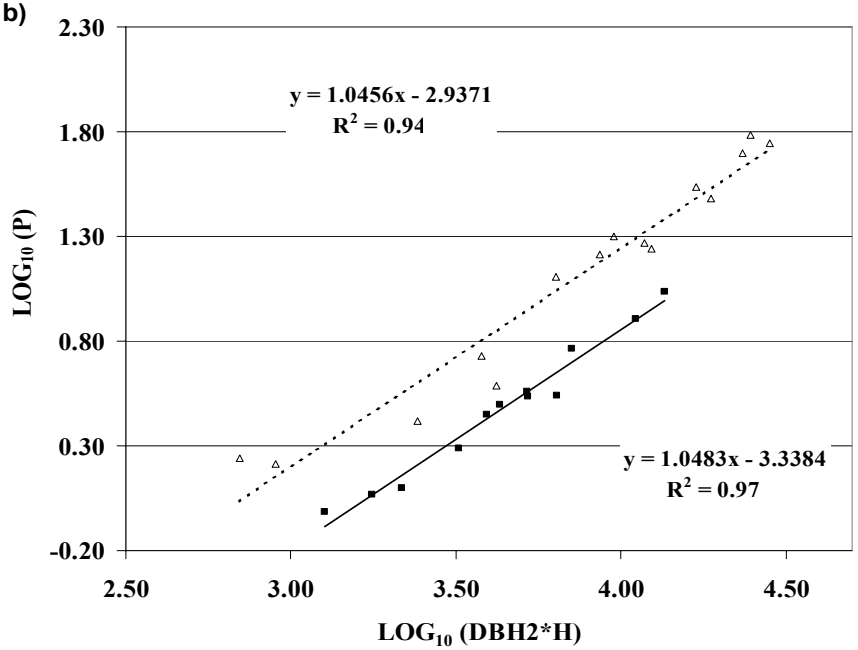




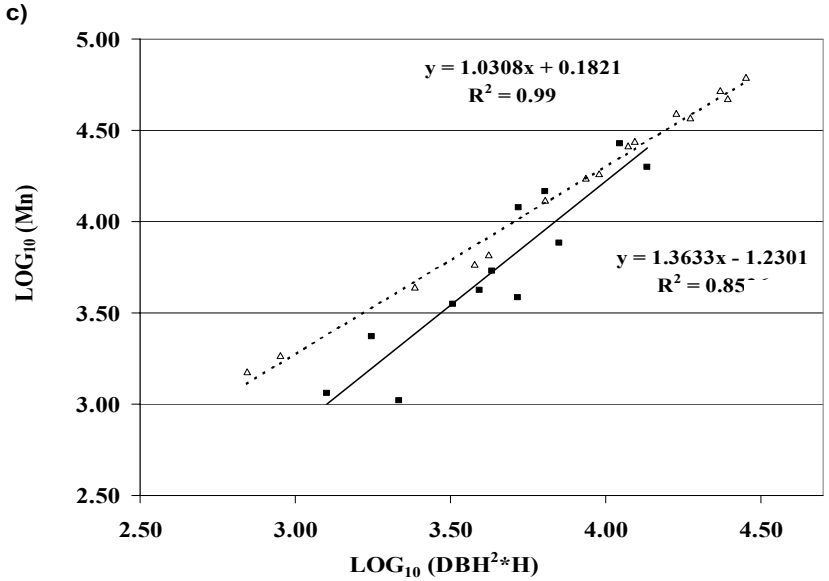
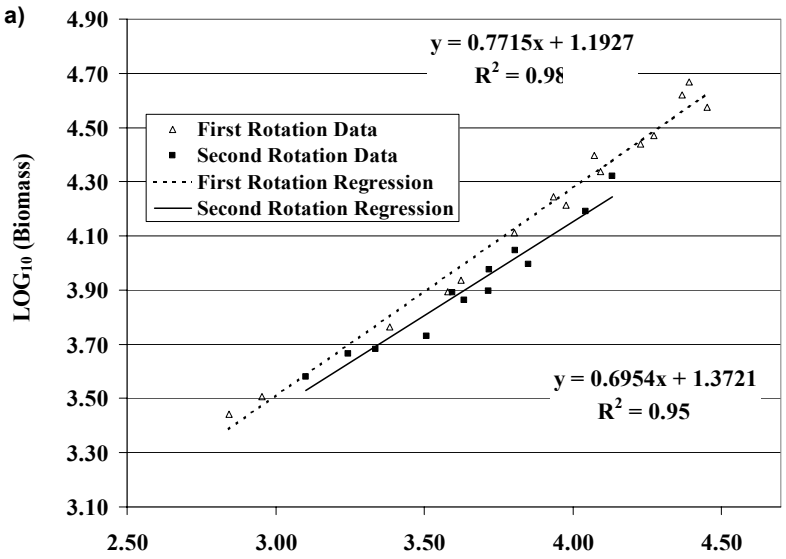
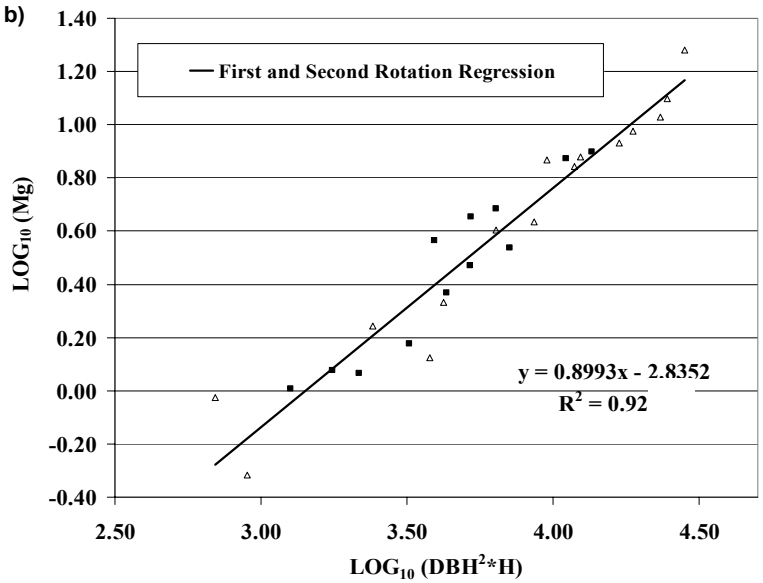
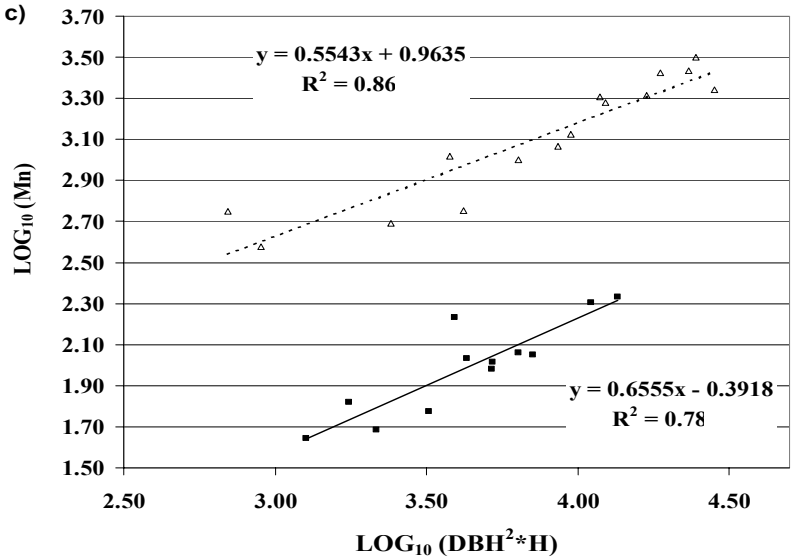


Figure 7.- Individual bark regression equations comparison between rotations a) Biomass, the same patterns were shown for N, P, K, and Ca b) Mg, the same patterns were shown for K c) Mn, the same patterns were shown for Zn, and B. Macronutrients in grams and micronutrients in milligrams.







CHAPTER 2

Biomass and Nutrient Accumulation between Successive Loblolly Pine Plantations on an Upper Coastal Plain Site.

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ABSTRACT

Upper Coastal Plain forest sites are characterized by highly weathered soils and an intensive agricultural use. These conditions predispose intensively managed sites to second rotation declines if managed carelessly. This study compares aboveground biomass and nutrient content changes between successive rotations of loblolly pine on the same site in the Upper Coastal Plain of Alabama and predict what first rotation factors are important in the biomass and nutrient accumulation in the second rotation. Stand biomass and nutrient accumulation for each rotation were calculated destructively sampling trees for each rotation. Forest floor biomass and nutrient accumulation for both rotations, soil samples obtained at harvesting of the first rotation stand characterized total N and available pools for other mineral soil nutrients.

Major results indicate that stand biomass accumulation with lower nutrient accumulation and lower foliage biomass, suggests declines in N, P and/or other nutrients availability for the second rotation site. Considering harvesting removals, micronutrient availability, and specially B may severely be affected as large proportions are allocated to the stemwood compared to macronutrients. Soil exchangeable P was the most important variable that predicted biomass and nutrient accumulation in the second rotation stand. Forest floor is a large C reservoir and seems to represent a large nutrient sink for N, P, K, S Zn and Cu. Stand and forest floor nutrient accumulations across sites presented log-linear relationships with biomass accumulation. Fires, storms and other ecological events seems to decrease the quality of these functional relationships for forest floor compared to stand estimates.

INTRODUCTION

Climatic constraints and nutritional limitations have been implicated as major factors that limit potential productivity of loblolly pine plantations in the southeastern USA (Allen et al., 1990). Extensively weathered soils, coupled with a 200-year history of intensive agricultural use, characterize many southeastern sites (Richter et al., 2000), and especially the Upper Coastal Plain (Stone, 1979). This combination of factors may predispose intensively managed sites to productivity declines if managed carelessly (Tiarks and Haywood, 1996, Terry and Campbell, 1981; Smith et al, 1994, 2000).

The assessment of major nutrient pools removed by harvesting, losses or displacements caused by site preparation, and intensive management of pine plantations have permitted speculation about the impacts on nutrient cycling and sustainability (Wells, 1983; Raison, 1984; Neary et al, 1983; Tew et al. 1986). Long-term negative impacts on site fertility and productivity caused by frequent removals of aboveground biomass, deterioration of soil properties by removal of organic matter and compaction, have been hypothesized by several authors (Flinn et al., 1980; Van Lear et al., 1982; Morris et al., 1983; Haywood, 1994). In fact, the issue of productivity decline has been controversial for fast growing plantations (Keeves, 1966; Squire et al 1985; Haywood, 1994; Allen et al, 1991; Burger, 1996; Smith et al, 2000; Gresham, 2002). However, due to the scarcity of long-term data, remarkably few reports have compared biomass and nutrient accumulation of successive rotations of loblolly pine on the same site (Allen et al, 1991; Burger, 1996, Gresham, 2002). In addition, successive rotation biomass comparisons have been criticized for the lack of belowground assessments (Kelting and Burger, 1999), and the climatic, genetic, competing vegetation and catastrophic event differences between rotations (Burger,

1996; Morris and Miller, 1994). However, considering site-specific conditions, these comparisons are valuable from a forest management point of view (Fox, 2000) and are the more reliable measurement of soil-plant interactions (Morris and Miller, 1994).

This study describes aboveground biomass and nutrient content changes between successive rotations of loblolly pine on the same site in the Upper Coastal Plain of Alabama. The main objectives were to compare inter-rotational accumulations and to predict what first rotation factors are important in the biomass and nutrient accumulation in the second rotation. In addition, several southeastern USA loblolly pine biomass and nutrient content studies were compared with our inter-rotational estimates.

MATERIALS AND METHODS

Stand and Site characteristics

The experimental site was established as part of a large study investigating the long-term effects of forest management practices on site productivity. Details about the study have been provided in Rubilar et al (2002, in press-Chapter1). The site was an old-field site, located in the Upper Coastal Plain in Butler County, AL. The soils are Smithdale, a fine loamy, siliceous, subactive, thermic Typic Hapludult. Annual rainfall averages 1473 mm, and average monthly temperatures ranged from a minimum value of 11.9ºC to a maximum value of 25ºC, with an annual mean of 18.5ºC (NOAA, 2000).

The first rotation was a 22-year old loblolly pine plantation thinned at age 17. At harvest, the stand averaged 695trees ha^{-1}, 21cm diameter at breast height (DBH), 19.2m in height, and 271m^3

ha^{-1} in stem volume. Basal area averaged 30.5 m^2ha^{-1} with 26.4 m^2ha^{-1} of loblolly pine, 2.3m^2ha^{-1} of hardwoods, and 10 plots averaged 5.7m^2ha^{-1} of slash pine (Pinus elliotti). The second rotation stand was an 18-year-old loblolly pine stand, averaging 1541 trees ha^{-1}, 16.4 cm DBH, 16.7 m in height, 34.1 m^2ha^{-1} in basal area and 296 m^3ha^{-1} in stem volume. Small vines and suppressed trees were not significant competition. Site index (base age 25), according to the equations of Clutter and Lenhart (1968), was estimated 23.8m and 22.1m for the first and second rotation respectively.

Experimental Design

Prior to harvesting the first rotation stand in 1982, three blocks, with twelve plots (15 m x 30 m) each, were laid out on the site considering pine dominant height and soil-site uniformity within blocks. After harvesting, a factorial experiment was established testing the combined effect of harvesting and site preparation at five levels and cultural treatments at two levels. Harvesting and site preparation considered complete tree (CT) vs. stemwood (ST) harvest types, and shear, pile and disk (SH), chop and burn (CB), and scalping (SC) soil preparation treatments. Cultural treatments applied during the first three years considered herbicide and insecticide (WC) vs. none (NC). The combinations ST+SC+WC and ST+SC+NC were not tested. All harvest and site preparation treatments were applied during 1982. Bareroot 1-0 loblolly pine seedlings were planted in January 1983 and WC plots received herbicide in 1982, 1984, and 1985, and one insecticide application in 1984.

Biomass and Nutrient Analyses

The development of biomass and nutrient content equations for individual trees was described in detail by Rubilar et al (2002, Chapter 1). Briefly, first and second rotation stand biomass and nutrient content was estimated from winter harvesting of fifteen and twelve trees respectively to represent the stand diameter distribution. Trees were felled, the stems were cut in sections, weighed in the field, and stem discs were obtained from each section to adjust for moisture contents. Stemwood:Stembark ratios were determined from dry weights of each disc, and subsamples were obtained for nutrient concentration analyses. For each tree, foliage and branch biomass and nutrient content were estimated different between rotations. First rotation weighed each component in the field, and representative sub-samples were obtained for moisture content adjustments and nutrient concentration determinations. Second rotation estimated branch and foliage in a two-stage process, first using individual branch equations (Rubilar et al, 2002 Chapter 1) and second adding these estimates for each tree. For each branch sampled, foliage and branchwood (wood + bark) tissues were weighed green in the field, and sub-sampled for moisture content adjustments and nutrient concentration determinations.

Understory biomass and nutrient content, for the first rotation stand, was estimated from sampling four 1-m^2 subplots per each trial plot. All the vegetation less than 2.5 cm DBH was clipped, dried at 70ºC, weighed, and subsampled for nutrient concentration analysis.

Forest floor biomass was sampled on each 15 x 30 m plot, using 0.566-m^2 subplots. In the first rotation stand, a single sample of all organic horizons was obtained in four subplots per plot. In the second rotation stand, separate samples for Oi, Oe and Oa organic layers were obtained from

eight subplots per plot on treatments CT+CB+WC, CT+SC+WC, CT+SH+WC, ST+CB+WC, ST+SH+WC. Forest floor tissue chemical analyses were the same as for foliage. Loss on ignition at 500ºC for 12 hours was determined for forest floor samples in order to adjust for mineral soil contamination, and concentrations were recalculated using the formula:

[1] $X_{loi} = (X_{ini} * W_{500oC} / W_{ini})$

Where, X_{loi} : Corrected concentration.

X_{ini} : Uncorrected concentration

W_{500oC} : Weight after loss on ignition at 500^{o}C for 12 hours.

W_{ini} : Initial weight of the sample

First rotation archived forest floor and pine biomass samples were reanalyzed and small differences in concentration estimates were found for old and new procedures. Additional S and micronutrient analyses were obtained, and new concentrations used for analyses.

Soil sampling and nutrient analyses

Soil was sampled at 10 cm increments to a depth of 60 cm from eight random located points per plot prior to harvesting of the first rotation stand. The samples were composited by depth for each 15m x 30m plot, and the final samples were air dried, and analyzed for nutrient concentrations. Bulk density samples were estimated from each soil sample as weight of sieved soil per scoop volume. Total soil N was determined colorimetrically after digestion in sulfuric

acid (Technicon Industrial Systems, 1975). Phosphorus, K, Ca and Mg were determined using atomic adsorption spectrophotometry on Mehlich III extracts (Mehlich, 1984).

Data Analysis

Biomass and nutrient contents of the stand were estimated by applying previously described regression equations to DBH and H data collected during year 1982 (1st rotation) and 2000 (2nd rotation) for all the trees on the 15m x 30m measurement plots. Independence or similarity of tree biomass and nutrient content equations between rotations (Rubilar et al. 2002) were tested, individual tree estimates added and plot estimates were scaled to a hectare basis. Equations applied had the form:

[2] $$LOG_{10}(Y)= a + b* LOG_{10} (DBH^2H)*CF$$

where Y is the biomass or nutrient content in grams or milligrams per tree, DBH in cm, H in m, a, and b coefficients of the model, and CF the correction factor for bias suggested by Baskerville (1962). All the models tested were selected based on best fit, R^2 value, and residuals analysis. Understory biomass and nutrient content per plot was estimated scaling average subplot information to a hectare basis, and averaging plots to obtain stand estimates. For the first rotation, inventory information was used to estimate slash pine biomass and nutrient content using biomass equations developed by Clark and Taras (1976). Slash pine nutrient concentrations were assumed the same as for loblolly pine. Hardwoods biomass and nutrient content was estimated from equations published by Clark (1986) and nutrient concentrations published by Messina et al. (1986) and Messina (1983). First and second rotation forest floor biomass and nutrient content per plot were estimated scaling subplot average to a hectare basis for each plot and averaging plots for stand level determinations.

Site index plot estimates were calculated using the equations of Clutter and Lenhart (1968) for the 250 tallest trees per hectare. Stand site index was obtained by averaging plot estimates.

Aboveground (stand and forest floor) biomass, nutrient accumulation, and site index were used to evaluate plot-by-plot differences using two-tailed bivariate Pearson correlations (Steel and Torrie, 1980). Significant correlations were further evaluated using linear regression, after transformation of non-normal distributed variables. In addition, forest floor average concentrations between rotations were compared using a t-test. ANOVA and ANCOVA were used to test stand and forest floor biomass and nutrient accumulation differences between rotations. Finally, data from our first and second rotation stands were compared with several biomass and nutrient content studies across the Southeast USA using regression analysis. All statistical analyses were performed using SAS software (version 8.2, SAS Institute Inc., Cary, NC, 2000)

RESULTS

Average stand biomass and nutrient accumulation comparison between rotations

Biomass accumulations by tissue type were similar for the two rotations but larger estimates for first rotation foliage and branches were the major differences. Stemwood accounted for 73% and 79%, branches for 13.9% and 8.2%, foliage for 3.6% and 2.6%, and stembark for 9.6 and 9.9%, for the first and second rotation stands respectively (Figure 1). Nutrient concentrations for each tissue and rotation are presented in Tables 1 and 2.

Proportional nutrient accumulations by tissue type were similar for the two rotations. However, tree nutrient distributions by tissue type were different from biomass distributions (Tables 3 and 4). Stemwood accumulated more nutrient accumulations during both rotations (35% to 80%). Micronutrients accumulated larger amounts compared to macronutrients. Lower nutrient accumulations for the second rotation were obtained for N and P. Branch and bark accumulated the larger amounts of Ca (16-25%). In addition, branches accumulated 13-29% of all micronutrients. Lower proportional accumulations for the second rotation branchwood were obtained for Ca, Mg, S, Zn, B and Cu; and for bark for Mn, Zn, B and Cu. Foliage, containing 20 to 25% of the N, P and S, and 11-20% of the K, did not represent a large pool in the stand for Ca (4-5%) or micronutrients (6 to 10%). Solely, foliage K proportional accumulation was lower for the second rotation.

Second rotation main increases in proportional nutrient accumulations were recorded for stemwood Ca, Mg, S and Zn (8-13%), and B and Cu (23-35%). Stembark N, P, and K also increased from 7% to 9.5%. (Tables 3 and 4)

Forest floor mass and nutrient accumulation comparison between rotations

Forest floor mass accumulation was greater in the first rotation, 21% of the first, and 16% of the second rotation aboveground biomass accumulation (Tables 3 and 4). Forest floor nutrient concentrations for the first and second rotation stands ranked N > Ca > S=K > P=Mg > Mn > Zn > B and Cu. Second rotation concentrations decreased 52% for K, 23% for Ca, 30% for Mg, and 36% for B ($p<0.001$). However, N concentrations were higher in the second rotation stand and P, Mn, Zn, and Cu concentrations showed no differences between rotations.

Forest floor accumulated 50 to 65% of the aboveground N, 43 to 55% of the P, 20 to 11% of the K, 46 to 44% of the Ca, 40 to 29% of the Mg, 57% to 59% of the S, 50% to 55% of the Mn, 32% to 36% of the Zn, 35 to 37% of the B, and 40 to 41% of the Cu in the first and second rotation respectively (Tables 3 and 4).

ANOVA analyses showed that, except for Cu, significant differences ($p<0.01$) in stand nutrient accumulation but not in biomass existed between rotations (Figure 2). In fact, comparing each plot by rotation, second rotation plots accumulated less P than first rotation plots (Figure 3). Forest floor showed significant differences ($p<0.01$) in biomass and nutrient accumulation, except for N. Details about treatment effects on stand biomass and forest floor are presented in Rubilar et al. (Chapter 1).

Inter-rotational factors predicting second rotation biomass and nutrient accumulation

Correlations at the plot level between second rotation and first rotation stand biomass (Figure 2), site index, or nutrient accumulations (Figure 3) were not significant. However, significant relationships (R^2=0.43-0.51, $p<0.01$) were found between second rotation biomass and soil P

(Figure 4). Soil exchangeable Mg also showed a significant (R^2=-0.29 to -0.47, $p<0.01$) but negative correlation with biomass and P, K and Ca accumulation of the second rotation stand.

Southeast biomass studies comparison

Biomass and nutrient content data for 39 stands (Table 5), and forest floor biomass and nutrient content (Table 6) were compiled for southeastern USA sites to compare with our inter-rotational changes. The stands ranged from four to 56 year old with a range of aboveground biomass of 2 to 253 Mg ha^{-1}. Nutrient content of stand biomass ranged 10 to 475 kg ha^{-1} for N, 1 to 48 kg ha^{-1} for P, 4 to 226 kg·ha^{-1} for K, 3 to 275 kg ha^{-1} for Ca, and 2 to 73 kg·ha^{-1} for Mg. Studies with forest floor biomass data ranged from 5 to 37 year old and biomass ranged from 7.1 to 69.7 Mg ha^{-1}. Forest floor nutrient content ranged 15 to 730 kgha^{-1} for N, 1 to 71 kgha^{-1} for P, 3 to 71 kgha^{-1} for K, 16 to 199 kgha^{-1} for Ca, and 2 to 39 kgha^{-1} for Mg.

Significant ($p<0.01$) linear relationships existed between stand and forest floor biomass and N, P, K, Ca and Mg nutrient contents (Figure 5). Stand biomass regression R^2 values were 0.80, 0.71, 0.83, 0.84, and 0.89 for N, P, K, Ca, and Mg respectively (Figure 5). Forest floors regressions R^2 values were 0.82, 0.78, 0.67, 0.47, and 0.32 for N, P, K, Ca, and Mg respectively (Figure 6). These estimates indicated higher variability in forest floor nutrient relationships for K, Ca and Mg for a given biomass accumulation compared to stand biomass nutrient estimates.

DISCUSSION

Average stand biomass and nutrient accumulation comparison between rotations

Major differences in biomass allocation between rotations existed in foliage and branches. Reduced foliage biomass allocation in the second rotation stand suggests nutritional limitations (Vose and Allen, 1988; Albaugh et al., 1998; Jokela and Martin, 2000). However, foliage differences may also be related to differences in genetic plant material (Pope and Graney, 1979). Branch biomass differences suggest an effect of differences in stand density (695 vs. 1500 trees ha^{-1}) as dominant trees have larger branches compared to suppressed trees (Naidu et al. 1998, Harms and Langdon, 1976). Genetic differences are less likely to cause differences in branch biomass considering the small genetic influence on the relative distribution of dry matter in loblolly pine plantations (Pope, 1979; Pope and Graney, 1979). As foliage, higher nutrient availability also may account for a large branch production (King et al., 1999; Jokela and Martin, 2000) during the first rotation.

Despite similar biomass amounts for the two rotations, nutrient accumulations were lower for the second rotation. In the first and second rotations, N aboveground accumulation represented almost 30% of the total soil capital to 60 cm depth (Table 7) and 7% to 12% was allocated to tree biomass (Table 3 and 4). Atmospheric N deposition for the area of 4.5 $kgha^{-1}yr^{-1}$ (EPA, 2000), and approximate estimates of average N fixation of 1.5 kg $ha^{-1}yr^{-1}$ (Jorgensen and Wells, 1986), indicates that important inputs exist to the N budget of the site. For the second rotation, annual inputs would have accumulated 102 kg ha^{-1} at this site. An aboveground whole tree harvest, of the second rotation stand, would have removed 128 kg ha^{-1} of N, producing a net site reduction of 26 kg $ha^{-1}$of N. These estimates would place this stand as a low degrading ecosystem (Richter

et al.,2000). A more detailed assessment of N soil changes will permit determination of increases or decreases on N ecosystem budget (Richter et al., in preparation). If no removals exist, the site could be considered a net aggrading ecosystem. Similar results have been obtained for a Piedmont site by Richter and Markewitz (2001).

At our site, despite similarities in stemwood dry weight biomass, N content was reduced by almost one-half in the second rotation. A possible explanation would be that the first rotation stand grew under luxury storage conditions, accumulating more units of nitrogen per unit of biomass. However, N availability decline and deficiency effects could be affecting second rotation stand development, in particular, considering the lower foliar biomass observed on the second rotation stand (Table 3). The fact that this aggrading N ecosystem has reached an N deficiency condition, seems paradoxical from a sustained productivity point of view. Declines in productivity may be present on aggrading ecosystems, as nutrient accumulation do not necessarily reflects nutrient availability. The tight dynamic of N and P in the forest floor, and the high demands for these nutrients from mineral soil sources, limit nutrient supply and tree growth (Richter and Markewitz, 2001). Assessments of sustainability, based on maintenance of site productivity between successive rotations considering a traditional budget balance approach (Van Lear et al., 1982; Neary et al., 1983; Wells, 1983, Gresham, 2000), may be misleading if changes in site fertility and their implications on current and future stand growth are not evaluated.

The lower second rotation accumulation of other nutrients, and potential removals at harvesting, indicates that P, K, Mg, Mn, Zn, B, and Cu may be exported at higher rates. In fact, second

rotation P showed a 75% lower accumulation in stemwood and 50% lower in total stand biomass suggesting a decline in P. However, very high soil P levels were observed at the beginning of the second rotation. Atmospheric deposition for K, Ca and Mg have been estimated as 0.2, 1.6, 2.8 and 0.7 kg $ha^{1}yr^{-1}$ (Wells, 1983), indicating low inputs for maintenance of soil fertility. Prior to harvest of the first rotation, soil extractable K, Ca, and Mg levels suggest low availability for these nutrients at the site (Table 7). Richter and Markewitz (2001) have observed that exchangeable pools of Mg and Ca decrease due to rapid growth and depletion by plantations uptake for Piedmont soils. The low levels of these highly weathered Ultisols indicate that nutrient availability may be reduced in the long-term if no amendments are applied (Wells, 1983). However, total pools for these soils should be large enough to maintain adequate buffering capacity for K, Ca, and Mg availability as these nutrients have not been indicated as major deficiencies on southern sites compared to N and P (Neary et al., 1983).

The large relative accumulation of micronutrients in stemwood biomass represent an important pool considering micronutrient availability in this low fertility soil (Buol, 1997) (Table 3 and 4). For example, between 45 to 70% of the stand aboveground B accumulation was allocated on stemwood. A stemwood harvesting, usually considered a low intensity nutrient removal impact, will export a large proportion of the site B compared to other nutrients. The traditional belief that micronutrient availability is of little concern due their extremely low requirements is not necessarily true. Extensive evidence around the world for B deficiencies has been provided (NCSFNC, Report Nº37, Schlatter and Gerding,1985; Lambert et al, 1990; Will and Madgwick, 1990; Stone, 1990). Comerford et al. (1982) have indicated that micronutrient fertilized loblolly pine plantations increase productivity once N, P, and K limitations were satisfied in several soil

types in the southeast. In addition, Jokela et al. (1991) suggested that micronutrient stress is possible on poorly to moderately well drained Ultisols, specifically on sites with intensive site preparation, fertilization with macronutrients, and weed control.

Forest floor mass and nutrient accumulation comparison between rotations

The large forest floor accumulation indicated its relevance as a carbon (C) storage sink (Richter et al., 1999). In fact, forest floor accounted for 20% to 25% of the total aboveground C accumulation at this site. Lower forest floor accumulation in the second rotation may be attributed to age differences or faster rates of decomposition caused by environmental conditions. Nutritional limitations may also have reduced second rotation foliage and then needlefall production. Second rotation forest floor nutrient concentrations suggest lower availability of all nutrients except N. Nevertheless, higher second rotation forest floor N concentrations may indicate lower N release, large immobilization (Piatek and Allen, 2001) or greater input from atmospheric deposition (Cole, 1992).

Despite similar stand biomass accumulation between rotations, first rotation forest floor biomass and all nutrient accumulations, except N, were significantly higher ($p<0.01$). This was coincident with the lower nutrient concentrations for biomass components and stand nutrient accumulations at the site, supporting our contention of a generalized decline in nutrient availability at the site.

Forest floor accumulated a large proportion of all the nutrients in both rotations, indicating the importance of this pool, and the amounts that have been transferred every year from needle fall. A hypothetical removal of the forest floor plus aboveground tree biomass will represent around

one third of the site N capital resources (Table 3 and 4). Therefore, understanding forest floor nutrient dynamics is critical to assess impacts of management and specifically site preparation activities (Morris et al., 1983). Other macronutrients long-term removal effects are less quantifiable considering the large existing soil total pools. Total aboveground biomass accumulation for the second rotation represents a 30%,102%,75%, and 66% of the soil extractable P, K, Ca, and Mg prior harvesting of the first rotation stand.

Inter-rotational factors predicting second rotation biomass and nutrient accumulation

Mehlich III extractable P was the most important variable correlating with biomass and nutrient accumulation in the second rotation stand (Figure 4), and significant declines in P accumulation at the stand and forest floor suggest the idea that P availability has declined at the site (Figure 3). However, soil available P levels are higher than usually found for these soils (Table 7). These high P levels may be explained by amendments remaining on this old field site (Richter et al., 2000). On the other hand, soil P availability could be a surrogate for N availability that we did not measured at the site. Reduced N availability would explain satisfactory both, our lower foliage accumulation estimates, and reductions in other nutrient accumulations of the second rotation stand (Table 4).

Southeast biomass studies comparison

Biomass and nutrient relative distribution by tree components change with age, and maximum rates of accumulation are limited by soil and the physiological characteristics of the trees (Wells and Jorgensen, 1975). However, total biomass by components (Figure 1, Table 8), and nutrient

accumulation in the first and second rotation stands were in agreement with other studies of similar ages (Tables 5 and 8).

The significant linear relationship between stand biomass and nutrient contents indicated that nutrient concentrations do not vary substantially across sites. The variation around the regression lines may be due to differences in sampling season and nutrient concentration determinations. These results do not support Van Lear et al. (1984), suggesting that nutrient equations at stand level are site specific. Regional average estimates of nutrient accumulation are possible using biomass accumulation as a predictor for nutrient content estimations. On the other hand, our results suggest that is more important to considerate potential site-specific N and P nutrient limitations. In fact, our second rotation N and P nutrient content showed a strong decrease (Figure 5a and 5b) compared to other nutrients (5c). Using a regional model would have overestimated second rotation nutrient accumulation.

Forest floor nutrient contents were well related with forest floor biomass, however N and P relationships showed lower variation and better linear relationships with forest floor biomass compared to K, Ca, and Mg. This suggests N and P less variability on a site by site basis or a better coupling with C dynamics. The larger variation compared to stand biomass was expected, considering foliar nutrient concentration variation, incidence of fires (Covington and Sackett, 1984), thinning regimes that would have increased decomposition and reduced the annual litterfall (Wells and Jorgensen, 1975), storms which would have increases amounts of needlefall (Urrego, 1993), and decomposition and forest floor mineralization rates across sites (Attiwill and Leeper, 1987).

Piedmont and Upper Coastal Plain sites dominated our compilation of biomass studies. Maybe one of the most interesting trends observed for forest floor variation was the higher biomass accumulations and nutrient contents attained for N and P at Piedmont sites compared to Upper Coastal Plain sites. Causes of variation may include differences in natural fertility of the Coastal Plain soils compared to Piedmont sites and climatic variations. Undoubtedly, agricultural amendments from the late 19th century have played a significant role in the region (Richter and Markewitz, 2001).

CONCLUSIONS

Stand biomass accumulation with lower nutrient accumulation and lower foliage biomass, suggests declines in N availability for the second rotation site. Considering harvesting removals, micronutrient availability, and especially B, may be critically reduced as large proportions are allocated to the stemwood compared to macronutrients. Forest floor is a large C reservoir and seems to represent a large nutrient sink for N, P, Ca, S, Zn, and Cu. Stand and forest floor nutrient accumulations across sites presented linear relationships with biomass accumulation but weaker relationships were found for forest floor K, Ca and Mg.

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Table 1. Mean and standard deviations in parenthesis of weighed nutrient concentrations by tree component (n=15), lower vegetation subplots (n=30) and forest floor (n=15) for the 22 year-old first rotation loblolly pine stand.

Tree Component	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	---------- % ----------						------ ppm -------			
Foliage †	1.075 (0.065)	0.139 (0.028)	0.538 (0.101)	0.177 (0.021)	0.101 (0.011)	0.110 (0.011)	466 (94)	21.3 (3.6)	11.9 (1.6)	3.1 (0.3)
Branches†	0.280 (0.082)	0.030 (0.013)	0.114 (0.050)	0.237 (0.043)	0.047 (0.009)	0.028 (0.010)	173 (32)	14.8 (3.6)	8.8 (2.3)	2.6 (0.7)
Stembark†	0.218 (0.029)	0.023 (0.006)	0.073 (0.036)	0.267 (0.078)	0.030 (0.009)	0.031 (0.008)	90 (37)	13.4 (2.8)	7.1 (1.3)	2.9 (0.2)
Stemwood†	0.139 (0.039)	0.013 (0.003)	0.073 (0.012)	0.079 (0.026)	0.026 (0.005)	0.010 (0.004)	143 (9)	6.3 (1.0)	2.9 (0.6)	0.8 (0.2)
Lower vegetation	0.697 (0.094)	0.110 (0.018)	0.657 (0.131)	0.470 (0.063)	0.125 (0.028)	NA NA	NA NA	NA NA	NA NA	NA NA
Forest floor*	0.826 (0.096)	0.066 (0.010)	0.105 (0.020)	0.464 (0.078)	0.091 (0.016)	0.091 (0.014)	654 (156)	17. 2 (1.0)	9.9 (2.4)	3.8 (0.5)

† From Rubilar et al. (2002)
* Values corrected for loss of ignition (LOI).
NA Not available

Table 2. Mean and standard deviations in parenthesis of weighed nutrient concentrations by tree component (n=12), and average weighted nutrient concentrations of forest floor (n=15), for the 18 year-old loblolly pine second rotation stand.

Tree Component	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	%						ppm			
Foliage †	0.971 (0.214)	0.110 (0.026)	0.374 (0.078)	0.141 (0.033)	0.103 (0.026)	0.112 (0.028)	394 (17)	22.4 (2.9)	9.1 (0.6)	3.4 (0.4)
Branches†	0.232 (0.033)	0.032 (0.008)	0.166 (0.026)	0.173 (0.012)	0.057 (0.010)	0.023 (0.006)	164 (13)	14.1 (1.8)	7.0 (0.7)	2.4 (0.4)
Stembark†	0.198 (0.021)	0.018 (0.005)	0.068 (0.019)	0.243 (0.074)	0.036 (0.009)	0.025 (0.003)	12 (3.4)	6.3 (0.7)	2.6 (0.3)	NA NA
Stemwood†	0.049 (0.004)	0.005 (0.001)	0.062 (0.007)	0.059 (0.007)	0.025 (0.001)	0.009 (0.002)	99 (41)	5.4 (1.4)	2.9 (0.8)	1.4 (0.2)
Forest floor*										
Oi	0.435 (0.069)	0.042 (0.005)	0.038 (0.009)	0.341 (0.043)	0.078 (0.010)	0.056 (0.008)	652 (171)	10.4 (1.4)	8.9 (0.7)	1.9 (0.3)
Oe	0.836 (0.081)	0.066 (0.008)	0.059 (0.008)	0.363 (0.045)	0.059 (0.008)	0.099 (0.013)	634 (199)	16.9 (3.8)	5.8 (1.3)	4.3 (0.9)
Oa	1.626 (0.166)	0.100 (0.021)	0.035 (0.021)	0.334 (0.049)	0.066 (0.008)	0.153 (0.014)	884 (327)	26.1 (4.6)	6.2 (3.3)	8.0 (1.2)
Total**	0.934 (0.059)	0.069 (0.006)	0.050 (0.006)	0.354 (0.042)	0.063 (0.008)	0.103 (0.010)	687 (212)	17.7 (3.3)	6.3 (1.1)	4.7 (0.6)

† From Rubilar et al. (2002)

* Values corrected for loss of ignition (LOI)

** Weighted average of Oi, Oe, and Oa horizons.

NA **Not available**

Table 3. Average winter dry weight by aboveground biomass components for the 22 year-old loblolly pine first rotation stand.

Component	Dry weight	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	Mg ha^{-1}	kg ha^{-1}						g ha^{-1}			
Foliage	5.1	55.8	7.2	27.5	9.3	5.2	5.3	2423	103	62	15
	(1.3)	(14.7)	(1.9)	(7.0)	(2.4)	(1.4)	(1.4)	(630)	(27.4)	(16.0)	(4.1)
Branches	19.9	54.4	5.7	21.8	57.9	9.2	5.0	3423	296	182	52
	(5.2)	(14.1)	(1.5)	(5.8)	(16.4)	(2.4)	(1.3)	(893)	(77.7)	(47.8)	(13.8)
Stembark	13.7	29.6	3.2	9.5	33.6	4.3	4.0	1099	178	98	39
	(3.5)	(7.5)	(0.8)	(2.4)	(8.9)	(1.1)	(1.0)	(295)	(45.9)	(4.9)	(10.1)
Stemwood	104.5	138.4	13.6	77.0	80.5	26.5	9.3	14983	658	280	88
	(26.2)	(33.6)	(3.6)	(19.1)	(20.4)	(6.7)	(2.4)	(3755)	(165.0)	(71.0)	(22.2)
Stand Total	**143.2**	**278.2**	**29.7**	**135.8**	**181.4**	**45.2**	**23.6**	**21928**	**1235**	**621**	**195**
Hardwoods	1.6	5.3	0.9	4.1	5.2	0.8	NA	NA	NA	NA	NA
	(1.4)	(4.6)	(0.7)	(3.6)	(4.6)	(0.7)	NA	NA	NA	NA	NA
Lower vegetation	0.3	1.7	0.3	1.5	1.2	0.3	NA	NA	NA	NA	NA
	(0.2)	(1.3)	(0.2)	(1.1)	(0.9)	(0.2)	NA	NA	NA	NA	NA
Forest Floor*	37.1	277.1	22.3	35.2	155.5	30.5	30.8	21811	574	332	129
	(8.2)	(80.2)	(6.9)	(11.5)	(48.2)	(9.2)	(10.0)	(7805)	(151)	(118)	(39)
Aboveground Total	**180.6**	**556.4**	**52.3**	**171.9**	**337.8**	**75.9**	**54.4**	**43739**	**1809**	**953**	**324**

Standard deviation in parenthesis

* **Forest floor dry weight expressed on an ash-free content basis averaged across treatments selected for comparison**

NA **Not available**

Table 4. Average winter dry weight by aboveground biomass components for the 18 year-old loblolly pine second rotation stand for all treatments.

Component	Dry weight	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
	Mg ha^{-1}	----------		kg ha^{-1}	----------			----------	g ha^{-1}	----------	
Foliage	3.4	29.6	3.5	11.5	4.3	3.0	3.3	1347	83	30	13
	(0.5)	(3.2)	(0.4)	(1.3)	(0.5)	(0.3)	(0.4)	(180.3)	(9.8)	(3.8)	(1.4)
Branches	10.6	22.5	2.8	18.4	15.9	5.3	2.0	1819	137	69	22.5
	(1.9)	(3.7)	(0.4)	(3.3)	(2.6)	(0.8)	(0.3)	(339.6)	(22.2)	(11.5)	(3.6)
Stembark	12.9	25.9	2.5	9.9	29.4	4.7	3.4	161	86	35	NA
	(0.9)	(2.0)	(0.2)	(0.9)	(1.4)	(0.4)	(0.2)	(10.6)	(6.0)	(2.3)	NA
Stemwood	103.1	50.4	5.2	60.4	62.0	26.2	9.5	10599	551	292	137
	(10.1)	(4.9)	(0.5)	(5.9)	(5.7)	(2.5)	(1.0)	(1328.6)	(56.8)	(26.5)	(13.3)
Stand Total	**130.0**	**128.4**	**14.0**	**100.2**	**111.6**	**39.3**	**18.2**	**13926**	**857**	**426**	**172**
Forest Floor	25.3	236.6	17.4	12.7	88.9	15.8	26.5	16935	489	253	119
	(3.7)	(34.2)	(2.1)	(2.1)	(9.3)	(1.9)	(1.5)	(3616)	(89)	(25)	(23)
Aboveground Total	**155.3**	**365.0**	**31.4**	**117.3**	**200.5**	**55.1**	**44.7**	**30861**	**1346**	**679**	**291**

Standard deviations in parenthesis

[a] **Forest floor dry weight expressed on an ash-free content basis and averaged across contrasting treatments.**

NA **Not available**

Table 5. Total stand aboveground biomass and nutrient content for several studies on loblolly pine plantations in the southeastern USA.

Age	TPH	Height	Site	Biomass	N	P	K	Ca	Mg	Author
yrs.	*	m		Mg ha^{-1}	----------		kg ha^{-1}	----------		
4	1665	4.3	PID	7.1	28	3	18	13	3	Haines and Sanderford, 1975
4	1495		LCP	2.1	10	1	4	3	2	Colbert, 1988
4	4485	2.4	-	6.9	38	-	-	-	-	Smith et al, 1971
5	4629	3.8	-	17.3	72	9	35	31	9	Nelson et al, 1968
5	-	-	CP	8.3	22	2	13	7	3	Switzer and Nelson, 1972
10	2125	13	CP	28.0	85	10	49	33	11	Switzer and Nelson, 1972
11	1349	10.5	LCP	77.4	-	-	56	138	29	Nemeth, 1972
11	1349	-	LCP	99.6	-	-	59	158	34	Wheeler, 1972
11	2990	9.8	HAK	88.5	195	27	129	-	-	Pope, 1979
13	1112	6.1	SAH	23.5	81	9	36	29	10	Albaugh et al,
13	1439	11.6	HCP	98.2	180	-	-	-	-	Larsen et al., 1976
15	1200	19.0	CP	63.0	140	16	82	62	17	Switzer and Nelson, 1972
16	2202	14.9	PID	156.0	257	31	165	187	46	Wells et al, 1975
16	2243	-	PID	192.0	321	48	226	-	-	Jorgensen et al., 1975
17	-	-	PID	146.1	475	21	142	275	56	Johnson and Lindberg, 1992
18	1383	17.7	UCP	185.8	245	34	168	212	56	Shephard, 1985 (Plantation 19,20,21)
18	**1544**	**16.7**	**UCP**	**130.0**	**128**	**14**	**100**	**112**	**39**	**Second Rotation Stand**
19	1420	17.3	UCP	169.1	213	31	146	191	52	Shephard, 1985 (Plantation 1,2)
20	1779	16.6	UCP	151.0	191	30	134	172	47	Shephard, 1985 (Plantation 4,5,31)
20	1001	-	CP	90.0	174	19	98	90	24	Switzer and Nelson, 1972
21	1349	13.7	UCP	110	138	20	96	124	34	Shephard, 1985 (Plantation 12,13,15,16,17)
21	1261	19.2	UCP	179	223	33	157	199	53	Shephard, 1985 (Plantation 18,24)
22	1276	18.9	UCP	182.2	201	33	153	203	54	Shephard, 1985 (Plantation 7,32)
22	1327	21.6	UCP	239.3	268	41	198	266	71	Shephard, 1985 (Plantation 29,30)
22	983	-	PID	85	135	11	64	85	23	Tew et al, 1986
22	**695**	**19.2**	**UCP**	**143**	**278**	**30**	**136**	**181**	**45**	**First Rotation Stand**
23	760		PID	101.4	205	26	130	128	31	Johnson and Lindberg, 1992
23	1112	20.4	UCP	237.0	230	37	177	238	63	Shephard, 1985 (Plantation 6)
24	1235	15.5	UCP	102	141	21	100	118	36	Shephard, 1985 (Plantation 8)
24	815	18.5	UCP	138	162	26	123	155	43	Shephard, 1985 (Plantation 9)

*** TPH Trees per hectare**

HAK Hilly region North Central Arkansas, LCP Lower Coastal Plain, PID Piedmont, UCP Upper Coastal Plain, SAH Sandhills, HCP Hilly Coastal Plain, TER, Terraces

continue

Table 5. Stand total aboveground biomass and nutrient content for several studies on loblolly pine plantations in the southeastern USA.

Age	TPH	Height	Site	Biomass	N	P	K	Ca	Mg	Author
yrs.	*	m		Mg ha^{-1}	----------		kg ha^{-1}	----------		
25	685	25.8	UCP	253.1	263	43	206	275	73	Shephard, 1985 (Plantation 26,27)
25	1108	22.4	UCP	202.3	213	34	166	223	59	Shephard, 1985 (Plantation 25,28)
25	1175	-	HCP	161.0	209	25	97	196	63	Pehl et al, 1984
34	1100-1500		PID	203.4	244	24	171	192	53	Urrego, 1993
35	430	-	TER-	117.1	140	16	96	97	26	Johnson and Lindberg, 1992 (plot1)
35	430	-	TER	119.7	143	16	99	99	26	Johnson and Lindberg, 1992 (plot2)
41	437	22.9	PID	109.6	123	10	56	111	-	Van Lear et al, 1984
48	437	-	PID	144.9	165	14	78	154	-	Van Lear et al, 1995
56	-	21.0	UCP	-	142	5.0	14.0	9.0	72	Switzer and Nelson, 1963

*** TPH Trees per hectare**

HAK Hilly region North Central Arkansas, LCP Lower Coastal Plain, PID Piedmont, UCP Upper Coastal Plain, SAH Sandhills, HCP Hilly Coastal Plain, TER, Terraces

Table 6. Forest floor biomass and nutrient accumulation for several studies on loblolly pine plantations in the southeastern USA.

Age yrs.	TPH *	Height m	Site	Biomass Mg ha^{-1}	N	P	K	Ca	Mg	Author
					----------		kgha^{-1}	----------		
5	-	-	CP	-	15	1	5	16	2	Switzer and Nelson, 1972
10	2125	13	CP	-	75	7	12	59	11	Switzer and Nelson, 1972
13	1439	11.6	HCP	15.7	102.7	-	-	-	-	Larsen et al., 1976
15	1200	19.0	CP	-	108	8	14	73	14	Switzer and Nelson, 1972
15	2523	11.9	PID	-	171	21	16	64	12	Van Lear and Goebel, 1976
16	2202	14.9	PID	-	307	30	28	93	20	Wells and Jorgensen, 1975
17	-	-	PID	32.0	310	21	30	125	39	Johnson and Lindberg, 1992
18	1383	17.7	UCP	21.2	186	12	14	133	13	Shephard, 1985 (Plantation 19,20,21)
18	**1544**	**16.7**	**UCP**	**25.3**	**236.6**	**17.4**	**17.1**	**88.9**	**15.8**	**Second Rotation Stand**
19	2244	14.9	PID	37.0	398	37	20	130	19	Jorgensen et al, 1980
19	961	18.0	UCP	12.1	69	12	3	76	4	Lockaby and Taylor-Boyd, 1986
19	1421	17.3	UCP	28.3	270	18	16	94	17	Shepard, 1985 (Plantation 1,2)
20	1779	16.6	UCP	20.6	163	13	15	88	14	Shepard, 1985 (Plantation 4,5,31)
20	1000	-	CP	15.0	124	9	16	81	16	Switzer and Nelson, 1972
21	1349	13.7	UCP	13	115	8	10	62	10	Shephard, 1985 (Plantation 12,13,15,16,17)
21	1261	19.3	UCP	17	164	11	14	81	9	Shephard, 1985 (Plantation 18,24)
21	2241	7.9	PID		327					Strader, 1981
22	1273	18.9	UCP	23.4	171	17	19	103	15	Shephard, 1985 (Plantation 7,32)
22	1327	21.6	UCP	13.1	122	10	12	63	11	Shephard, 1985 (Plantation 29,30)
22	983		PID	30.0	360	23	41	199	36	Tew et al., 1986
22	692	22.0	UCP	40.3	270	22	35	158	31	Rodriguez and Allen
22	**695**	**19.2**	**UCP**	**37.1**	**277**	**22**	**35**	**156**	**31**	**First Rotation Stand**
23	761	-	PID	63.0	450	71	50	145	18	Johnson and Lindberg, 1992
23	1112	20.1	UCP	18.4	118	12	15	66	10	Shepard, 1985 (Plantation 6)
24	1235	15.5	UCP	28	317	18	21	97	21	Shepard, 1985 (Plantation 8)
24	815	18.5	UCP	21	234	15	16	77	14	Shepard, 1985 (Plantation 9)
24	1154	14.9	LCP	7.1	67	8	3	24	4	Rodriguez and Allen
25	685	25.8	UCP	13	117	8	10	58	8	Shephard, 1985 (Plantation 26,27)
25	1108	22.4	UCP	9	98	8	10	52	9	Shephard, 1985 (Plantation 25,28)
31	640	17.1	LCP		205					Strader, 1981
34	1100-1500		PID	69.7	730	46	71	178	27	Urrego, 1993

*** TPH: Trees per hectare**

HAK: Hilly region North Central Arkansas.
LCP: Lower Coastal Plain
PID: Piedmont
UCP: Upper Coastal Plain
SAH: Sandhills
HCP: Hilly Coastal Plain
TER: Terraces

Table 7. Average soil N total nutrient content (Kjeldahl) and soil extractable P, K, Ca, and Mg (Mehlich III).

	N	P	K	Ca	Mg
Depth (cm)	---	kg ha^{-1}		---	
0- 10	388	41	16	27	7
10- 20	227	42	16	46	12
20- 30	163	12	16	49	15
30- 40	164	5	20	51	17
40- 50	171	3	24	47	16
50- 60	172	2	24	47	16
Total profile (0-60 cm)	**1285**	**104**	**115**	**268**	**83**

Bulk density values were assumed equivalent as gr/cm3 from scoop air-dry 2 mm sieved sample

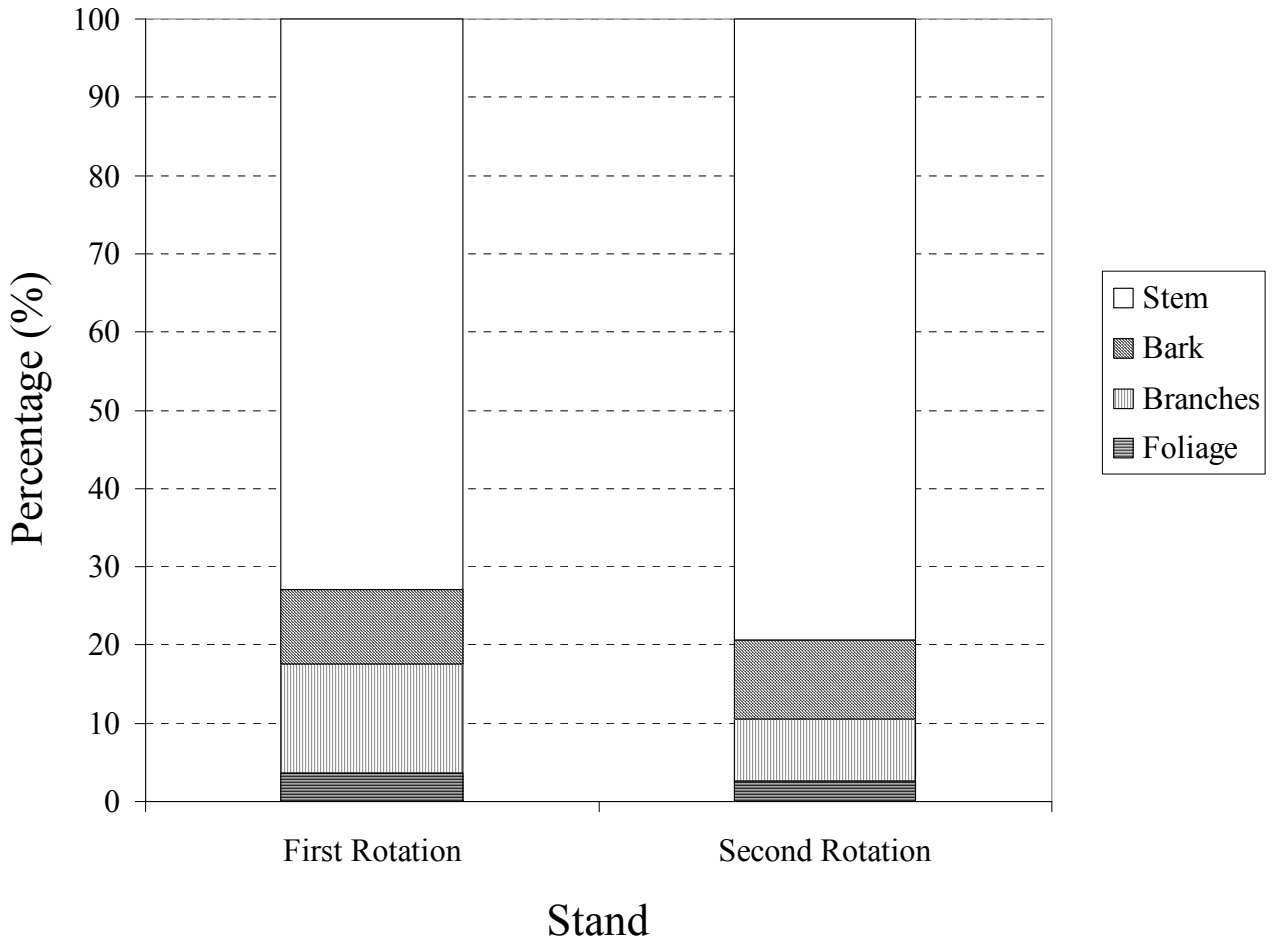

Figure 1.- Relative biomass distribution of the first and second rotation stands

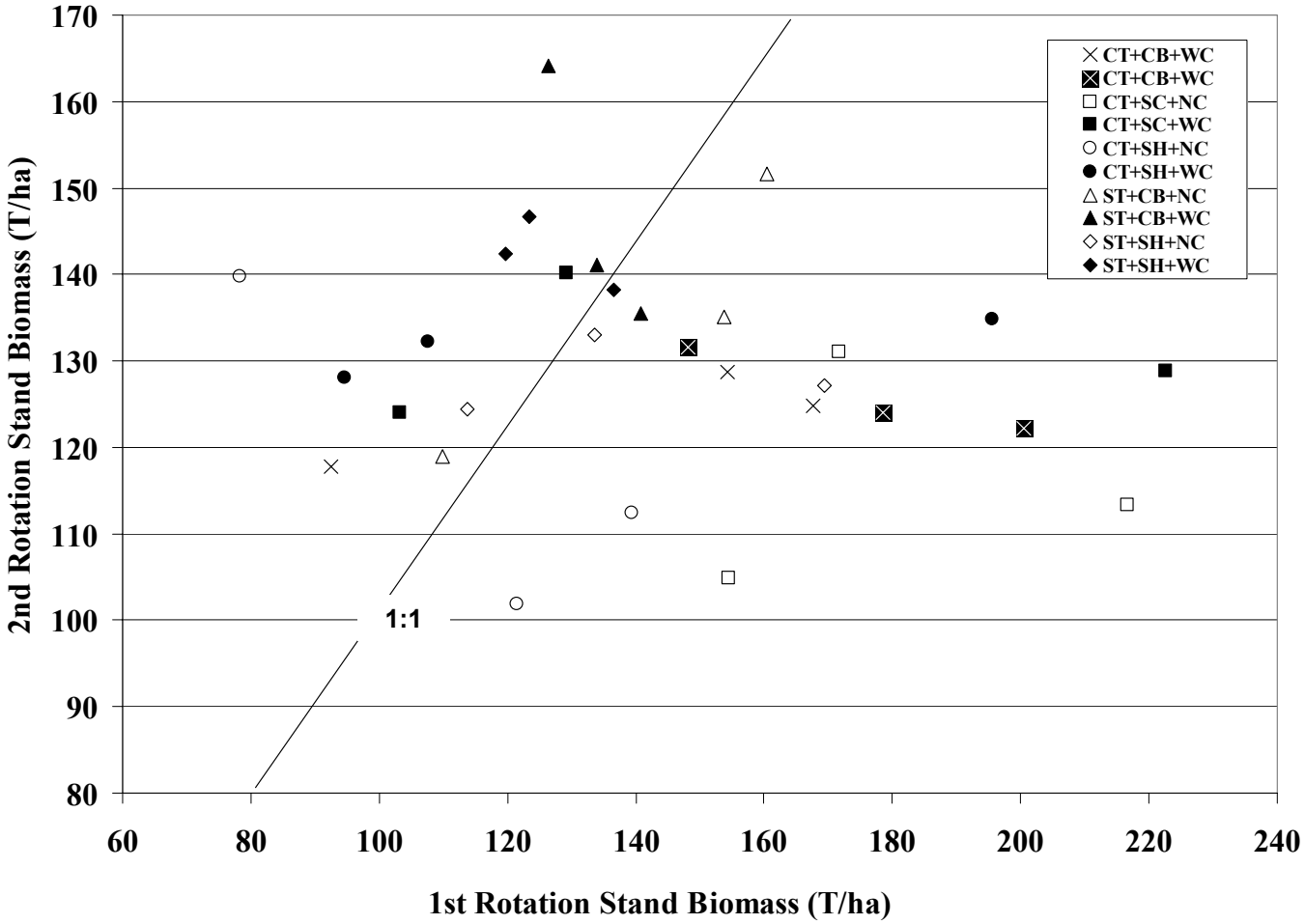

Figure 2.- First and second rotation biomass comparison in a plot by plot basis.
CT : Complete tree harvesting, ST : Stem removal harvesting, CB: Chop and Burn site preparation, SH: Shear and pile, SC: Scalping, NC: no weed control, WC: Weed control during 3 years.

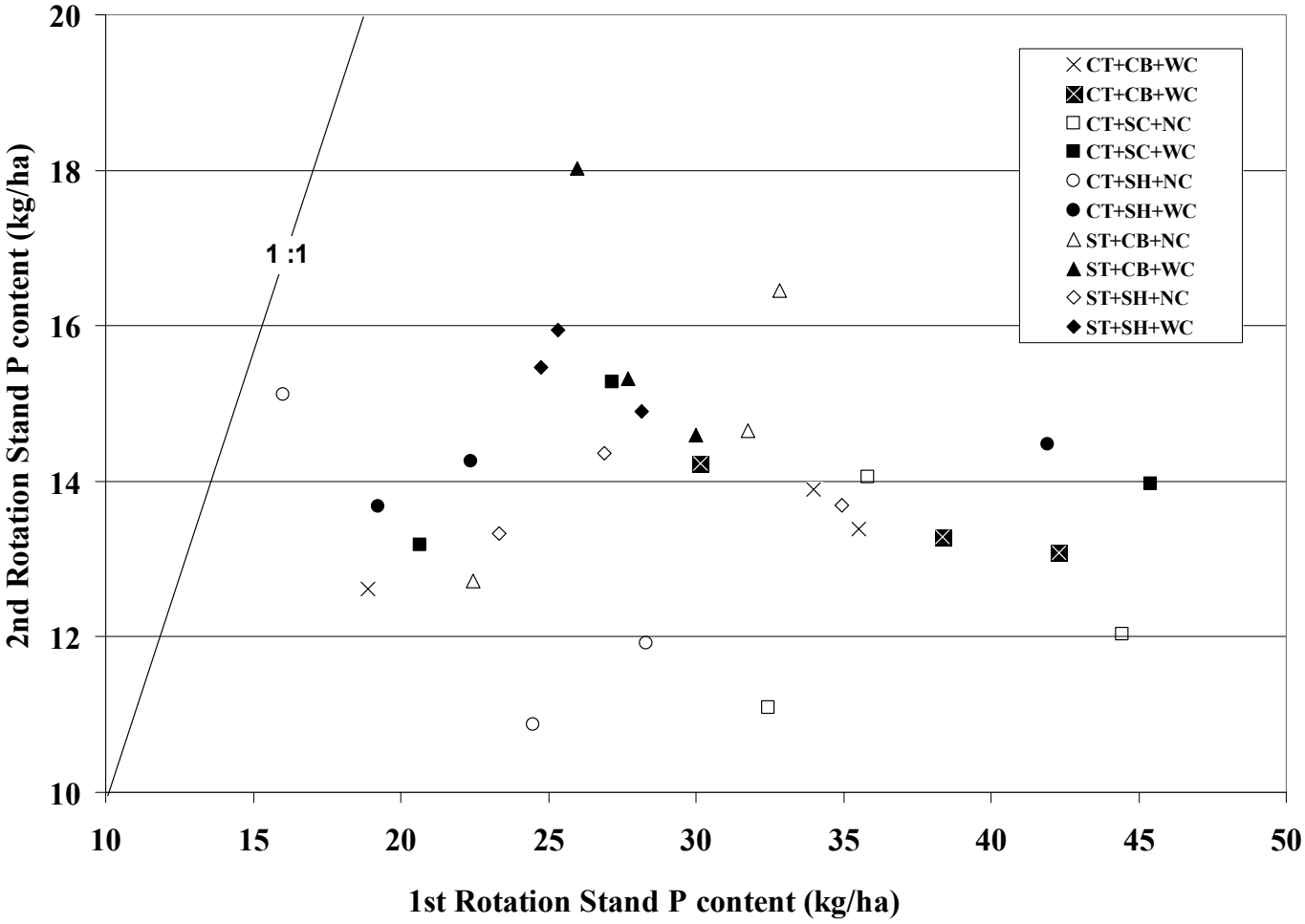

Figure 3.- First and second rotation P content comparison in a plot by plot basis.
CT : Complete tree harvesting, ST : Stem removal harvesting, CB: Chop and Burn site preparation, SH: Shear and pile, SC: Scalping, NC: no weed control, WC: Weed control during 3 years.

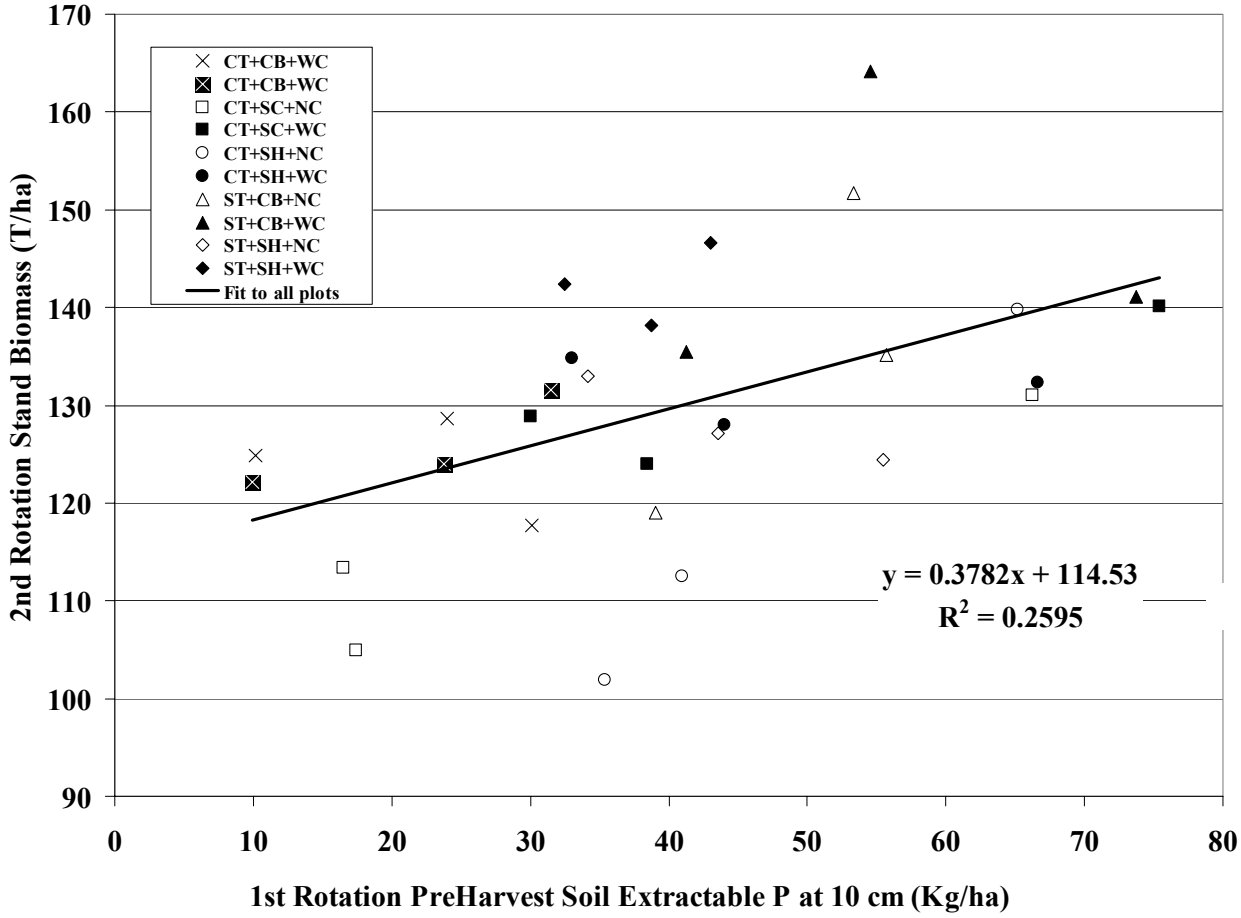

Figure 4.- Second rotation biomass versus soil extractable P on a plot by plot basis.
CT : Complete tree harvesting, ST : Stem removal harvesting, CB: Chop and Burn site preparation, SH: Shear and pile, SC: Scalping, NC: no weed control, WC: Weed control during 3 years.

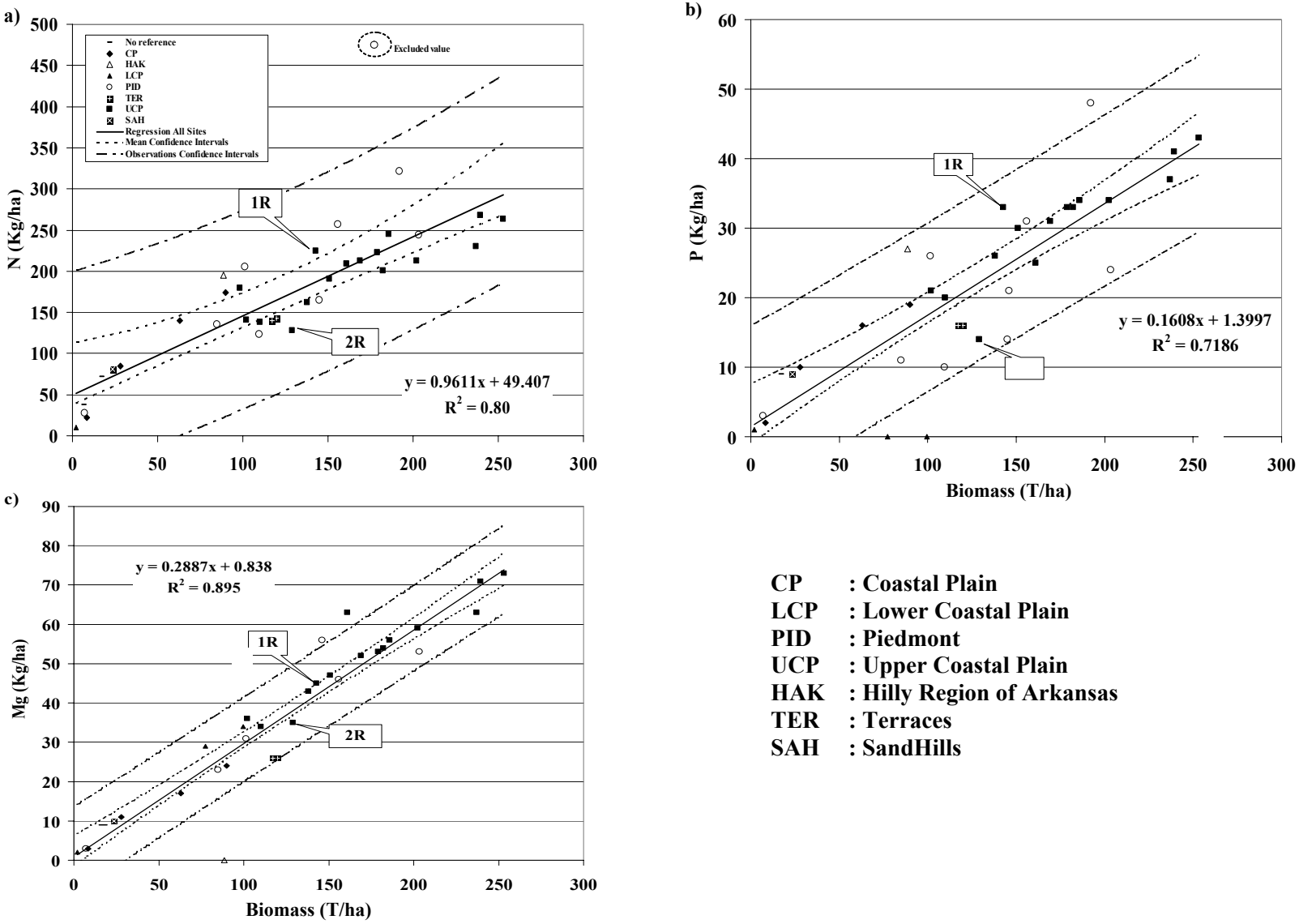

Figure 5.- Stand biomass and nutrient content relationship among Southeastern biomass studies, a) N nutrient content, b) P nutrient content b) Mg nutrient content, the same pattern was shown for K and Ca.

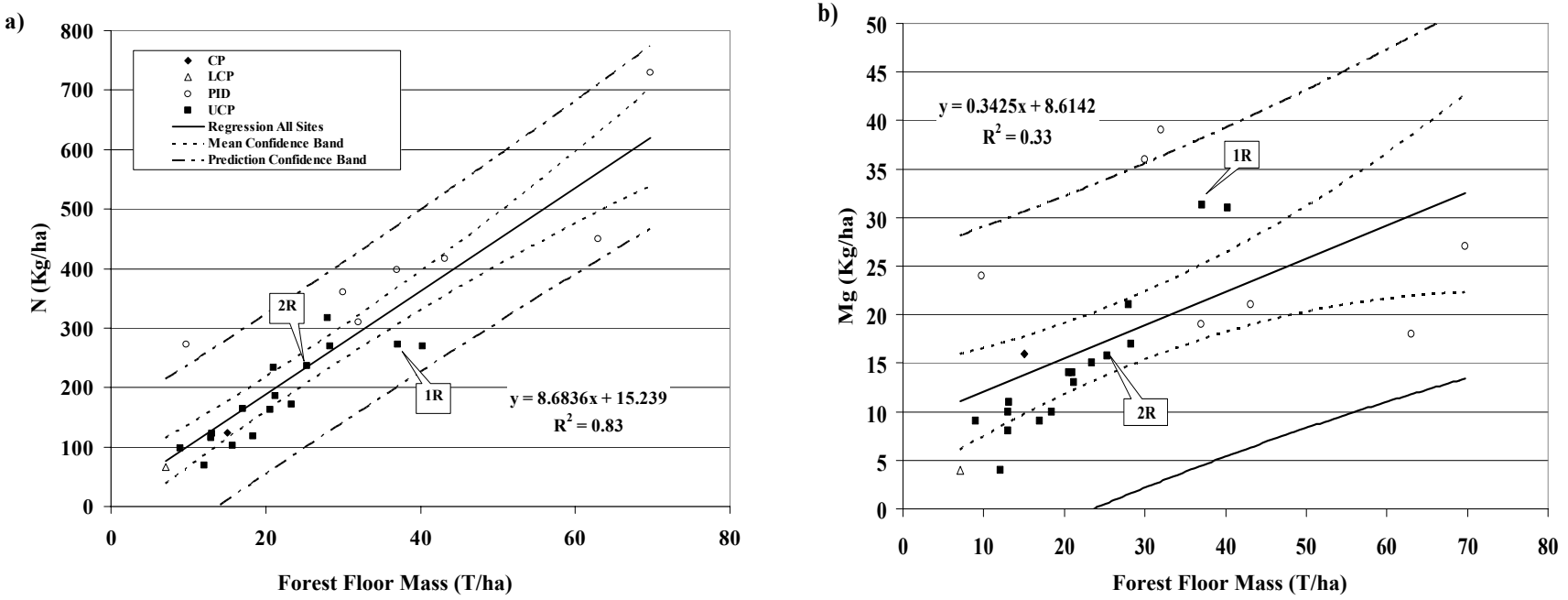

Figure 6.- Forest floor mass and nutrient content relationships among southeastern biomass studies. a) N nutrient content, the same pattern was shown for P, b) Mg nutrient content, the same pattern was shown for K and Ca.