ABSTRACT

AGUIAR, VITOR HERINGER DE. Effects of Silvicultural Intensity, Genetics, and Planting Density on Above and Belowground Carbon Allocation of Loblolly Pine (*Pinus taeda*). (Under the direction of Dr. Rachel L. Cook).

Over the last decades, atmospheric carbon dioxide has reached unprecedented levels. One way to offset greenhouse gas emissions is to increase the productivity of forest systems, which has increased the interest to account for carbon sequestration. However, carbon accounting usually does not consider belowground sequestration in root systems, as it is much harder to estimate. Decades of research in fertilization, vegetation control, site preparation, planting density and tree improvement have made loblolly pine (*Pinus taeda*) the most commercially important pine species in southeastern United States. However, little is known about the effects of silviculture, genetics and planting density, and their interactions, on belowground carbon sequestration.

To address this issue we sampled 8 year-old loblolly pine trees from two genotypes (an open-pollinated family and a clone), planted at two densities (618 and 1853 trees ha^{-1}), and managed under two silvicultural levels (operational and intensive). We developed treatment-specific allometric equations, using whole-tree harvesting techniques, to estimate aboveground (bole, branches and foliage) and belowground (root) biomass. We used these estimates to evaluate treatment effects on tree- and stand level biomass accumulation and on belowground to aboveground ratios.

In general, silviculture affected biomass accumulation at the tree level, with intensive silviculture increasing foliage, branch, root, and total biomass, but not bole biomass. Planting density was also significant, with low density resulting in bigger individual trees and more biomass in all components. At the stand level, only planting density had a significant effect on

biomass accumulation, with high density resulting in more biomass in all tree components. A high level of mortality was observed in the open-pollinated family, especially under intensive silviculture, which most likely confounded treatment effects. There were differences in root:shoot ratios due to a three-way interaction and on root:bole ratios due to two way interactions. Root:shoot ratios ranged from 0.29 to 0.40 and root:bole ratios ranged from 0.39 to 0.65. The low stand density resulted in higher ratios, but the magnitude of the effect was dependent on genotype and the level of silviculture. Overall, this study provides better understanding of silviculture, genetic, and density effects on biomass accumulation and the relationship between above and belowground biomass allocation.

Effects of Silvicultural Intensity, Genetics, and Planting Density on Above and Belowground Carbon Allocation of Loblolly Pine (*Pinus taeda*).

by
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DEDICATION

To my beloved wife and parents

BIOGRAPHY

Vitor Aguiar grew up in the small town of Timóteo, in the state of Minas Gerais, Brazil. He started his undergraduate studies in Biochemistry, because of his interest in biological processes. However, he also had a strong interest in mathematics and engineering, which led him to later switch majors to Forest Engineering at Federal University of Viçosa. During his undergraduate career, Vitor was given an opportunity to travel to the United States for a period of one year, to study and conduct research focusing on biofuel processing. Though this international research experience, Vitor was able to improve his English skills, as well as to travel through the country. It was also what made him decide to pursue a graduate degree in America. After returning to Brazil and completing his undergraduate degree, Vitor went on to pursue a Master of Science at NC State University, researching biomass production and allocation in loblolly pine plantations.

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CHAPTER 1: Review of Literature

As human population continues to grow, forest land decreases while the demand for forest products increase (Wear and Greis, 2002; Fox et al. 2007b). In addition, human activity has increased carbon dioxide (CO_2) emissions to record levels (IPCC, 2013). In order to reduce the pressure on native forests and ensure their conservation while meeting the increasing demand for wood and fiber, and reduce (CO_2) net emissions, production from intensively managed production forests must increase (Sedjo and Botkin, 1997; Cacho et al., 2005). Well-designed forest management activities have the potential to meet the human population growing need for forest products but also protect ecological and social values (Bettinger et al., 2009).

Plantation forests are more effective than naturally regenerated forests in accumulating biomass and, therefore, providing wood to a growing consumer market while sequestering more carbon. These tree plantations become more relevant as the human population continues to grow and expand into rural areas, converting forestland into higher-valued uses such as residential property (Salwasser, 2004).

Roundwood (wood in its natural state as felled, with or without bark) is the chief economical product of forests, and it can be converted into other wood products, such as sawtimber, pulpwood, fuelwood, veneer, etc. Tree plantations supply around 35% of all forest products despite the fact that they account for only 5% of the forest cover around the world (Food and Agriculture Organization, 2006). The southern United States supplies almost 290 million m^3 of roundwood to wood markets annually, and of this total, about 28% comes from plantation forests (Smith et al., 2004).

From a carbon sequestration perspective, considering that plants sequester atmospheric carbon in living biomass, pine plantations have incredible potential to mitigate greenhouse gas

emissions. Overwhelmingly, the generic assumption is that biomass consists of 50% carbon, and this value has been used in a variety of carbon stock estimates in natural forests (tropical and temperate), managed forests, experimental forest sites, and agroforest systems (Thomas and Martin, 2012). However, in a review study, Thomas and Martin (2012) noted that this assumption can introduce estimation errors up to 8%, and observed that conifer species exhibited greater wood carbon content compared to angiosperm species. Analyzing 47 conifer species, they found that mean carbon fraction of conifers in subtropical biomes and in temperate/boreal biomes was 50.5% ± 2.8 and 50.8% ± 0.6, respectively. Forest belowground biomass is often ignored when accounting for carbon sequestration, since carbon markets usually do not consider belowground biomass when estimating carbon credits (Lin and Lin, 2013). In addition, there is little knowledge regarding belowground carbon sequestration due to the laborious work involved in root sampling (Kapeluck and Van Lear, 1995; Wang et al., 2012).

From 1952 to the turn of the 21st century, pine plantation areas in the south have increased from about 0.7 million hectares to about 13 million hectares (Fox et al., 2007b), and are projected to rise to about 18 million hectares by 2040 (Wear and Greis, 2002). During the same period, productivity has also increased while rotation age has dropped due to improved silvicultural practices, such as site preparation, weed control and fertilization as well as improvements in genetics (Fox et al., 2007b). In southeastern U.S. the most common and commercially important pine species is Loblolly pine (*Pinus taeda*) (Harms et al., 2000). Its natural range extends from southern New Jersey to central Florida and west to eastern Texas, making it well adapted to a wide range of soils, sites, and environments (Baker and Langdon, 1990).

Fertilization and Vegetation Control

Studies show that productivity in southern U.S is still below what is biologically possible (Jokela et al., 2000; Borders and Bailey, 2001) and that the growth potential of loblolly pine is far greater than growth records in the region indicate (Harms et al., 2000). For instance, even unimproved stock can have its growth double in comparison to loblolly pine plantations in its natural range, when grown in very favorable conditions (DeBell et al., 1989; Schultz, 1997). The use of superior genotypes under intensive management (fertilization and competition control) can increase productivity up to three-fold (Borders and Bailey, 2001). Therefore, it is important to identify and quantify the specific tree, and stand physiological, and environmental factors responsible for high growth rates, as well as site-specific factors that are limiting to loblolly pine in the Southeast (Harms et al., 2000).

Poor productivity is directly related to low levels of leaf area (Albaugh et al., 1998). Leaf area index (LAI) is defined as the total one-sided area of leaf tissue per ground surface area (leaf area / ground area, $m^2\ m^{-2}$) (Watson, 1947). It is sometimes expressed on the basis of all leaf surfaces. The total for broad-leaf trees is twice the projected area, while the conversion factor for needle-leaf trees is between 2.4 and 2.6 (Bennett and Rook, 1978; Waring et al., 1982) and only in rare occasions pi (π), since leaves are usually not perfect cylinders (Grace, 1987). Aboveground production is strongly correlated to LAI, but the magnitude of stemwood biomass increments depends on genetics, site characteristics and management intensity (Samuelson et al., 2004). LAI is greatly affected by soil nutrient availability, and low levels of available soil nutrients reduce not only leaf area, but also growth efficiency, and stand production (Sampson and Allen, 1999; Albaugh et al., 2004). Studying the effects of fertilization on production and leaf area efficiency in loblolly pine, Jokela and Martin (2000) observed a decline in stemwood

growth after restricting fertilizer applications, which led them to hypothesize that stemwood growth reduction following peak LAI (LAI at peak season, i.e, following leaf expansion) was due primarily to decreasing nutrient availability. Forest fertilization is, therefore, an important mechanism to increase production rates (Fox et al., 2007a).

Fertilization is now a common practice in managed pine plantations in southern U.S., with typical applications of phosphorus and nitrogen (Albaugh et al., 2012). Phosphorus applications are often performed at or soon after stand establishment (Fox et al., 2007a) and the response to a single application may last for over 20 years (Pritchett and Comerford, 1982). Throughout the rotation, volume growth gains average 2.8 to 3.5 m^3 ha^{-1} yr^{-1} in soil deficient sites (Fox et al., 2007a). Mid-rotation fertilizer applications usually consist of nitrogen and phosphorus. A common prescription used for loblolly pine on most sites consists of 170 to 225 kg ha^{-1} of N plus 28 kg ha^{-1} of P, and growth gains average 3.5 m^3 ha^{-1} $year^{-1}$ during the first 8 years after application (Fox et al., 2007a).

Another strategy that can improve productivity is site preparation, which can reduce competing vegetation, facilitate planting and improve the soil conditions of the site (Shiver and Martin, 2002; Zhao et al., 2009). Mechanical site preparation has been a common practice since the 1950s, and the methods applied include bedding, chopping, disking, and shearing (Zhao et al., 2009). It is, however, a costly practice. More viable alternatives or complements to mechanical site preparation are chemical site preparation and post-plant vegetation control. Herbaceous and woody competition has negative impacts in loblolly pine development. They affect nutrient and water availability, moisture, and rooting volume (Shiver and Martin, 2002). Chemical herbicides can be used (with little soil disturbance) to reduce the influence of

competing vegetation on site resources, increasing overstory productivity (Martin and Jokela, 2004; Zhao et al., 2009).

Pienaar and Shiver (1993) reported that complete control of competing vegetation during plantation establishment doubled the yield of genetically improved 8-year-old loblolly pine stands. Colbert et al. (1990) observed that the effects of complete and sustained elimination of competing vegetation on productivity and stand development of juvenile loblolly pine stands in nutrient-impoverished sites could be similar to annual fertilization applications. In addition to increasing tree development and stand yield, control of competing vegetation alone can reduce tree mortality (Allen, 2001). However, the effects of chemical herbicide application will depend on the nature of the herbicide being used, as well as the intensity and frequency of applications.

Planting density

Research on the influence of initial planting density on tree growth and stand development has a long history (Sjolte-Jorgensen, 1967). Particularly, a considerable amount of experimental studies have been conducted on the responses of loblolly pine plantations in the southeastern US (Owens, 1974; Arnold, 1978; Harms and Loyd, 1981; Clutter et al., 1984; Buford, 1991). There is no single planting density optimal for all management objectives, as planting density will influence the quantity and quality of the wood material produced at final harvest (Amateis and Burkhart, 2012). Therefore, when choosing a planting density, it is critical to consider management objectives and products desired at the end of the rotation, as well as the implementation of silvicultural interventions during stand development, such as thinning (Amateis and Burkhart, 2012).

There are important tradeoffs related to stand densities. While lower planting densities contribute to increasing tree diameter, it reduces total, stand-level biomass production. On the other hand, higher planting densities result in smaller individual trees but greater stand level biomass production. Management plans focused on sawtimber production typically use a lower planting density while plans focused on biomass production generally use higher planting density. Thinning treatments can be applied to planted stands, reducing stand density, in order to increase resource availability (light, mineral nutrients, and water) to fewer trees. Thinning reduces total stand production (Burkhart and Amateis, 2012) However, it allows the early capture of economic values of harvested trees, improves the health and vigor of the remaining trees, and promotes diameter and volume growth, increasing trees potential to become high quality, valuable timber (Albaugh et al., 2017). In addition, silvicultural practices such as fertilization, weed control, and the deployment of advanced genotypes may change the appropriate spacing of plantations, as they tend to accelerate stand development, new genotypes with differing crown characteristics may compete for resources in different ways.

Clonal Forestry and Crown Ideotype

Another contributing factor for the increasing forest productivity in southern US, especially for loblolly pine, is the extensive research focused on selecting, breeding, and testing advanced genotypes that display desirable characteristics (Li et al., 1999). A great number of half-sib families (produced from open pollination, having one parent in common) and full-sib families (produced from control pollination, having both parents in common) that possess desirable traits has been made available (McKeand et al., 2006). In addition, technological advances in vegetative propagation has allowed the clonal multiplication of elite loblolly pine

genotypes (Bettinger et al., 2009). A few clonal populations used in experimental settings have been produced as rooted cuttings. Clones being deployed for production forestry are propagated entirely by somatic embryogenesis (Stoval let al., 2012). These genetically improved pines have shown to be more disease resistant than their unimproved genotypes (Schmidt, 2003) and yield between 20 and 40% more stem volume at rotation age (McKeand and Svensson, 1997; McKeand and Bridgwater, 1998). There are varying amounts of inherent genetic variation in open-pollinated, control pollinated, and clonal trees, with open pollinated trees having the greatest amount of genetic variation, and clones having the least. These differences allow land managers to balance the benefits and risks involved in the deployment of genotypes that are less diverse but potentially more productive (Bridgwater et al., 2005; Aspinwall et al., 2011).

The general premise is that clonal plantations will result in more uniform stand growth and development because clones possess less tree-to-tree variation (Bettinger et al., 2009). Aspinwall et al. (2011), however, observed the opposite when testing stand-level uniformity and biomass production in ten different juvenile loblolly pine genotypes. In their study, clones showed the least uniformity as well as the lower productivity, while some half-sib families and some full-sib families showed the most uniformity, and greater stand-level production. Increased resource-use efficiency and productivity, in addition to a reduced number of suppressed trees, can be achieved with greater stand uniformity (Nilsson and Allen, 2003; Stape et al., 2010; Aspinwall et al., 2011).

Significant variability exists among clonal varietals in terms of nutrient use efficiencies, stem form, internode length, growth rate, branch size and angle and crown characteristics. From a diversity standpoint, it is important to preserve and actually broaden the variability between genotypes in order to meet specific goals as well as challenges and opportunities in the future,

such as climate change, the occurrence of new pests and diseases, or the expansion to new ranges (Wright and Dougherty, 2007). As new clones are developed they need to be tested under a range of sites and silvicultural treatments to be effectively and efficiently evaluated, in order to identify the ones that are best suited for specific conditions, mitigate high costs involved in clonal development and deployment, and increase productivity and financial gain (Albaugh et al., 2016).

One possibility for screening clones and their response to silvicultural treatments is to work with the concept of ideotype. This concept was introduced by Dickmann (1985) to describe woody perennials grown on long rotations. An ideotype has a consistent set of properties or characteristics that tend to respond to management practices in a uniform and consistent manner. In forestry, it is defined by crown architecture, and includes characteristics such as number of branches, branch diameter and branch length, branch angle relative to the bole and tendency to self-prune (Martin et al., 2001).

Management objectives will determine the appropriate ideotype to plant in specific stands. Albaugh et al. (2016) observed that tree growth is related to crown volume, and that bigger crown would result in more stem volume on a given tree. That led them to suggest that trees with broad, large crowns may be desired in plantations with low stocking levels managed for sawtimber production, while trees with narrow crowns may be desired in highly stocked plantations designed for biomass production. McCrady and Jokela (1998) observed that discrepancies in branch and foliage biomass production, as well in other crown characteristics among open-pollinated loblolly pine families resulted in differences in stem volume production.

In a study conducted in Hawaii, Harms et al. (1994) proposed that the capacity of loblolly pine plantations to carry higher levels of stocking were related to the crown architecture of the

trees. Intermediate dominance stands had crowns that extended from the main canopy to below the live crown base of the dominant stand, increasing the occupancy of the canopy space with functioning leaf area (Harms et al., 2000). Albaugh et al. (2016) suggests that the use of crown ideotype to classify genotype response to silvicultural treatments and environmental conditions could reduce the need for empirical testing to predict responses of newly developed genotypes.

Carbon Allocation

By shifting carbon between above and belowground biomass, as well as between ephemeral and lasting tissues, carbon allocation is a major factor influencing forest ecosystem carbon cycling, and changes in allocation can significantly affect plant growth and carbon sequestration (Litton et al., 2007). The idea behind the carbon allocation theory is that plants allocate carbon to different components in order to optimize absorption of limiting resources, and maximize growth (Friend et al., 1994; Litton et al., 2007).

Carbon allocation terminology is inconsistent in the literature, and the term *carbon allocation* has been used to refer to flux of carbon to plant parts, to the distribution of flux as fraction of gross primary productivity, and/or to patterns in the amount of biomass in a given component (Litton et al., 2007). In order to standardize the vocabulary of carbon allocation for forest ecosystems, Litton et al. (2007) propose the terms *biomass* (the amount of material present), *flux* (the flow of carbon to a given component per unit time), and *partitioning* (the fraction of gross primary productivity used by a given component). They use the term carbon allocation as a general, overarching term that can refer to pattern (biomass) or process (flux and partitioning), or both. In this study, carbon allocation refers to patterns in biomass (live and nonliving tissues) and its distribution in different components (e.g. root:shoot).

Accurate estimates of biomass allocation to above and belowground are important to determine and understand differences in growth efficiency, ecosystem carbon balance, and carbon sequestration in root systems. (Albaugh et al., 2006; Stovall et al., 2012). This information could be used, for instance, to manipulate carbon allocation towards the aboveground portion of the trees in order to attain more efficient production, or towards the belowground portion if the main objective is to increase carbon sequestration.

Genetic, ontogenetic and environmental characteristics (nutrient and water availability, light levels, etc.) have strong influence on the relationship between above and belowground biomass (Retzlaff et al., 2001). According to Stovall et al. (2012), greater nutrient availability typically results in greater carbon allocation to woody perennial tissues and reduced root:shoot ratios. Retzlaff et al. (2001) suggests that as more nutrients become available, the carbon demand of root systems for fine root production and mycorrhizal colonization decreases, providing extra carbon for aboveground growth. Differences in allocation patterns have been observed between clonal genotypes and open-pollinated families (Barnes 2002; Tyree et al., 2009; Stovall et al., 2012). In addition, carbon allocation is probably highly constrained by ontogeny, and patterns in allocation may change with stand development and growth (Gedroc et al., 1996). Therefore, in order to determine if treatment effects are actually changing allocation and or simply altering growth rates, it is necessary to directly compare plants of similar size (Ledig et al., 1970), or to use statistical methods that can separate ontogenetic effects to treatment effects (King et al., 1999).

While the effects of silvicultural treatments and stand density on aboveground biomass are known, there is little information available regarding belowground carbon allocation, which is more difficult to quantify (Aspinwall et al., 2011). Root growth may be influenced by soil

physical and morphological characteristics of a given site (Parker and Van Lear 1996; Schenk and Jackson 2002), stand age (Adegbidi et al., 2002; Samuelson et al., 2004), and stocking (Litton et al., 2003; Russell et al., 2009). Root morphology may even be modified by wind stress, causing lateral roots to increase in number and size (Nicoll and Ray, 1996).

Trees in soils with low mechanical resistance tend to produce more root biomass relative to stem biomass compared to trees in soils with high mechanical resistance. In the same way, lower soil water potential tends to increase root:shoot ratio, compared to higher soil water potential (Albaugh et al., 2006). Schenk and Jackson (2002) observed greater rooting depths in sandy soils compared to loam and play soils, as well as greater depths in water-limited ecosystems. In poorly drained soils, roots stay shallow in order to avoid oxygen stress below the water table, while in well-drained soils roots follow infiltration depth (Fan et al., 2017). In a study established in a well-drained sandy soil, King et al. (2009) observed coarse roots penetrating the soil to depths of 4 m. They concluded that these deep roots are important for the uptake of water stored at greater depths, despite the fact they represent only a small fraction of total root biomass.

Albaugh et al. (2006) lists a variety of methods used to estimate coarse and fine root biomass, including the direct excavation of individual roots, excavation of roots found away from tree stumps, excavation using water or air, and soil coring, and warns that these methods may not be precise or consistent when quantifying roots in different conditions. Soil excavation may account for as little as 65% of total root mass (Le Goff and Ottorini, 2001) and another 20 to 40% of sampled root material could be lost during handling, washing and storage (Oliveira et al., 2000).

Whole-tree excavation demands great amount of time and resources, usually limiting the number of sampled individuals or the depth and area excavated around the tree, ultimately resulting in limited information on a stand level (Vogt and Persson, 1991). Nevertheless, it provides better estimates than soil cores on total root biomass, on proportions allocated to different classes (e.g., coarse roots, fine roots, etc.) and on the root distribution throughout the soil profile (Retzlaff et al., 2001).

Genetic x Management x Environment Interactions

The response of loblolly pine plantations to silvicultural intensity, genetic variability, and planting density are commonly reported in literature, but not many studies compare differences due to interactions among treatments and environmental conditions (Zhao et al., 2016). Information regarding site-specific responses can be very enlightening and help increase our understanding of factors affecting biomass production and allocation in loblolly pine plantations.

Albaugh et al. (2015) observed that response to fertilization in loblolly pine natural stands and plantations was influenced by soil texture and drainage. Zhao et al (2016) found that response to silvicultural treatments was dependent on site quality, in that lower quality sites showed more significant response to silvicultural intensity than higher quality sites. Litton et al. (2007) observed that changes in resource availability (due to irrigation and fertilization) within a site had significant effects on allocation to above versus belowground biomass. In addition, the range of changes in allocation across sites far exceeded the changes observed within a given site. They also found that competition (stand density) had a small effect on allocation to foliage and aboveground wood material, and that shifts in allocation were site specific.

Studying the combined effect of silvicultural intensity and planting density on seven open-pollinated loblolly pine families, in two locations, through age 5 years, Roth et al. (2007) observed significant genotype x site interaction, genotype x silvicultural intensity interaction, and silvicultural intensity x density interaction for basal area and standing stem volume.

McKeand et al. (2006) found that open-pollinated loblolly pine families are generally stable in performance across sites within a climatic zone, while Baltunes et al. (2008) observed high height variability in clones across sites. Similar results led Aspinwall et al.(2011) to suggest that loblolly pine genotypes with greater genetic variability (i.e. open-pollinated families) are more resistant to changes in environmental conditions, while genotypes with little or no genetic variability (i.e. clones) are more susceptible to environmental heterogeneity.

Significant interactions involving different genotypes, silvicultural treatments and environmental conditions emphasize the importance of understanding how elite genotypes respond to silvicultural treatments in association with site-specific conditions (Roth et al. 2007). Deployment and management strategies must be carefully considered in order to improve yield gain, and adjustments in silvicultural intensity and stand density with consideration of genetic and environmental conditions, could maximize growth rate and carbon sequestration (Zhao et al. 2016).

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CHAPTER 2: Effects of Silvicultural Intensity, Genetics, and Planting Density on Above and Belowground Carbon Allocation of Loblolly Pine (*Pinus taeda*)

Introduction

Concerns over the increasing levels of carbon dioxide (CO_2) emissions in the atmosphere have intensified the demand for climate mitigation and the interest to account for carbon credits (Cacho et al., 2005; Daigneault et al., 2010). Increasing the productivity of forest systems is a convenient and efficient way of capturing carbon from the atmosphere and reduce net emissions (Cacho et al., 2005). Pine plantations have been extremely successful in increasing productivity in the 1950's in southern United States making it the wood basket of the world (Fox et al., 2007b), and the most common and commercially important pine species in the region is Loblolly pine (*Pinus taeda* L.) (Harms et al., 2000).

Carbon accounts for about fifty percent of biomass, therefore accurate biomass estimates are necessary to improve carbon assessments in forest plantations at different locations and stages of development (Rubilar et al., 2010). Carbon accounting typically does not consider belowground sequestration in root systems (usually left behind at harvest), and only accounts for aboveground carbon sequestration. Adequate above and belowground biomass estimates can provide a better understanding of differences in growth efficiency associated to changes in carbon accumulation (Albaugh et al., 2006) and help develop better carbon sequestration models. Therefore, it is important to have a good understanding of allometric relationships and carbon allocation patterns in loblolly pine trees. The general hypothesis behind the carbon allocation theory is that plants will allocate carbon to specific organs in order to enhance capture of limiting resources, optimizing growth rate (Litton et al., 2007). Thus, allocation patterns are subject not

only to genetic and ontogenetic influences but also environmental ones, such as nutrient and water availability, light levels, growth regime, etc. (Retzlaff et al., 2001).

Fertilization and vegetation control increase nutrient availability, resulting in faster growth and greater stand development. It will also typically result in greater carbon allocation to woody perennial tissues and reduction of root:shoot ratio (Ingestad and Agren, 1991; Albaugh et al., 2006; Stovall et al., 2012). Decades of selection, breeding and testing of genotypes with desirable characteristics has generated a wide variety of full-sib and open-pollinated families that display considerable production levels over a range of sites and silvicultural conditions (McKeand et al., 2006; Aspinwall et al., 2011). There is, however, limited information concerning the effects of genetics on production and biomass allocation, especially belowground biomass, which is more difficult to quantify (Aspinwall et al., 2011). Chmura et al. (2007) observed that differences in productivity between different full-sib families of loblolly pine were associated with changes in biomass allocation patterns. Stovall et al. (2012) found significant differences in carbon allocation towards foliar, branch, bole and root material in 10 loblolly pine clones at age 6 in control and operationally fertilized plots in the Virginia Piedmont. The genetic control of biomass allocation to above and belowground components may affect the tree's capacity to compete for resources and endure environmental stress (Retzlaff et al., 2001).

In early stages of development, loblolly pine stand-level biomass production increases with increasing stand density, though not linearly (Burkes et al., 2003; Zhao et al., 2012). Stand density will also have an effect on carbon allocation. Zhao et al. (2012) observed a reduction in allocation to bole and bark and an increase in allocation to branches as stand density decreases. Studying allocation patterns over the first 25 years of loblolly pine stands, Sheldon (1984) found significant differences in biomass allocation to above and belowground tissues, especially during

early development, due to different planting densities. Aspinwall et al. (2011) observed that interaction between ten different loblolly pine genotypes and two levels of planting density had a significant effect on biomass accumulation and carbon allocation, suggesting that, as higher stand density accelerate tree-to-tree competition, genotype growth and allocation patterns are affected by genetic related sensitivity to competition.

Overall, our understanding of how carbon allocation in loblolly pine varies across different management intensities, genotypes and planting density is limited. Generally, studies investigating these differences, particularly with an emphasis on belowground components, are lacking (Retzlaff et al., 2001). Most studies relating loblolly pine and the effects of silvicultural intensity, genotype or stand density investigate these effects alone. A few (Aspinwall et al., 2011; Jokela & Martin, 2000; Stovall et al., 2012; Zhaoet al., 2012) were designed to study the effects of two of these treatments and their interaction on biomass production and allocation patterns. Moreover there are inconsistencies with regards to their effects, especially on carbon allocation (Zhao et al., 2012). The objective of this study was to evaluate biomass production and biomass allocation patterns of two loblolly pine genotypes with inherent genetic differences, managed under two levels of silvicultural intensity, planted at two initial stand densities, and the occurrence of genetic x management interactions, both at the individual tree and stand level.

Materials and Methods

Study site

The study was stablished in 2009 in the southeastern United States in the Coastal Plain of North Carolina at Bladen Lakes State Forest (34°49'50"N 78°35'18"W). From 2009 to 2016 the

average annual precipitation was 1144 mm yr^{-1} and the average daily maximum and minimum air temperature were 25°C and 9.5°C, respectively. The soils at the site are somewhat poorly to poorly drained Ultisols mapped as the Rains series (Fine-loamy, siliceous, semiactive, thermic Typic Paleaquults) (Vickers et al., 2012). The study site is approximately 21 hectares (51 acres) in size.

The study was installed as a split-split plot design with 3 replicates (Gomez and Gomez 1984). The main plot treatments are two levels of Silviculture (Low - "typical" operational and weed control versus High - no nutrient deficiencies and intensive weed control). The split-plot treatments (subplots) are six different loblolly pine genotypes (1 open pollinated, 1 mass control pollinated and 4 clones). The split-split-plot treatments (sub-subplots) are three initial planting densities (618, 1235 and 1853 trees ha^{-1}) (**Figure 2.1**). Therefore, the study has a total number of 108 plots, with 36 plots in each of the 3 replicates. Each sub-subplot had 63 trees in a 7 by 9 configuration (row by planting spacing, respectively). This allowed for a 5 by 5 internal measurement plot with additional rows functioning as buffers. Because of the differences in spacing, the size of each individual plot varies. The main plots (silvicultural intensity) were separated by large buffers with several planting rows (Vickers et al., 2012).

For this project, certain treatments were selected for biomass harvest: two of the three planting densities, 618 and 1853 trees ha^{-1} (250 and 750 trees ac^{-1}, respectively), and two of the 6 genetic entries, one of the clones and the open pollinated family. The result is a total of 24 plots (2 silvicultural levels x 2 genotypes x 2 stocking levels x 3 replicates) selected for destructive sampling.

Silvicultural intensity

The entire site (all treatments) was chemically prepared in the fall of 2008 with ground application of 11.69 L ha^{-1} of Krenite (active ingredient: amonium salt of fosamine 41.5%), 2.33 L ha^{-1} of Chopper (active ingredient: isopropylamine salt of imazapyr 27.6%) and 1.53 L ha^{-1} of Garlon XRT (active ingredient: triclopyr as butoxyethyl ester 83.9%) with 2.33 L ha^{-1} of methylated seed oil. The site was V-blade bedded using a Savannah plow, with a 3.65 m (12 ft) distance between the centers of the beds.

The "Low" level of Silviculture followed typical operational practices commonly used by landowners for the region in terms of weed control and fertilization. Low silviculture plots also received banded herbaceous weed control after planting (spring of 2009). It consisted of 0.29 L ha^{-1} of Arsenal AC (active ingredient: isopropylamine salt of imazapyr 53.1%) and 0.15 L ha^{-1} of Oust XP (active ingredient: sulfometuron methyl 56.25%). The "High" level of silvicultural intensity was designed to achieve near maximum growth for the existing soil and climate conditions of the site. The site preparation in high silviculture plots was followed by broadcast herbaceous weed control (0.29 liters of Arsenal AC and 0.15 liters of Oust XP in 94 liters of water per hectare) after planting and during the first two years (spring of 2009, 2010 and 2011). The plots in high silviculture received tip moth control (soil injection of fipronil at a rate of 1.5 ml per tree) after planting. These plots were fertilized with Arborite phosphate coated urea fertilizer (38.8% N and 3.9% P, with 0.12% B) one year after planting. Due to the differences in planting densities, this fertilization treatment was applied to individual trees at a rate of 0.24 kg $tree^{-1}$. A total of 57.31 kg ha^{-1} of elemental N and 5.76 kg ha^{-1} of elemental P were applied in high density plots, and 171.83 kg ha^{-1} of elemental N and 17.27 kg ha^{-1} of elemental P were applied in low density plots.

Genetic entries

Six different genetic entries were used as the subplots, including an open-pollinated family, a mass control pollinated family and four clones (**Table 2.1**). All the genetic entries were provided by ArborGen. All clonal seedlings were containerized, while control-pollinated and open-pollinated seedlings were bare-root stock. Among the genotypes in this study, clone 3 (GE34) and open pollinated family (AG89S) were selected for biomass harvest because they provided the widest range on crown size. Based on field measurements, clone 3 (C3) presented the narrowest crown while the open pollinated family (OP) presented the widest. Crown ideotype classification was based on measurements of the same genotypes planted in other trials, completed prior to the establishment of this study (**Table 2.1**).

Planting density

Three different planting densities were employed in this study. The lowest planting density is 618 trees ha^{-1} (250 trees ac^{-1}) is meant to represent a sawtimber regime, in which diameter growth is maximized. The medium planting density is 1235 trees ha^{-1} (500 trees ac^{-1}) represents a mixed product regime that includes both pulp and sawtimber production objectives. The high planting density is 1853 trees ha^{-1} (750 trees ac^{-1}) represents a biomass or pulpwood regime.

In all three planting densities the spacing between planting rows is 3.65 m (12 ft) while the distance between trees within the row varies. For the low, medium and high planting densities, the distances within rows are 4.42 m, 2.20 m and 1.48 m (14.5 ft, 7.26 ft and 4.84 ft), respectively. Prior to planting, planting spacing was measured and marked with pin flags. All seedlings were planted by hand. The two planting densities selected for biomass harvest, 618

trees ha^{-1} (250 trees ac^{-1}) and 1853 trees ha^{-1} (750 trees ac^{-1}), provided the widest range on stand density.

Data collection

Growth measurements were taken annually (from 2010 to 2017) in the dormant season (December to February) and included diameter at breast height (1.3 m), tree height, live crown height (height of the lowest branch with live foliage) and crown width (average of the across row and on row widths). Mortality and damage assessments were made on all trees in each plot.

A total of 24 trees (2 silvicultural levels x 2 genotypes x 2 stocking levels x 3 replicates) were destructively sampled in the months of February and March of 2017, one for each treatment type. Trees were divided into three size categories (small, medium and large) to cover the range of diameter and height at the site at the time of sampling. For each treatment combination each size group was randomly assigned to a replicate. Trees were than randomly selected from each size group, considering that trees were not damaged, and had a full complement of living neighbors.

Each sampled tree was measured for diameter at breast height (DBH), total height, live crown length and width, and the diameter and distance from the top of the tree of all live branches. All trees were cut at ground level. A total of 6 branches per tree were sampled and their branch wood and foliage collected. This generated 144 branch wood and 144 foliage samples. All remaining branches were cut from the stem as close to it as possible. The remaining boles were cut into smaller sections and their fresh weight was recorded.

The coarse root harvest included the root ball (taproot and all connected roots, limited to a 1 m^2 square centered on the stump) plus the roots sieved from soil in a 1 m^2 pit (0.5 m deep)

centered on the stump. In addition, 0.5 m wide and 0.5 m deep trenches extended from the edge of the pits to half the distance between tree rows (**Figure 2.2**) and coarse roots were sieved from soil as well. The size of the mesh screens used was 1.27 cm (0.5 in). Fine root biomass was sampled using 7 cm (2.75 in) cores. In low density plots, two locations halfway between rows, two locations between trees on the same row, and two locations approximately 91 cm (3 ft) from the tree along the row were randomly selected. In high density plots two locations halfway between rows, and two locations between trees on the same row were randomly selected. Cores were divided by three different depths, 0-10 cm, 10-20 cm, and 20-50 cm. After washed, roots were sorted into fine (diameter < 2 mm) and coarse (diameter > 2 mm) size classes. Roots from other species (present in stands with competing vegetation) were removed during the sifting process or after root material was washed in laboratory. All tissues (root material, branches, foliage, and bole sections) were oven dried at 65^{o}C to a constant weight to obtain standing-crop dry mass, hereinafter referred to as biomass, estimates.

Estimation of biomass production and allocation

The average amount of fine root biomass from the cores in each plot was scaled to the stand level. In order to estimate the amount of biomass in each of the other tree components for standing trees (foliage, branch, bole, and coarse root), models used in other allometry studies were tested in order to determine the one with the best fit for each of the tree components, including small variations or the same models used by Albaugh et al. (1998), King et al. (1999), Litton et al. (2003), Samuelson et al. (2004), Albaugh et al. (2006), and Russell et al. (2009). However, the model presented by Schumacher and Hall (1933) proved superior for all tree components.

A mixed model approach was applied to develop treatment-specific equations to estimate individual components. Branch-level regression equations were developed with data from the sampled branches. Branch diameter and distance from the top of the tree were used as predictor variables for branch and foliage biomass (Gillespie et al., 1994). The equations were applied to each branch (all branches had their diameter and distance from the top of the tree measured) on each of the 24 harvested trees and the results summed by tree for whole-tree branch wood and foliage biomass estimates. The estimates were used to develop regression equations predicting whole-tree branch wood and foliage, using tree DBH as predicted variable.

The root biomass in the trench was scaled to the total area occupied by the tree (subtracting the area of the pit) based on the initial planting density. Regression equations predicting whole-tree root biomass in the pit and in the area occupied by the tree were developed using DBH as predictor variable as tree height was not significant at an alpha level of 0.05, which has also been found in other studies (Albaugh et al., 1998; King et al., 1999). Whole-tree bole biomass regression equations were developed using DBH and tree height as predictor variables. Each plot represents a combination of treatments (silvicultural intensity, genotype and planting density). For any allometric equation, treatment effects were assigned to the intercept. These regression equations were of the form presented by Schumacher and Hall (1933):

$$ln(y) = (\beta_0 + t_i) + \beta_1 ln(d) + \beta_2 ln(h) + \mathcal{E}$$

and

$$ln(Y) = (\beta_0 + t_i) + \beta_1 ln(D) + \beta_2 ln(H) + \mathcal{E}$$

where *ln(y)* is the natural logarithm of one component biomass (individual branch wood or foliage in grams), *ln(d)* is the natural logarithm of branch diameter (cm), *ln(h)* is the natural logarithm of the branch distance from the top of the tree (m), *ln(Y)* is the natural logarithm of one

component biomass (whole-tree foliage, branch, bole or root material biomass in kilograms), *ln(D)* is the natural logarithm of tree DBH (cm), *ln(H)* is the natural logarithm of tree height (m), t_i is the effect to be estimated being assigned to the i^{th} treatment combination (**Table 2.2**), $\beta_{0\text{-}2}$ are fixed parameters to be estimated and $\mathcal{E}$ is the error associated with each observation. $\mathcal{E}$ ~N(0, σ^2) and t_i ~N(0, σ^2D).

Models were evaluated by examining the distribution and magnitude of the residuals for each variable (bole, root, branch and foliage biomass, at tree and branch level). Data points with values that were more than three standard deviations away from the mean were considered outliers. To determine goodness of fit of the models, absolute and relative biases (T), mean absolute error (MAE), root mean square errors (RMSEs), Akaike information criterion (AIC), and plots of observed versus estimated values were evaluated. Models with smaller values for these statistics were selected.

$$T = \frac{1}{n}\sum_{i=1}^{n}(Ob - Pr)$$

$$MAE = \frac{1}{n}\sum_{i=1}^{n}|Ob - Pr|$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(Pr - Ob)^2}{n}}$$

where, Pr is the predicted value, Ob is the observed value and n is the number of observations.

The regression equations developed were used to predict the total amount of root biomass in the area occupied by each tree, root biomass in the pit, bole wood, branch wood and foliage of all the trees in each plot. The results for all tree biomass variables (roots, bole, branch, and foliage) were averaged by plot and scaled up to a per hectare basis based on how many living trees were left in each plot.

ANOVA with a mixed effect model was used to analyze the effects of the different levels of silvicultural intensity, planting density and genotypes on biomass accumulation (at tree and stand-level) and allocation patterns. Silviculture, genotype, planting density, and all their interactions were treated as fixed effects. Analyses were conducted on individual biomass components (foliage, branch, bole, fine root, and coarse root), total aboveground biomass, whole-tree biomass, percentage of total biomass allocated in each component, and root:bole and root:shoot ratios. The linear model was:

$$Y_{ijk} = \mu + S_i + G_j + D_k + S_iG_j + S_iD_k + G_jD_k + S_iG_jD_k + \mathcal{E}_{ijk}$$

where Y_{ijk} is the observed amount of biomass on individual components (foliage, branch, bole, fine root, and coarse root), total aboveground biomass, whole-tree biomass, percentage of total biomass allocated in each component, and root:bole and root:shoot ratios. S_i is the effect of the i^{th} level of silviculture, G_j is the effect of the j^{th} genotype, D_k is the effect of the k^{th} planting density, S_iG_j is the silviculture x genotype effect, S_iD_k is the silviculture x genotype x density effect, G_jD_k is the genotype x density effect, $S_iG_jD_k$ is the silviculture x genotype x density effect. $\mathcal{E}$ is the error associated with the model. $\mathcal{E}_{ijk} \sim N(0, \sigma^2)$.

Tukey's Honestly Significant Difference (HSD) test was used to compare means at an alpha level of 0.05, but differences at the 0.05 to 0.1 level were also discussed. All statistical analyses were performed using RStudio (version 1.1.423, RStudio Inc., 2009-2018) and SAS Enterprise Guide 6.1 (SAS Institute Inc., Cary, NC, USA, 2013).

Results and Discussion

Different predictors were tested in the tree-level models of biomass in individual components, such as tree DBH, tree height, live crown length, and dominant height. The final models included DBH for coarse root, branch and foliage estimates, and DBH and height for bole estimates (**Table 2.3**). Diameter at breast height (DBH) was the most effective predictor of coarse root biomass. The relationship between tree DBH and coarse root biomass was nonlinear (**Figure 2.3**) and highly significant. The results of the statistics calculated to determine the accuracy of the predictions can be seen in **Table 2.4**. Plots of observed versus estimated values are shown in **Figure 2.4** for branch-level equations and in **Figure 2.5** for tree-level equations.

The analysis of the results for biomass accumulation was performed at a tree level and at a stand level. This allowed us to evaluate treatment effects on individual trees in comparison to the whole stand. It also allowed us to assess how changes in stand density due to mortality influenced biomass accumulation. Because fine root biomass was estimated from cores distributed around the plots and not related to the harvested trees, fine root analysis was performed only at the stand level. The amount of root biomass found in the trench was relatively small, but highly variable, ranging from 28 g m^{-2} to 2060 g m^{-2}, in trenches about 0.66 m^2 wide. Therefore, roots from trench samples were excluded from the analysis and only the 1 m^2 pit coarse root biomass and fine root biomass were included. Our results suggest that future root harvests should include a greater area for harvesting roots between tree rows.

Mortality

The mortality rate observed at the time of biomass harvest was 22% in the OP family and 5% in C3. The higher mortality rate was most likely due in part to the use of bare root seedlings

for the OP family as opposed to containerized seedlings in the C3 treatment. While initial planting densities were 1853 trees ha^{-1} (750 trees ac^{-1}) and 618 trees ha^{-1} (250 trees ac^{-1}) in high and low densities, respectively, the effective stand densities in the OP were reduced to 1675 trees ha^{-1} (678 trees ac^{-1}) and 424 trees ha^{-1} (172 trees ac^{-1}), and in C3 to 1779 trees ha^{-1} (720 trees ac^{-1}) and 585 trees ha^{-1} (237 trees ac^{-1}). Within the OP family, there was a considerable difference in survival due to the level of silviculture, and a statistical analysis of mortality shows an interaction between genotype and silviculture ($p = 0.0021$). Surprisingly, in high silviculture mortality was approximately 32%, while 11% in low silviculture for OP, while rates for C3 reached 7% in high silviculture and 3% in low silviculture. In high silviculture plots, the extra herbicide applied to the seedlings at year one and year two, which did not happen in low silviculture plots, may have caused herbicide damage. In high silviculture the OP effective stand densities were reduced to 1445 trees ha^{-1} (585 trees ac^{-1}) and 363 trees ha^{-1} (147 trees ac^{-1}) and in low silviculture to 1828 trees ha^{-1} (740 trees ac^{-1}) and 486 trees ha^{-1} (197 trees ac^{-1}). We also observed a significant interaction between genotype and planting density ($p = 0.001$), with higher mortality of OP trees in low density. The causes driving the higher mortality in low density are unclear.

Mortality may be affecting accumulation and allocation patterns due to creating variation in stand density, making it more difficult to evaluate treatment effects. The reduction in the number of trees due to mortality results in greater availability of resources such as nutrients, water and light. This will directly affect tree and stand-level biomass increment, generally with individual trees growing bigger but overall stand volume decreasing (Russell et al., 2009). Mortality also affects crown structure. At canopy closure, crowns grow upward since they can no longer expand outward due to self-shading (Albaugh et al., 2016). Extra space available due to

mortality allows for greater outward expansion of crowns and maintenance of live branches at lower heights, increasing canopy space occupancy with functioning leaf area (Harms et al., 2000). Because of the high mortality observed in OP, additional separate analyses were performed considering only C3 trees (removing the genotype treatment and transforming the study design into a split-plot).

Tree-level analysis

Clone and open pollinated family

No significant differences in bole biomass due to interactions between the level of silviculture, genotype and stand density were observed (p = 0.1348) (**Figure 2.6**). Although nutrition is often the primary limit to productivity in the southeastern US (Albaugh et al., 1998), no significant differences in bole biomass between the two levels of silviculture were observed (p = 0.1271). The lack of response to different levels of fertilization and weed control was surprising considering the low fertility characteristics of the soil where the study was established. However, it suggests that, at this stage in the stand development, soil supplies meet the trees demands for nutrients. Stand density was the most significant effect on bole biomass (p = 0.0055), with lower stand density increasing average bole biomass from 17.9 kg to 21.4 kg.

At the tree level, aboveground biomass (bole + branches + foliage biomass) was also greater in low stand density (**Figure 2.7**). There was an interaction between the level of silviculture and stand density at the p = 0.081 level. The amount of aboveground biomass is consistently greater in low stand density than in high stand density, regardless of silvicultural treatment. However, in high silviculture the differences in accumulation are more prominent than in low silviculture (42.5 kg vs. 29.3 kg for low vs high density, respectively in high silviculture,

and 27.5 kg vs. 20.4 kg for low vs high density, respectively in low silviculture). There was also an interaction (at the $p = 0.055$ level) between stand density and genotype. While there is no significant difference in aboveground biomass between genotypes in high stand density (about 25kg), OP yielded more biomass than C3 in low stand density (38.4 kg vs. 31.7 kg, respectively). This difference could be the effect of the high mortality in the OP family in low stand density, which reduced the competition among surviving trees. Studying stand density and genetic effects on tree growth and stand productivity of juvenile loblolly pine, Aspinwall et al. (2011) also observed that different genotypes (clones, full-sib families, and half-sib families) responded differently to stand density. They noted that full-sib families and half-sib families were more productive than clones, but the differences were more pronounced in higher stand density compared to lower stand density (110% and 82% increase, respectively, from the least productive genotype to the most productive one).

Low stand density also increased pit root biomass ($p = 0.0002$). There was a three-way interaction at a $p = 0.057$ level. The interactions were all due to magnitude rather than a rank change (**Figure 2.6**). In high silviculture, the amount of root biomass is higher, but there are no significant differences between the genotypes. In low silviculture, however, the difference in root biomass between the two levels of stand density is much greater for the OP genotype. Aspinwall et al. (2011) observed similar differences in woody root dry mass between open-pollinated families and clones in low stand density. In high stand density, however, the difference between the genotypes was greater than the estimates from our study, with some open-pollinated families producing almost twice as much as some clones.

The amount of root biomass found in the trenches, which we initially used to estimate root biomass between rows was highly variable. Therefore, belowground estimates at the tree

level consider only the root material harvested from the one m^2 square around each tree and underestimate total root allocation. As trees age and increase in size, the difficulty in extracting entire root systems also increases (Retzlaff et al., 2001). Friend et al. (1991) calculated that root mass recovery by direct excavation of 2-year-old hybrid poplar trees (*Populus deltoids x P. trichocarpa*) was around 60%. Comparing root material of 30-year-old beech trees (*Fagus sylvatica*) recovered after excavation and after meticulous sampling, Le Goff & Ottorini (2001) found that excavation recovered about 87% of root biomass, but could account for as little as 65%. In addition, another 20 to 40% of sampled root material could be lost during handling, washing and storage (Oliveira et al., 2000). However, based on tracing of lateral roots and tree canopy size of 5-year-old loblolly pine trees, Retzlaff et al. (2001) estimated that the amount of roots harvested inside one m^2 correspond to 85 to 90% of the total. Considering the amount of roots in the pit and in the trench, and the more advanced age of the trees in our study, we believe that the amount of root biomass harvested inside the one m^2 pit fall closer to the lower end of the range estimated by Retzlaff et al. (2001).

As with all tree components, stand density had an unsurprisingly significant effect on whole-tree (above and belowground) biomass at the tree level ($p = 0.0002$), with whole-tree biomass increasing in low density (41% increase). There was an interaction between genotype and stand density at the $p = 0.058$ level, suggesting that variation in standing dry mass among genotypes was primarily dependent on stand density. Whole-tree biomass yield in high stand density was the same for both genotypes, while OP had greater whole-tree biomass than C3 in low stand density (49.4 kg vs. 40.9 kg). Once again, we are uncertain if the difference in accumulation between genotypes is due to difference responses to density or to the high mortality seen in the OP family in low density. At the $p = 0.086$ level, high silviculture increased

whole-tree biomass by 52% (from 30.6 kg to 46.4 kg). The maximum whole-tree biomass accumulation was found in the OP family in high silviculture and low stand density (67.0 kg). This may also be due to the fact that this treatment had the highest mortality rate. The reduced competition in these treatments contributed to greater tree development, especially branches and foliage, which were considerably higher (**Figure 2.6**). The amount of branch and foliage biomass in this treatment was 46% and 91% greater, respectively, than branch and foliage biomass observed for C3 in high silviculture and low stand density, which was the treatment with the second highest amount of biomass for these tree components.

Clone only

Because of the high mortality observed in the OP family, we performed a separate analysis with only C3. In this analysis, all tree components (roots, boles, branches and foliage) showed substantial changes in accumulated biomass in response to the treatments at the tree level (**Table 2.5**). However, there were no significant differences in total biomass accumulation due to the interaction between stand density and the level of silviculture. Although less significant now compared to its effects considering both genotypes (**Table 2.5**), low stand density increased production of root biomass from 7.05 kg to 9.19 kg, branch biomass from 4.62 kg to 7.79 kg, and foliage biomass from 2.05 kg to 2.94 kg. Unsurprisingly, the differences in branch and foliage biomass due to stand density were the most significant (**Table 2.5**). While the low stand density generally increased the amount of bole biomass, the difference in accumulation was not significant at an alpha-level of 0.05 (p= 0.071). However, differences in aboveground and total biomass production were significant, despite the fact that at this stage of development bole accumulates considerably more biomass than other tree components.

High silviculture also increased accumulation in all tree components except for foliage (p = 0.06). Bole biomass increased from 15.18 kg to 24.13 kg, root biomass from 5.6 kg to 10.64 kg and branch biomass from 4.13 kg to 8.29 kg. As expected, high silviculture resulted in greater aboveground and total biomass accumulation. These results are in agreement with results found by (Zhao et al., 2012) who observed significant differences in bole, branches and total aboveground biomass, but not foliage biomass, between operational and intensive silvicultural treatments. McKeand et al. (1999) and Retzlaff et al. (2001) observed similar results when studying the effects of fertilization and genetics on loblolly pine whole-tree biomass and carbon allocation. In their studies, fertilization increased biomass accumulation of all tree components in all tested genotypes, more than doubling the amount of some of them.

These results highlight the confounding effects of the high mortality observed in the OP family. The reduced number of OP trees reduced the competition for nutrients, water and light. The increased availability of these resources might have allowed the tree's demands to be met, even in the low silviculture conditions. This reduced tree response to fertilization and the response to silvicultural treatments. The opposite can be observed when considering the effects of stand density. In low stand density there is greater availability of resources such as nutrients, water and light (wider spacing between trees and less trees per hectare). Higher levels of mortality within the OP family were observed in low stand density compared to C3, allowing the remaining trees to grow even bigger. As a result, the effect of stand density when considering both genotypes is more significant than when considering just the clone.

Stand-level analysis

Clone and open pollinated family

Silviculture had no effect on bole biomass, and aboveground and total biomass, which are composed mostly by bole, were also not affected by it. Silviculture affected branch ($p = 0.0647$), and foliage biomass ($p = 0.0942$). Branch biomass increased from 4.8 Mg ha^{-1} in low silviculture to 7.7 Mg ha^{-1} in high silviculture, while foliage biomass increased from 2.5 Mg ha^{-1} to 3.4 Mg ha^{-1}. Genotype had no effect on biomass accumulation in any of the components, except for foliage ($p = 0.0501$), with the OP family accumulating 23% more than C3 (3.2 Mg ha^{-1} and 2.6 Mg ha^{-1}, respectively). This increase in foliage accumulation can be attributed to the extra space and light available due to the high mortality observed in the OP family.

As expected, stand density was highly significant ($p < 0.001$) for biomass accumulation in all tree components at the stand level (**Table 2.6**). High stand density increased standing crop biomass due to the higher number of trees per hectare. The amount of bole biomass for high stand density was almost three times the amount for low stand density (30.7 Mg ha^{-1} and 10.7 Mg ha^{-1}). Aboveground biomass for high density was 42.7 Mg ha^{-1} and low density was 17.2 Mg ha^{-1}. The maximum aboveground biomass observed was 51.8 Mg ha^{-1} for C3 and 44.1 Mg ha^{-1} for OP in high stand density and high silviculture. King et al. (1999) reported similar maximum aboveground biomass (44 Mg ha^{-1}) in response to fertilization and irrigation in a loblolly pine plantation stocked at 1260 trees ha^{-1}. Samuelson et al. (2004) reported a maximum of 72.3 Mg ha^{-1} of aboveground biomass in 6-year-old loblolly pine trees from an open-pollinated family, which is considerably higher than the values observed in this study, but their most intensive silvicultural treatment included irrigation, annual doses of fertilization, and had a mortality rate of less than 5%.

There was an interaction for fine root biomass between silviculture and stand density. There was no difference in fine root biomass between the two densities in low silviculture (both densities yielded 1.2 Mg ha^{-1}). In high silviculture, fine root biomass increased from 1.1 Mg ha^{-1} in low density to 1.6 Mg ha^{-1} in high density. Across all treatments fine root biomass occupied between 2.5% and 6.1% of total stand biomass (**Figure 2.8**), in agreement with results found by Knight et al. (1994) which ranged from 3% to 7% in pine forests in general. The average amount of fine root biomass relative to total stand biomass was 3.9%, but as trees in this study continue to develop, this percentage should decrease to values close to what was reported by Van Lear and Kapeluck (1995), who found that fine roots represented 2% of total stand biomass in mature (48-year-old) loblolly pine plantations.

There was a significant interaction between the level of silviculture and stand density for coarse root biomass as sampled in the one m^2 pit. Naturally, root biomass is greater in high stand density, but the magnitude of the difference between the stand density levels is more prominent in high silviculture (**Figure 2.9**). In low silviculture, coarse root biomass increased from 4.2 Mg ha^{-1} in low density to 9.6 Mg ha^{-1} in high density. In high silviculture it increased from 5.8 Mg ha^{-1} in low density to 14.5 Mg ha^{-1} in high density. There was also an interaction between the level of silviculture and genotype ($p = 0.0518$). There was no difference in coarse root biomass for OP between the two levels of silviculture, but C3 yielded almost twice as much biomass in high silviculture compared to low silviculture. McKeand et al. (1999) and Retzlaff et al. (2001) found that fertilization increased stand level coarse and fine root biomass in fast- and slow-growing families from two provenances of loblolly pine at age 5 planted at very infertile excessively drained sandy soils. However, they reported no significant interaction between silviculture and genetic origin, with fertilizer additions having similar responses across families.

Comparing stand- and tree-level biomass accumulated in each component, we observe the most significant differences in the treatments with high mortality rates, especially OP family in low density and high silviculture. While OP in low density and high silviculture showed the second highest values in biomass accumulation in bole and coarse roots at the tree level, it showed to lowest values for the same components at the stand level. Since mortality is accounted for when analyzing stand-level production, and mortality rates were different not only among genotypes but also among levels of silvicultural intensity and planting density, it may have confounded treatment effects on biomass accumulation. Therefore, we performed the same analysis on C3 alone.

Clone only

A separate analysis without the OP family (due to its high mortality) showed that, at a stand level, the level of silviculture intensity and stand density were significant factors influencing all considered variables (**Table 2.6**), with high silviculture and high stand density resulting in greater biomass yield.

In response to high silviculture, bole biomass increased to 26.3 Mg ha^{-1} compared to 19.3 Mg ha^{-1} in low silviculture. Aboveground biomass increased to 37.7 Mg ha^{-1} compared to 24.9 Mg ha^{-1} in low silviculture (51% increase), with branch biomass increasing from 4.4 Mg ha^{-1} to 8.2 Mg ha^{-1} (86%). Foliage biomass showed a silviculture by stand density interaction (p = 0.0055) where for low stand density, the amount of foliage between high and low silviculture was not different, but for high density, high silviculture resulted in 131% more foliage (4.4 Mg ha^{-1}) than low silviculture (1.9 Mg ha^{-1}). The amount of root biomass was 73% higher in high silviculture (11.3 Mg ha^{-1}) than in low silviculture (6.5 Mg ha^{-1}). Total stand biomass was

increased by 56% from 31.4 Mg ha^{-1} in low silviculture to 49.1 Mg ha^{-1} in high silviculture. Stovall et al. (2012) also observed significant increases in root, branch, and foliage biomass due to fertilization and weed control in plots of 6-year-old loblolly pine clones, but no significant differences in bole biomass. Samuelson et al. (2004) reported similar increases in root biomass accumulation (70%) and more prominent increases aboveground biomass (94%) due to fertilization, vegetation control and irrigation.

As expected, stand density effects were highly significant. Bole biomass increased from 12.3 Mg ha^{-1} in low density to 32.4 Mg ha^{-1} in high density stands. Aboveground biomass increased from 18.6 Mg ha^{-1} in low density to 44.1 Mg ha^{-1} in high density stands. Root biomass accumulation also increased from 5.4 Mg ha^{-1} to 12.4 Mg ha^{-1} from low to high density stands. Total biomass more than doubled in high stand density compared to low stand density (56.5 Mg ha^{-1} and 24 Mg ha^{-1}, respectively). Similarly, testing the effects of stand density on 12-year-old-loblolly pine plantations in the Upper Coastal Plain and Piedmont of the southeastern United States, Zhao et al. (2012) observed significant differences in bole and total aboveground biomass. In their study, biomass accumulation was not statistically different between all six planting densities tested (ranging from 741 to 4448 trees ha^{-1}), but increased significantly (although not proportionally) as planting density changed from the lowest (741 trees ha^{-1}) to intermediate (1483 and 2224 trees ha^{-1}) to the highest densities (2965, 3706, and 4448 trees ha^{-1}). In our study, the amount of bole biomass in high stand density was 2.6 times greater than in low stand density, which is close to the three times greater number of trees planted in the high density stands. This indicates that the trees have recently began competing with each other. The difference in the amount of whole-tree biomass was less substantial, 2.3 times greater in high stand density compared to low stand density. This was primarily due to the effect of competition

on crown biomass (branch + foliage), which was only 1.8 times greater in high stand density. The magnitude of the difference in root biomass when comparing stand density levels was slightly smaller than the difference observed in whole-tree biomass. This suggests not only the occurrence of competition but also that roots could have been underestimated due to the inherent difficulties in belowground estimation techniques.

Biomass allocation

There was a three-way interaction for bole:whole-tree biomass ratio (**Figure 2.11**, **Table 2.7**). Bole:whole-tree ratio was always higher with high density compared to low density, but the magnitude of the difference varies with genotype and silviculture. This result was not surprising in that although a wide spacing results in larger diameter boles and more bole biomass at a tree level, it also allows the tree to develop much wider and longer crowns. The greatest difference in bole:whole-tree ratio between the two densities was found in the OP family in high silviculture. Bole:whole-tree ratios ranged from 0.39 to 0.58. The greatest ratio was observed for C3 in low silviculture and high stand density. The lowest ratio was observed for the OP family in high silviculture and low stand density, and it was significantly smaller than all the others. This might be explained by the high mortality rate observed for the OP family in high silviculture and low stand density, and the high biomass accumulation found in branches and foliage.

Comparing root:bole ratios, we observed an interaction between silviculture and stand density with changes in slope. Root:bole ratios are higher in low density regardless of silvicultural treatment, but the magnitude of the difference is more pronounced in low silviculture. In high silviculture, the ratio goes from 0.49 in high density to 0.59 in low density, whereas in low silviculture it goes from 0.40 in high density to 0.57 in low density. There was

also an interaction between genotype and density. Once again, root:bole ratios are higher in low density regardless of genotype, but the difference is more significant in the OP family. The ratio increased from 0.43 in high density to 0.53 in low density for the C3 and from 0.46 to 0.64 for OP. Across all treatments, root:bole ratio was approximately 0.44 (**Figure 2.12**). These results do not support the general perception that increased availability of nutrients would result in decreased biomass allocation to roots relative to shoots. Measuring root and stem biomass at three sites with varying soil texture, genetic makeup, environmental conditions, and stand densities (between 990 and 1650 trees ha^{-1}), Albaugh et al. (2006) found a root:bole ratio of about 0.5 (33% root and 67% shoot), though in this case "root" consisted of coarse root biomass inside and outside the square meter centered on the tree stump (down to 0.5 m into the soil). Considering that the amount of fine root biomass is less than coarse root outside the square meter, including fine roots while removing coarse roots outside the square meter to their estimates would reduce belowground mass pool, resulting in a smaller numerator and consequently a smaller root:bole ratio.

Analyzing root:shoot ratios (root meaning coarse roots and fine roots, and shoot meaning aboveground biomass) we observed a three-way interaction (**Figure 2.11**, **Table 2.7**). In high silviculture there are no significant differences in the ratio, regardless of genotype and stand density. The average root:shoot ratio in high silviculture was 0.34 (about 25% root and 75% shoot). In low silviculture the ratios for both genotypes in high stand density is the same, 0.29, but in low stand density, the root:shoot ratio for C3 increases to 0.34 while the ratio for the OP family increases to 0.40. The lower ratio observed for both genotypes in low silviculture and low density was the opposite result from what we expected to find. The higher ratio observed for the OP family in low silviculture and low stand density was due primarily to its substantial coarse

root biomass production (although its biomass accumulation was high for all other tree components, it was more significant for coarse roots).

Root:shoot ratios ranged from 0.29 to 0.40. Across all treatments root:shoot ratio was approximately 0.32 (about 24% root biomass and 76 % shoot biomass) (**Figure 2.12**). Retzlaff et al. (2001) suggested that the root:shoot ratio in loblolly pine is around 0.43, which represent 30% root and 70% shoot (with shoot including bole, branch and foliage biomass). In their study trees were 5 years old (juvenile) but the stand density was approximately 3330 trees ha^{-1} (1.5 x 2 m spacing), which is much higher than both densities tested in our study. The higher stand density might have suppressed crown development and allocation towards branches and foliage. The higher stand density, however, might not be enough to explain the ratio differences observed between their study and ours, considering how much more biomass is found in the bole compared to the crown. Although their study was stablished in a droughty, very infertile site, and fertilization substantially increased total amount of biomass in all measured tree components, they observed no significant effect of fertilization on biomass allocation.

Samuelson et al. (2004) reported root:shoot ratios ranging from 0.40 to 0.47 in a study with 6-year old loblolly pine stands under different management intensities. Their study was established in a low fertility soil where annual doses of fertigation (addition of fertilizer solution to irrigation water) were applied from May to October. Although fertigation greatly accelerated stand development and biomass accumulation, it had no effect the amounts root biomass relative to shoot biomass. Allocation within different compartments of aboveground biomass (bole, branches and foliage) also had no response to silvicultural intensity. Annual measurements revealed greater allocation to branches and foliage than bole at younger ages (3 and 4 yr), in contrast to greater allocation to bole than branches and foliage at older ages (5 and 6 yr), but

within any given year there were no differences in allocation to these components due to treatments.

Ovington (1957) observed that the relative biomass allocation among tree components changes as trees increase in size, indicating that allocation patterns change throughout the life of the tree. Studying chronosequence data from *Pinus sylvestris* plantations he found that maximum root:shoot ratios were reached around age 7 and then declined over the life of the stand. Ontogenetically, our stands seem to be in the stage of decreasing root:shoot ratio, and that could help explain the lower ratios found in this study. King et al. (1999) suggests that accelerated growth caused by fertilization may alter allometry in loblolly pine simply because they increase plant size, and that fertilization slightly reduces the rate at which root:shoot ratio decline occurs. King et al. (1999) reported a small but significant increase in perennial root tissue relative to perennial aboveground tissue (bole and branches) as a result of fertilization. They observed that root:shoot ratios of 8-year-old loblolly pine trees increased from about 0.32 in control plots to about 0.36 in fertilized plots. In addition, they found that, at age 10, the ratios were slightly smaller, 0.30 in control plots and 0.35 in fertilized plots, which supports the idea that carbon allocation is constrained by ontogeny, as root:shoot ratios tend to decrease as trees continue to develop.

Our results show a shift in allocation towards belowground biomass at the expense of aboveground biomass as a result of low stand density. Once again these results are contrary to the general idea that ratios would be greater (i.e. greater allocation to belowground biomass) in high density stands due to reduced nutrient availability caused by greater competition among crop trees. In addition, if shifts in biomass allocation towards roots was driven primarily by reduced nutrient availability, we would have seen a more significant silvicultural effect, which

was not the case. The differences in allocation to aboveground versus belowground biomass between the two densities are due primarily to competition happening aboveground. In high density, trees are considerably closer together, which resulted in canopy closure happening much sooner than in low density (**Figure 2.13**). As the canopy closure process takes place, light becomes the main resource limiting development, and trees compete for light more than they compete for soil nutrients or water. To better compete for light, trees allocate a greater percentage of the biomass being produced to aboveground tissues in detriment of belowground tissues. Furthermore, our estimates show that coarse root biomass is strongly correlated to DBH. DBH is highly affected by stand density, increasing as planting density decreases (Harms et al., 2000; Zhao et al., 2012). In a review study, Litton et al. (2007) analyzed the effects of stand density (among other treatments) on carbon allocation patterns in different species of pine and eucalyptus. They concluded that intraspecific competition (stand density) had no large or consistent effect on allocation patterns. Shifts in allocation to wood (bole and branches) and foliage were site specific, showing both small increases and decreases, while allocation to roots varied minimally with competition. In contrast with our results, higher root:shoot ratios as a result of higher stand density have been reported for lodgepole pine (Litton et al., 2003) and red pine (King et al., 2007). Russell et al. (2009) also observed an increase in root:shoot ratio with increasing planting density for 5- and 6-year-old loblolly pine trees at eight planting densities in a miniature-scale spacing trial, though the range of planting densities were far superior to the densities in this study.

Aspinwall et al. (2011) found root:shoot ratios between 0.25 and 0.33 (20% root and 80% and shoot and 25% root and 75% shoot, respectively), which are slightly smaller than the results observed in this study. The lower ratios found by them may be due to the lower planting

densities tested (~540 and ~1075 trees ha^{-1}) compared to our study (618 and 1853 trees ha^{-1}), which contributes to greater allocation to branches and foliage, increasing total aboveground (shoot) biomass and reducing the ratios. Studying 10 different genotypes divided between clones, open-pollinated families and control-pollinated families, Aspinwall et al. (2011) observed small but statistically significant differences in biomass partitioning to bole, branches, foliage and tap root among the genetic entries. Our results also show the effect of genotype, and its interaction with silviculture and stand density, on allocation patterns, with significant differences in root:bole and root:shoot ratios between the two genotypes. We must consider, however, the high mortality rate observed in the OP family and its cofounding effects. It is affecting not only biomass accumulation, but also biomass allocation patterns. These results, therefore, must be interpreted with caution.

Performing the same analysis without the OP family, we observed very similar results for bole:whole-tree ratio. When considering just C3, there were significant differences in bole:whole-tree biomass ratio due to the level of silviculture by stand density interaction (p = 0.0104). The lowest ratios were found in low stand density and are not statistically different between the levels of silviculture (0.49 in high silviculture and 0.50 in low silviculture). Both ratios increase in high stand density, although more significantly in low silviculture, changing to 0.54 in high silviculture and 0.59 in low silviculture.

Contrary to the results from the analysis with both genotypes, there was no interaction between silviculture and stand density for root:bole or root:shoot ratios, and while silviculture was not significant, stand density continued to have an effect on both ratios (**Table 2.7**). Root:bole ratio increased from 0.43 in high density to 0.53 in low density, a 23% increase, while root:shoot ratio increased from 0.31 in high density to 0.35, a 13% increase. These results show

how density is the main factor driving changes in allocation. In addition, it indicates that the influence of silvicultural treatments in root:bole and root:shoot ratios when considering both genotypes is due to the high mortality seen in the OP family in high silviculture.

Management Implications

Overall, the management implications for our results show that different objectives for biomass or carbon sequestration can be met in different ways. However, we must first consider the effect of mortality on biomass production. Our results emphasize the importance of using appropriate methods for producing and planting loblolly pine seedlings, and its effect on plant survival. It also highlights the importance of adequate control of competing vegetation. While insufficient herbicide application limits vegetation control, too much herbicide may damage seedlings and lead to high mortality.

Intensive fertilization and vegetation control are often applied in order to increase plantation tree development. Lower stand densities are regularly planted to maximize sawtimber production, because the extra space provided by a lower stand density increases diameter growth. Although the extra space results in bigger branches (and pruning might be necessary), individual bole size increases significantly. Our results confirm these ideas, with both genotypes producing more individual bole biomass in low density and high silviculture. Therefore, if the management objective is to maximize individual tree production of bole biomass for sawtimber, low density and high silviculture is the best treatment. On the other hand, if the management objective is to optimize total biomass production for bioenergy, individual tree diameter is of little importance. When managing for bioenergy, all aboveground biomass is considered, and planting density

must be high. Although individual tree development is limited, total aboveground stand biomass is greater.

As observed in our results, loblolly pine plantations, especially when intensively managed, have great potential to be a carbon sequestration mechanism on both above and belowground. These plantations can be highly responsive to planting density as well as silvicultural intensity, having the potential to achieve high rates of carbon stocks when aimed at carbon sequestration. Generally, tree biomass is considered to consist of fifty percent carbon, but forest carbon accounting often does not consider belowground biomass. In loblolly pine plantations aiming at long-term carbon sequestration, carbon storage can be accounted from whole-tree biomass (if trees are left for use as carbon sink) or from belowground biomass (if aboveground material is harvested). Similar to when managing for biomass production, individual tree size is not important, but total stand-level biomass must be maximized, and planting density is high. Considering the treatments tested in this study, high density and high silviculture yield more root biomass. Although silvicultural intensity had no effect on stand level whole-tree biomass (likely due to confounding effects of mortality), the analysis with just the clonal material shows that high silviculture increases biomass accumulation and, as a result, carbon sequestration.

The effects of silviculture and planting density on aboveground growth are well known. However, little is known about how these treatments (and their interaction) affect belowground biomass accumulation and allocation. Our results provide better understanding of how silviculture and planting density affect the relationship between above and belowground components, which can be used to develop better carbon sequestration models. Furthermore, the low and high densities tested in this study are frequently employed in sawtimber regimes and

biomass or pulpwood regimes, respectively, and the silvicultural treatments, especially low silviculture (operational), are also commonly used by landowners in the region. The information generated in this study regarding above and belowground allocation patterns under these treatments can be applied to similar stands in order to estimate belowground biomass from aboveground biomass, and better estimate total carbon budget.

Conclusions

The results of this study show that easily obtained tree measurements can be useful for estimating above and belowground biomass accumulation. This is especially true for tree DBH, due to its strong relationship with belowground biomass. This information could be used to evaluate production efficiency (aboveground) or carbon sequestration (belowground).

Changes in resource availability due to silvicultural intensity had significant effects on biomass accumulation and allocation. Increased fertilization and vegetation control resulted in more biomass allocated to roots and less allocated to shoots. These results are not consistent with the idea that increased nutrient availability will decrease root systems carbon demand, resulting in decreased root:shoot ratios.

The genotypes showed differences in biomass accumulation and allocation patterns in response to silviculture and planting density. The different responses to these treatments from the open pollinated family and the clone indicate that different genotypes may have fundamentally different capacities to respond to nutrient availability and stand density, although mortality might have confounded some treatment effects. As new and highly productive genotypes become

available, it is important to understand how silvicultural treatments and stand density might affect their development.

Planting density had the most significant effect on biomass accumulation and allocation patterns of loblolly pine. It is common knowledge that high planting densities yield smaller diameter trees but more total stand volume, while low planting densities yield less total stand volume but trees with larger DBH. This variation in biomass accumulation and allocation influences capacity at the stand level to generate forest products such as sawtimber, chip-and-saw, pulpwood and residuals used for energy. This study offers insight into the mechanisms that control belowground growth and allocation, and how they are affected by silviculture and planting density. Our results provide a better understanding of how trees grow as a whole, and how these treatments influence belowground carbon sequestration and total carbon budget. Understanding this influence will allow for better assessment of traditional forest products and biomass for carbon credit markets.

It is important to consider that changes in allocation patterns can be greatly affected by the ontogenetic development of the trees, as ontogenetic effects could confound direct treatment effects. In addition, further research with greater number of genotypes, across a variety of different sites is necessary to validate conclusions drawn from this study. Nonetheless, considering the economic as well as the ecosystem importance of loblolly pine, the results observed in this study highlight the importance of understanding how above and belowground biomass accumulation and allocation patterns are affected by different silvicultural intensities, genetics, planting densities, and their interactions, in order to optimize forest management, accurately model carbon dynamics and estimate belowground carbon stocks, and improve the sustainability of forest ecosystems.

Table 2.1 Genetic sources, family ID and crown ideotypes of the genetic sources in the block plot plantings.

Genetic Source	Color of Plot	Arborgen Family or Variety ID	Crown Ideotype
Open Pollinated (OP)	White	AG89S	Broad
Mass Control Pollinated (MCP)	Pink	AGM20	Moderate +
Clone 1	Orange	PM212	Moderate –
Clone 2	Yellow	NQ26	Moderate –
Clone 3	Blue	GE34	Narrow
Clone 4	Green	PT1056	Moderate +

Table 2.2 Estimates assigned to the mean in regression equations predicting branch and foliage biomass at the branch level and in regression equations predicting branch, foliage, bole and root biomass at the tree level.

Treatment			Coefficients					
			Branch-Level		Tree-Level			
			Branch	Foliage	Branch	Foliage	Bole	Root
High Silviculture	C3	High Density	-0.030	-0.057	-0.077	-0.130	-0.014	0.075
		Low Density	-0.026	-0.114	-0.105	-0.269	-0.044	-0.067
	OP	High Density	0.081	0.066	-0.165	0.037	-0.013	0.020
		Low Density	-0.017	0.044	0.326	0.406	-0.021	-0.054
Low Silviculture	C3	High Density	0.031	-0.055	-0.076	-0.284	0.023	-0.016
		Low Density	-0.057	-0.042	0.143	0.152	0.078	0.008
	OP	High Density	0.011	0.118	-0.095	0.117	0.018	-0.033
		Low Density	0.008	0.040	0.049	-0.030	-0.027	0.066

Table 2.3 Estimates and standard errors of parameters for branch- and tree-level models, with natural log transformed independent variables for branch diameter (bdia), branch distance to the top of the tree (distop), tree diameter at breast height (dbh), and tree height (ht). All parameters are significant at $p < 0.001$.

	Branch		Foliage		Root		Bole	
	Value	Std. Error	Value	Std. Error	Value	Std. Error	Value	Std. Error
Branch-level								
Intercept	-4.739	0.169	-4.993	0.499				
Ln(bdia)	2.714	0.054	2.223	0.081				
Ln(distop)	0.245	0.042	0.744	0.115				
Tree-level								
Intercept	-6.634	0.302	-4.018	0.225	-4.246	0.207	-3.947	0.069
Ln(dbh)	3.265	0.110	1.975	0.079	2.457	0.078	1.857	0.053
Ln(ht)	-	-	-	-	-	-	1.012	0.075

Table 2.4 Metrics used to measure accuracy of prediction of models based on mean absolute error (MAE) and root mean square error (RMSE). The bottom row (Max) refers to the maximum amount of biomass observed for each of the components, in grams for branch-level and kilograms for tree-level.

	Branch-level		Tree-level			
	Branch	Foliage	Bole	Root	Branch	Foliage
Bias (%)	-2.50	-5.60	-0.76	-0.82	-1.07	-0.41
MAE	38.76	17.01	1.22	1.23	1.68	0.28
RMSE	110.59	28.96	2.94	1.64	2.95	0.41
Max	2015.30	487.14	78.99	34.31	41.54	10.46

Table 2.5 P-values (P > F) from ANOVA for biomass accumulation for branch, foliage, bole, roots, aboveground (branch + foliage + bole), and total (whole tree), at the **tree level**, considering both genotypes and considering just the clone.

Effect	**Pr > F**					
OP and C3	**Branch**	**Foliage**	**Bole**	**Coarse Root**	**Aboveground**	**Total**
S[a]	0.0547	0.0571	0.1271	0.0721	0.0914	0.0865
G[b]	**0.0361**	**0.0067**	0.9628	0.1586	0.1904	0.1824
D[c]	**0.0001**	**<.0001**	**0.0055**	**0.0002**	**0.0002**	**0.0002**
S x G	0.8056	0.0803	0.1196	0.0881	0.3769	0.2766
S x D	**0.019**	**0.019**	0.4729	0.8064	0.0814	0.1412
G x D	**0.0132**	0.0127	0.3674	0.0794	0.0549	0.0582
S x G x D	0.4156	**0.0023**	0.1348	0.0569	0.8864	0.5628
C3	**Branch**	**Foliage**	**Bole**	**Coarse Root**	**Aboveground**	**Total**
S	**0.0355**	0.0629	**0.0313**	**0.0223**	**0.034**	**0.0307**
D	**0.0053**	**0.0042**	0.071	**0.0135**	**0.0184**	**0.0171**
S x D	0.0778	0.1658	0.109	0.1054	0.1299	0.1238

[a] Main-plot treatment factors: High silviculture or low silviculture.

[b] Subplot factors: Open pollinated family (OP) or clone (C3).

[c] Sub-subplot factors: High planting density or low planting density. In the analysis without the OP family planting densities become the subplot factors.

Table 2.6 P-values (P > F) from ANOVA for biomass accumulation for branch, foliage, bole, roots, aboveground (branch + foliage + bole), and total (whole tree), at the **stand level**, considering both genotypes and considering just the clone.

Effect	**Pr > F**					
OP and C3	**Branch**	**Foliage**	**Bole**	**Coarse Root**	**Aboveground**	**Total**
S[a]	0.0647	0.0942	0.2086	0.0657	0.1411	0.1182
G[b]	0.8621	0.0501	0.193	0.3272	0.3907	0.3768
D[c]	**0.0002**	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
S x G	0.1562	0.4718	0.142	0.0518	0.1532	0.1248
S x D	0.4249	0.3097	0.4905	**0.0411**	0.4542	0.3076
G x D	0.5710	0.1313	0.9705	0.9426	0.9943	0.9942
S x G x D	0.9562	0.1513	0.8932	0.5336	0.9724	0.9273

C3	**Branch**	**Foliage**	**Bole**	**Coarse Root**	**Aboveground**	**Total**
S	**0.0005**	**0.0006**	**0.0114**	**0.0003**	**0.0043**	**0.0025**
D	**0.0007**	**<.0001**	**0.0001**	**<.0001**	**0.0001**	**<.0001**
S x D	0.3894	**0.0055**	0.5697	0.1143	0.4162	0.3315

[a] Main-plot treatment factors: High silviculture or low silviculture.

[b] Subplot factors: Open pollinated family (OP) or clone (C3).

[c] Sub-subplot factors: High planting density or low planting density. In the analysis without the OP family planting densities become the subplot factors.

Table 2.7 P-values (P > F) from ANOVA for bole biomass to whole-tree biomass, root biomass to shoot biomass, and root biomass to bole biomass ratios, where "root" equals coarse roots plus fine roots, and "shoot" equals aboveground (branch, foliage, and bole).

Effect	**Pr > F**		
OP and C3	**Bole:Whole-tree**	**Root:Shoot**	**Root:Bole**
S[a]	**<.0001**	0.4268	0.0797
G[b]	**<.0001**	0.1006	**0.0001**
D[c]	**<.0001**	**0.0001**	**<.0001**
S x G	**0.0153**	0.0518	0.8915
S x D	0.3434	**0.0005**	**0.0153**
G x D	**0.0004**	0.4487	**0.0076**
S x G x D	**0.0019**	**0.0139**	0.6809

C3	**Bole:Total**	**Root:Shoot**	**Root:Bole**
S	**0.0012**	0.2019	0.1117
D	**<.0001**	**0.0303**	**0.0044**
S x D	**0.0104**	0.2540	0.1774

[a] Main-plot treatment factors: High silviculture or low silviculture.

[b] Subplot factors: Open pollinated family (OP) or clone (C3).

[c] Sub-subplot factors: High planting density or low planting density. In the analysis without the OP family planting densities become the subplot factors.

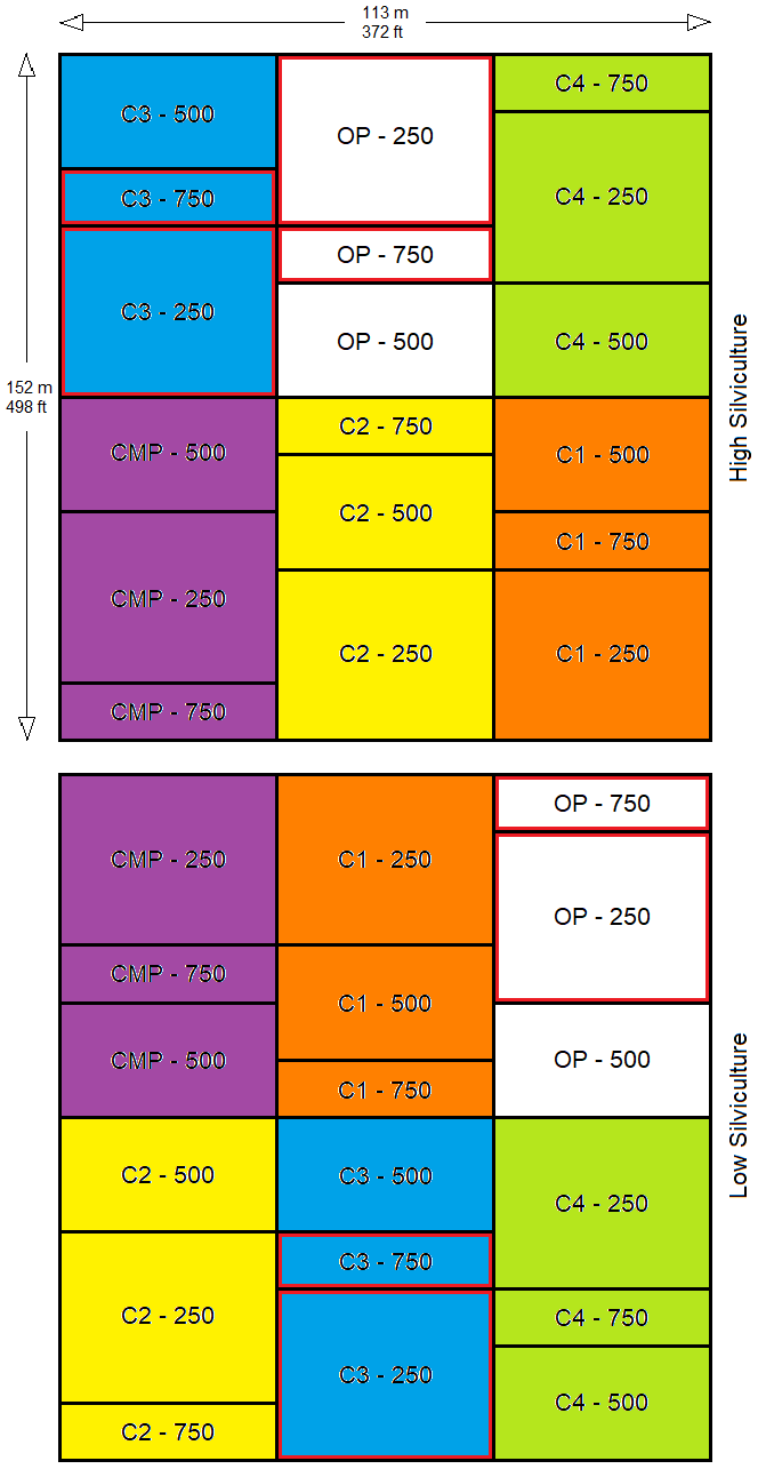

Figure 2.1 Layout of three different planting densities, 618 trees ha^{-1} (250 trees ac^{-1}); 1235 trees ha^{-1} (500 trees ac^{-1}) and 1853 trees ha^{-1} (750 trees ac^{-1}), and six genetic entries (OP = open-pollinated family; CMP = control mass-pollinated family; C = clone) a at two levels of silvicultural intensity (figure represents one replicate). Treatments selected for biomass harvest are highlighted in red.

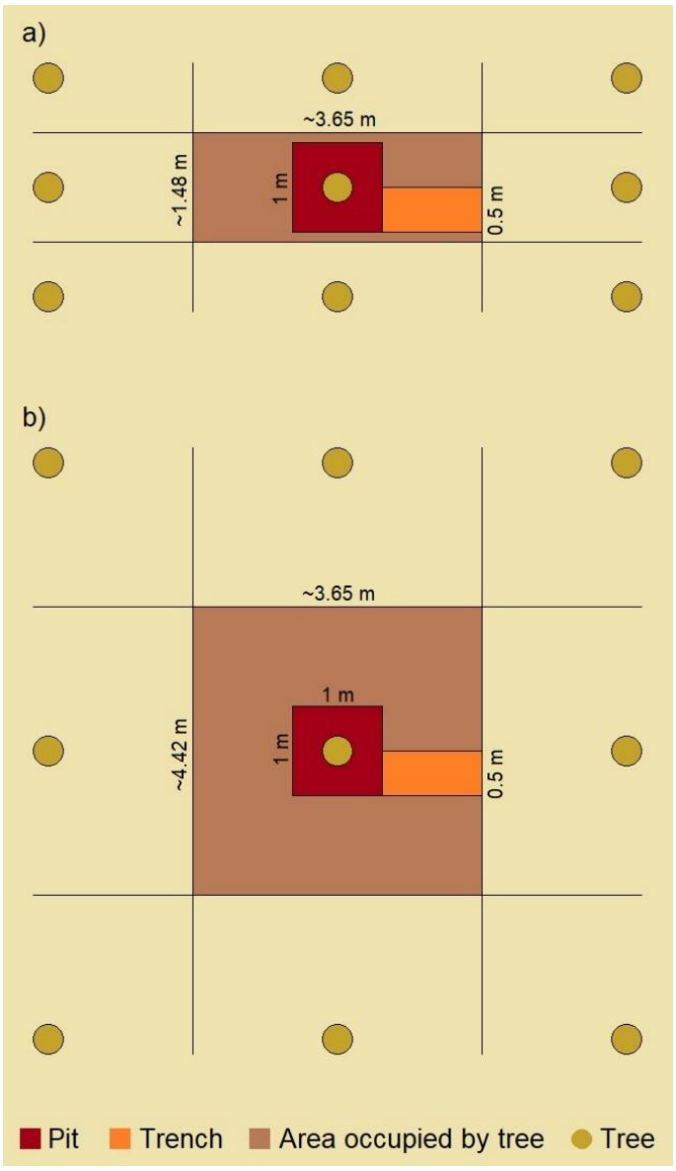

Figure 2.2 Root harvest diagram in (a) high and (b) low planting density plots. Figure not drawn to scale.

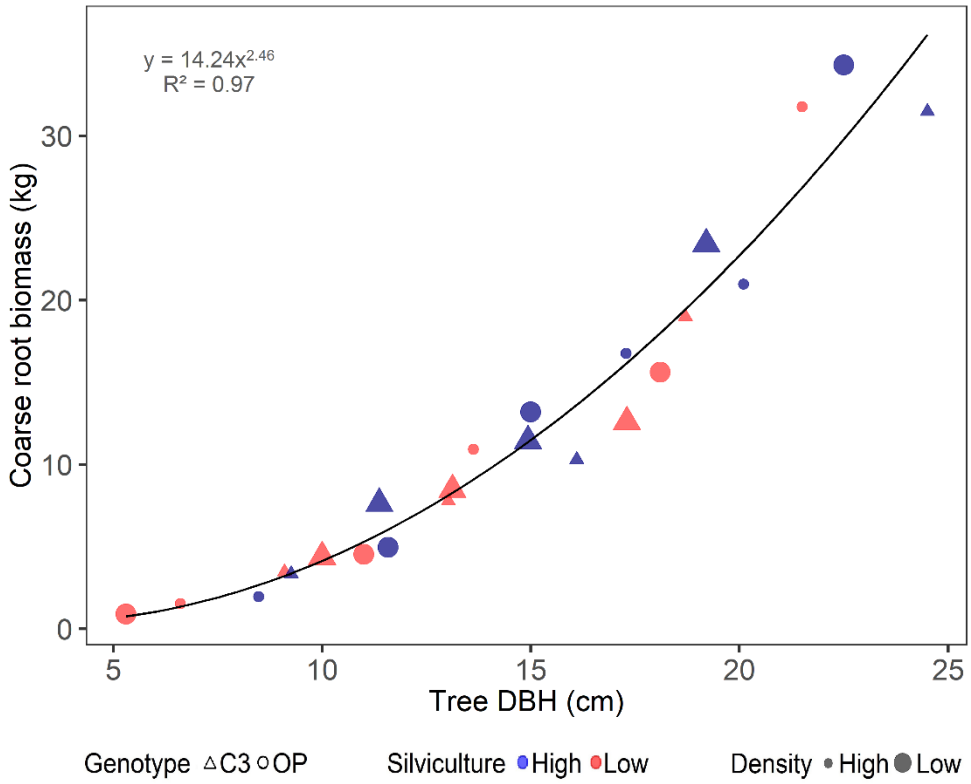

Figure 2.3 Allometric relationship between coarse root (> 2 mm) biomass and tree diameter at breast height for 8-year-old loblolly pine trees.

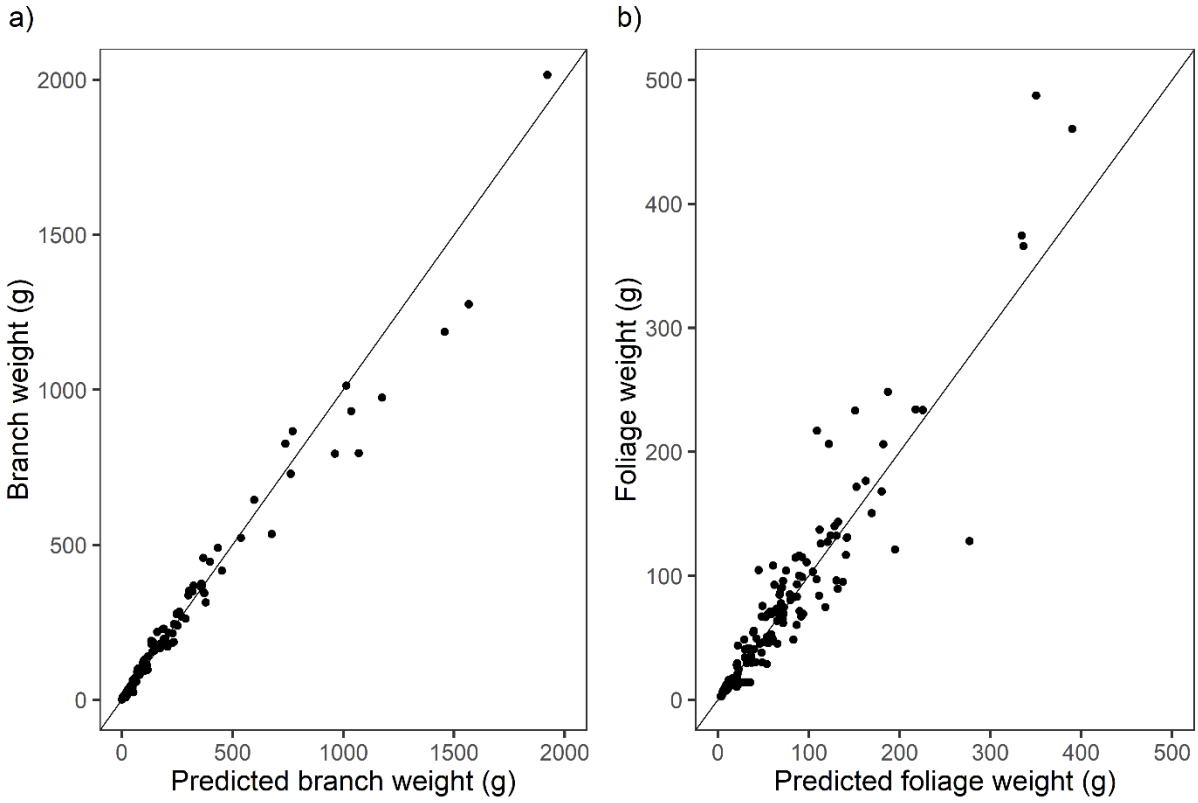

Figure 2.4 Observed versus predicted values of (a) branch and (b) foliage biomass for models at the **branch level**.

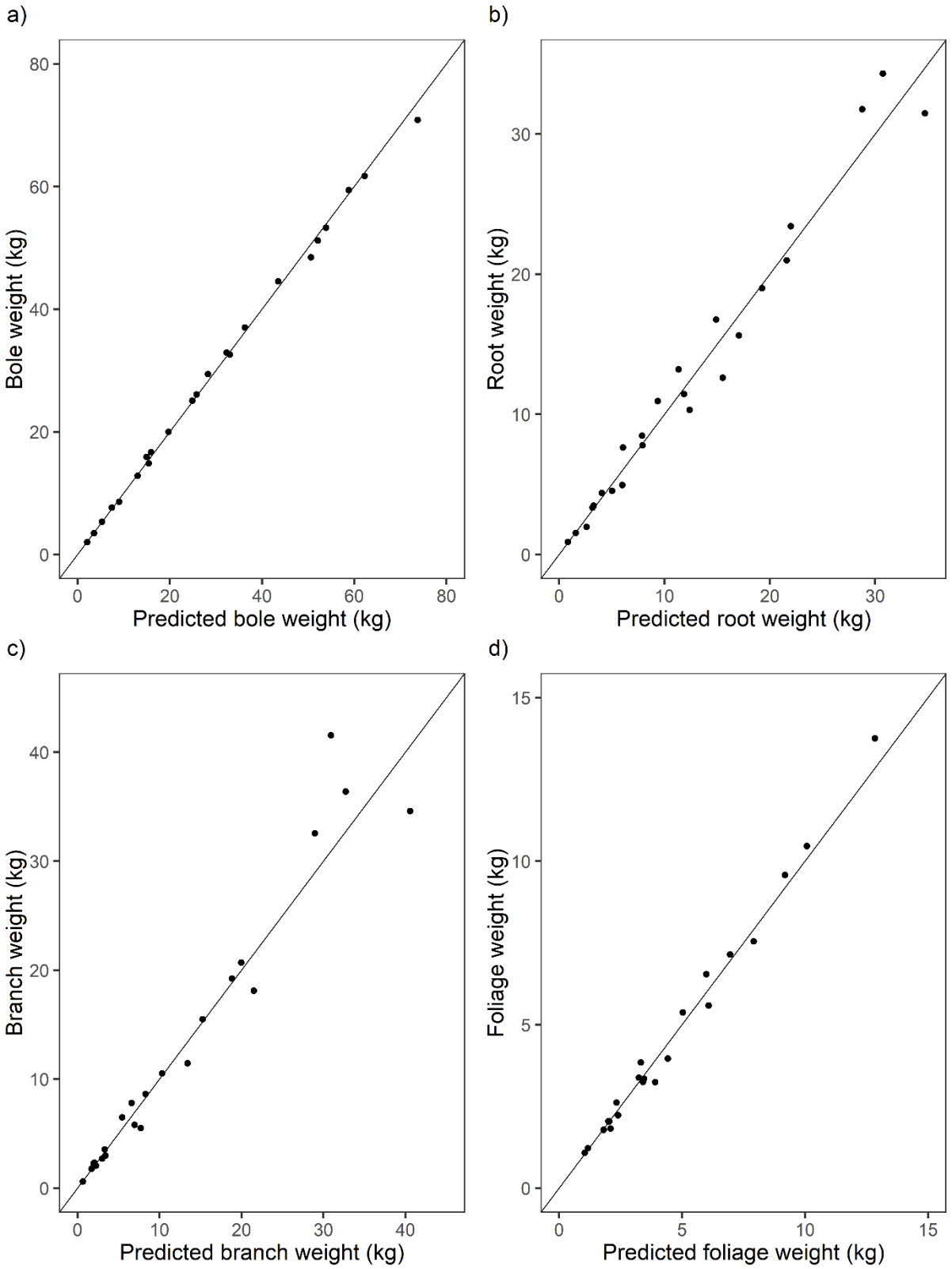

Figure 2.5 Observed versus predicted values of (a) bole biomass, (b) coarse root, (c) branch, and (d) foliage biomass for models at the **tree level**.

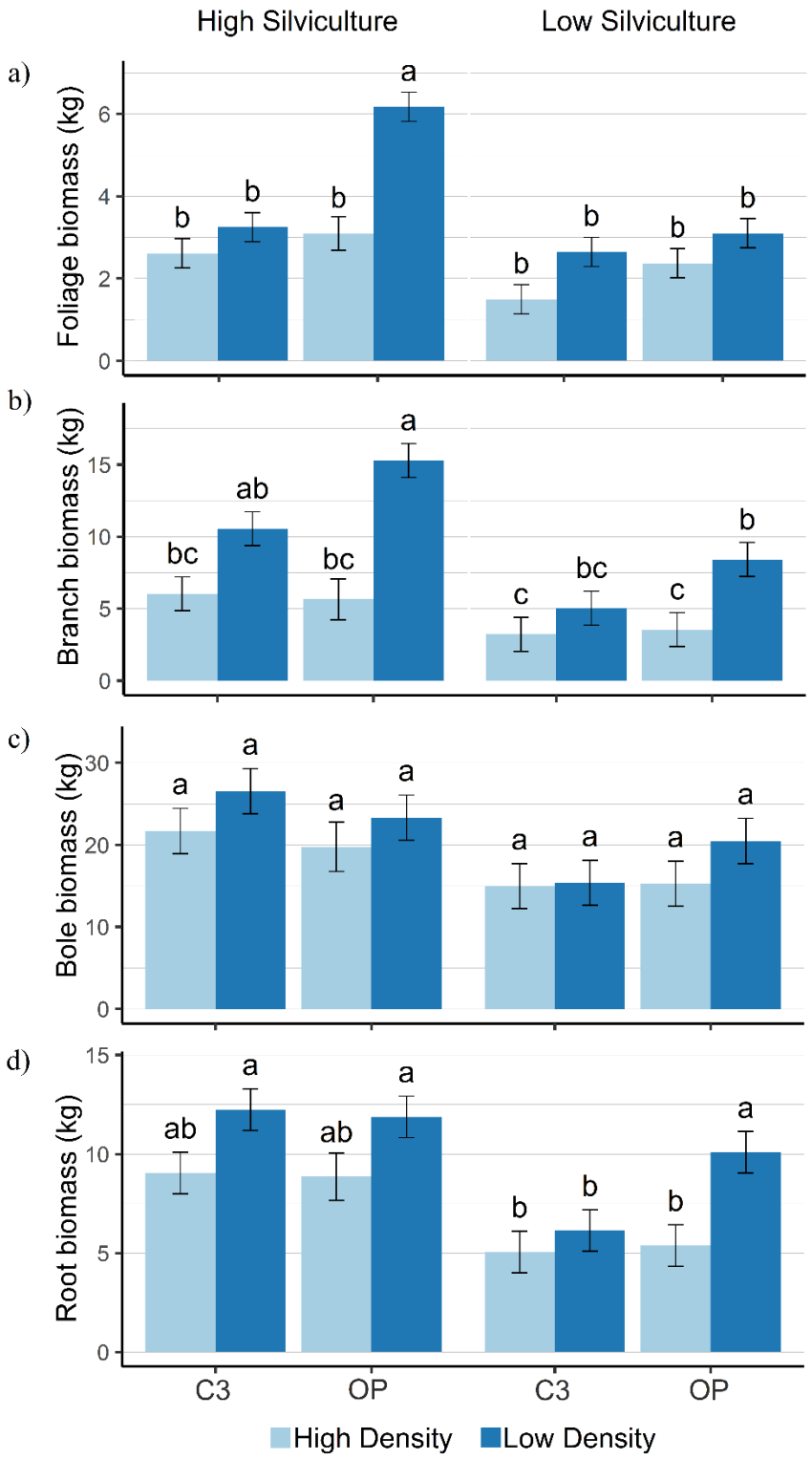

Figure 2.6 Mean biomass accumulation in (a) bole, (b) coarse root, (c) branch, and (d) foliage at the tree level, with different planting densities, genotypes, and silvicultural intensities. Within each tree component, treatments with the same letters are not significantly different at the p = 0.05 significance level. Error bars represent model standard error.

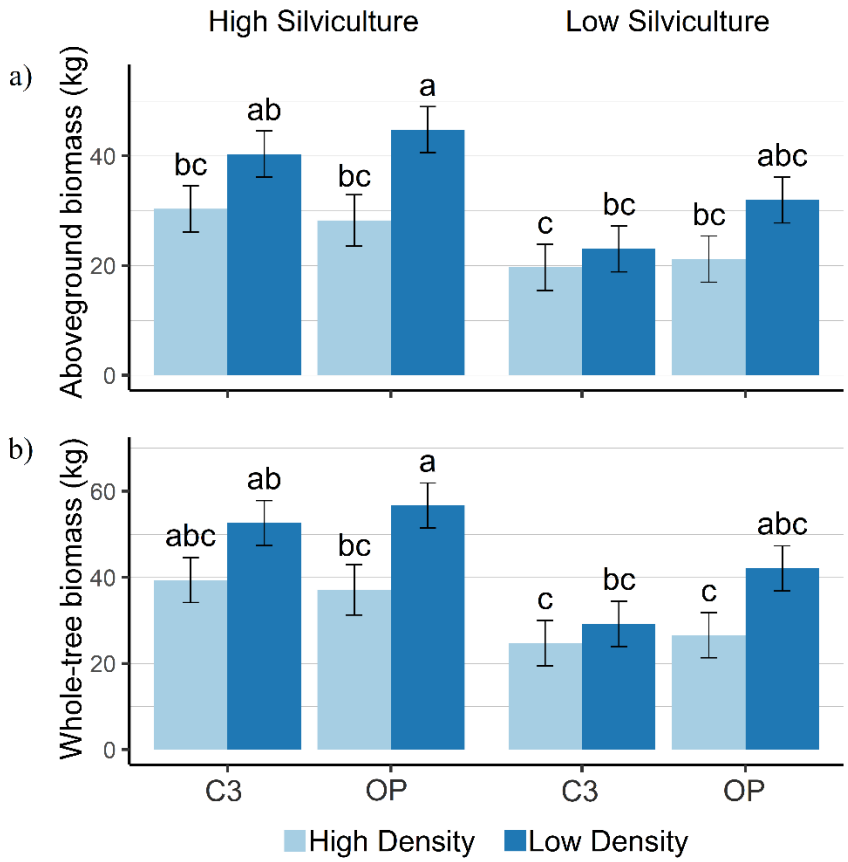

Figure 2.7 Mean aboveground (a) and whole-tree (b) biomass accumulation at the tree level, with different planting densities, genotypes, and silvicultural intensities. Treatments with the same letters are not significantly different at the p = 0.05 significance level. Error bars represent model standard error.

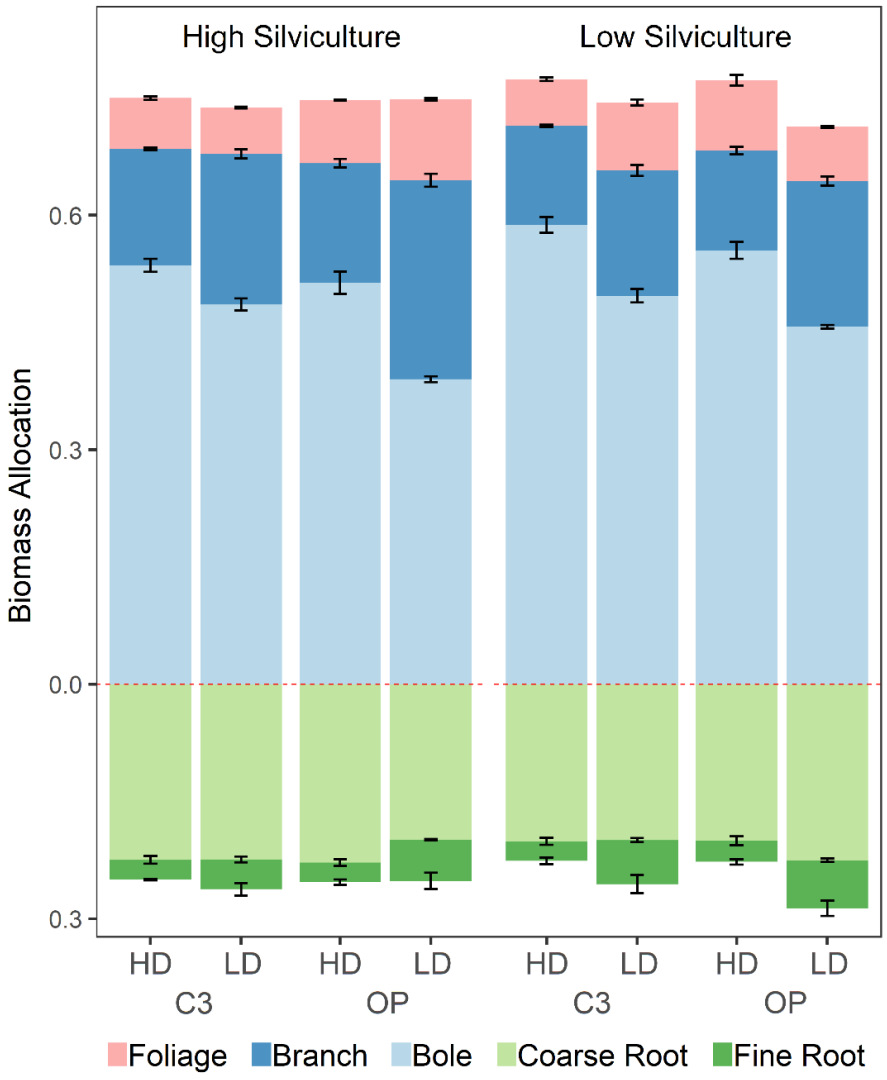

Figure 2.8 Estimates of biomass proportions within tree component between the two loblolly pine genotypes, planted at two different densities, under two levels of silvicultural intensity. Components below the red line are belowground components. C3 = clone 3; OP = open-pollinated; HD = high density; LW = low density.

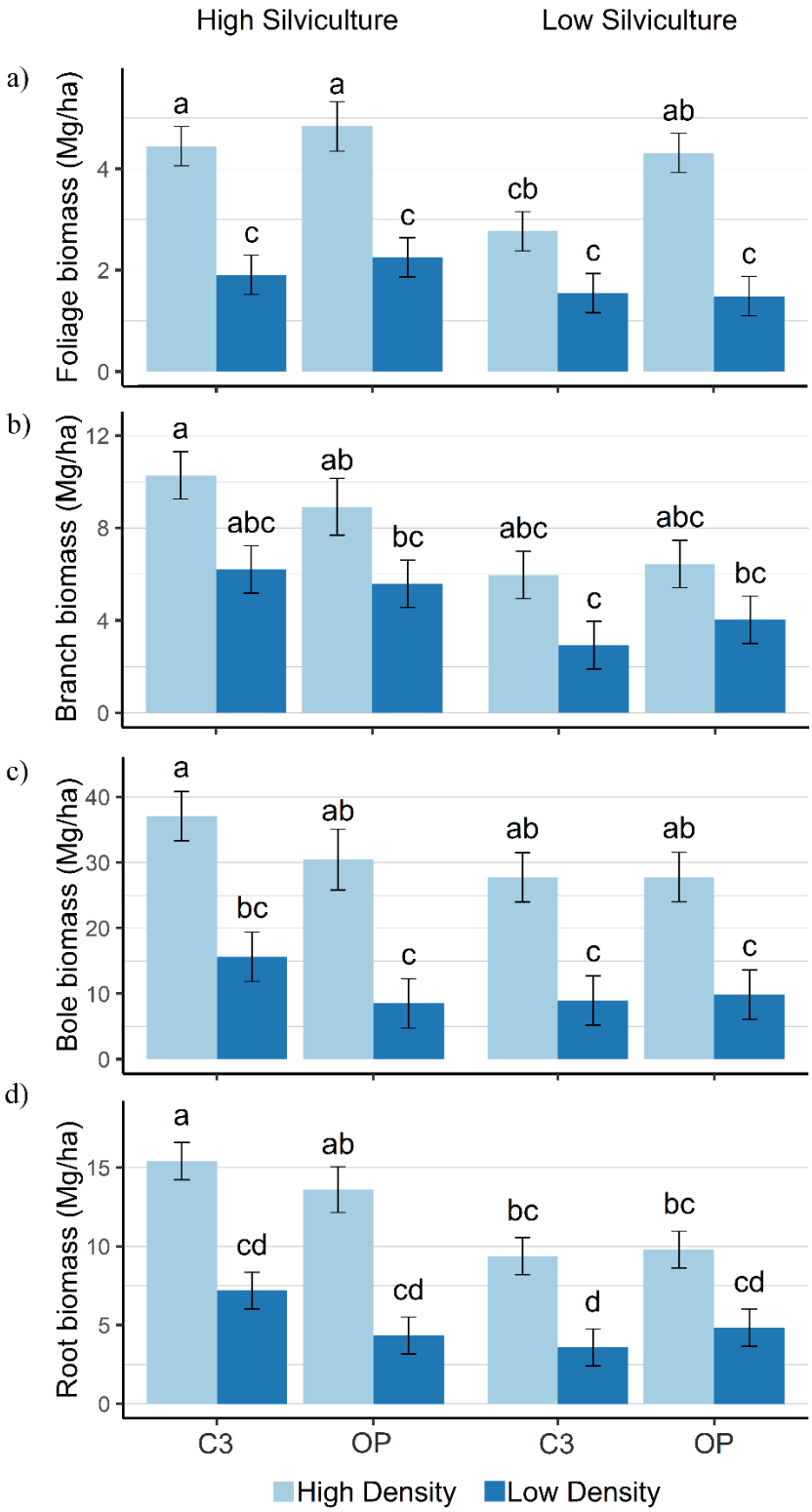

Figure 2.9 Mean biomass accumulation in (a) bole, (b) coarse root, (c) branch, and (d) foliage at the stand level, with different planting densities, genotypes, and silvicultural intensities. Within each tree component, treatments with the same letters are not significantly different at the p = 0.05 significance level. Error bars represent model standard error.

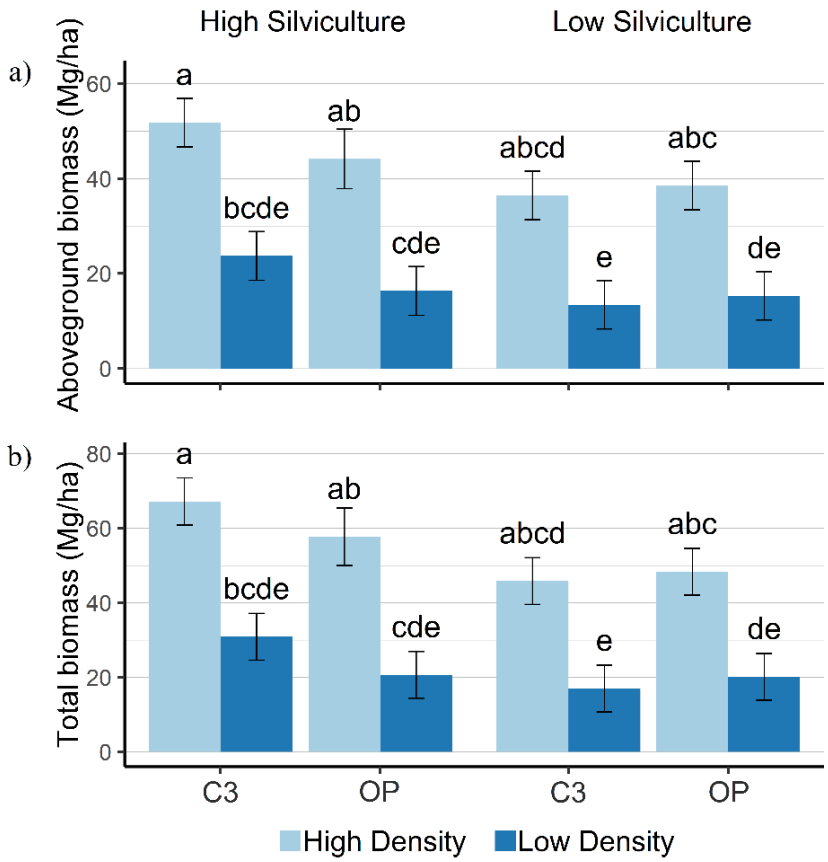

Figure 2.10 Mean aboveground (a) and total (whole-tree) (b) biomass accumulation at the stand level, with different planting densities, genotypes, and silvicultural intensities. Treatments with the same letters are not significantly different at the p = 0.05 significance level. Error bars represent model standard error.

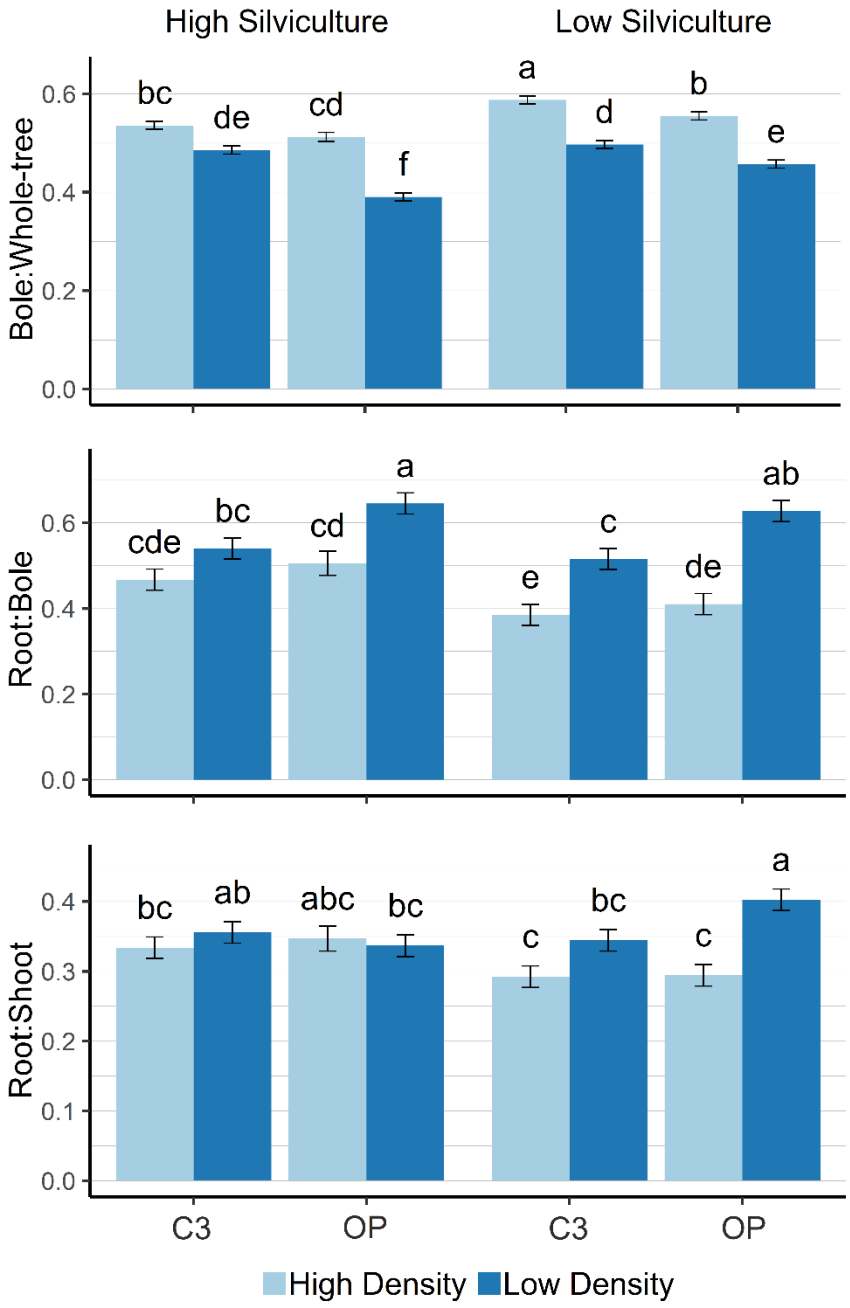

Figure 2.11 Bole:whole-tree ratio (a), root:bole ratio (b), and root:shoot (c), where root equals coarse and fine root biomass, and shoot equals aboveground biomass (bole +branch + foliage). Error bars represent model standard error.

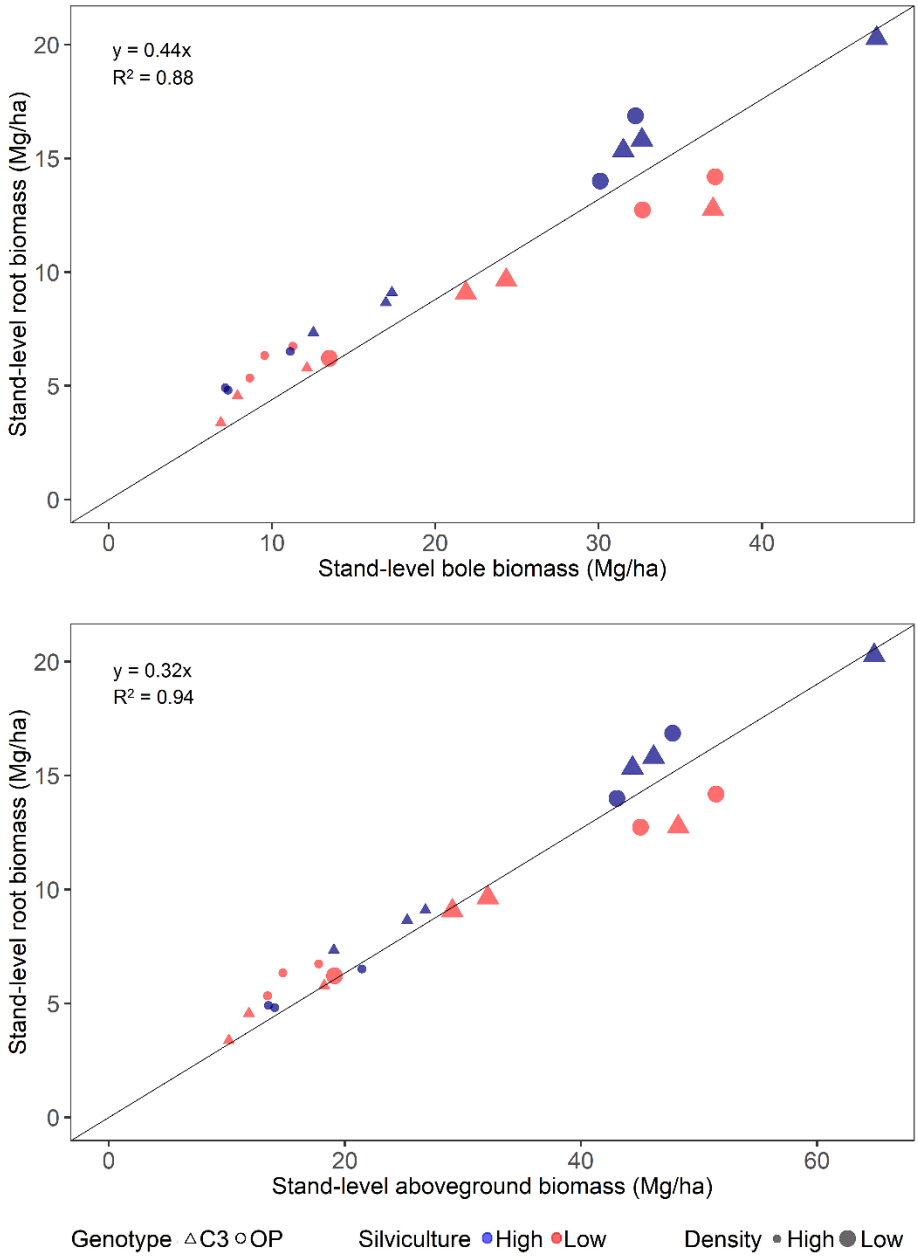

Figure 2.12 Total root (coarse root and fine root) biomass (Mg ha^{-1}) by (a) bole biomass (Mg ha^{-1}) and (b) aboveground biomass (Mg ha^{-1}).

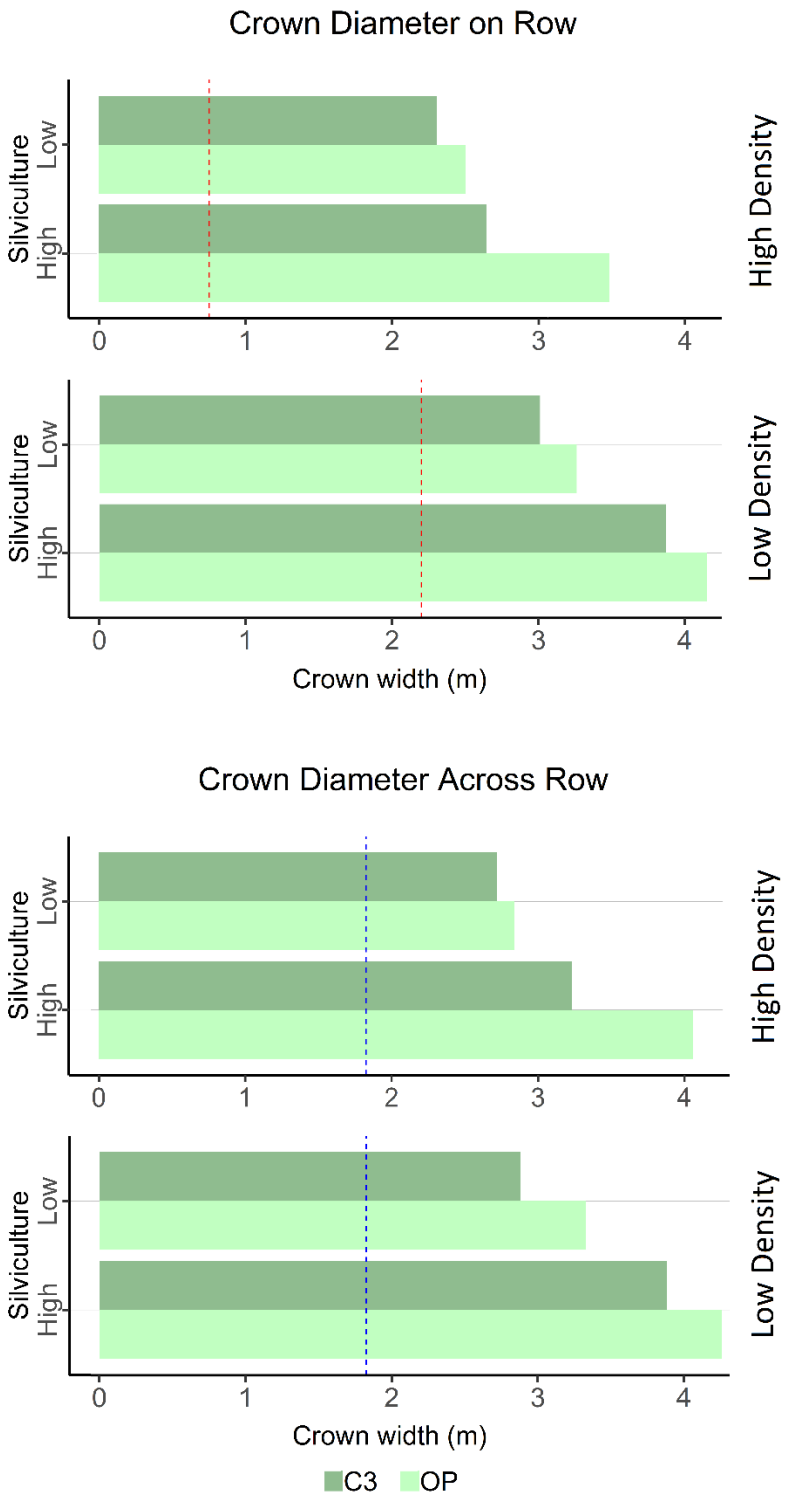

Figure 2.13 Crown dimensions measured along tree row and across tree row. Red lines in top two graphs represent half the distance between trees on the same row. Blue lines in bottom two graphs represent half the distance between trees on adjacent rows.

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