

PRODUCTION ECOLOGY OF THREE SHORT-ROTATION HARDWOOD
SPECIES ACROSS A RESOURCE GRADIENT

By

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I want to thank those women that have influenced my life, become role models, mentors, friends, and have taught me to expect more from and for myself.

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in
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PRODUCTION ECOLOGY OF THREE SHORT-ROTATION HARDWOOD SPECIES
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The objective of this study was to examine the production ecology of three economically important hardwood species, *Populus deltoides*, *Quercus pagoda*, and *Platanus occidentalis*, to varying levels of resource application. Specifically, we wanted to determine how biomass production was altered, physiologically supported, and how nutrient uptake and storage within various biomass components were influenced by the applications of irrigation and the combined treatment of irrigation and nitrogen application at 56, 112, and 224 kg N ha⁻¹ yr⁻¹. Allometric equations were used for woody biomass production and litter traps were used to determine actual foliar biomass. Overall, our results suggest that biomass accrual is highly correlated with LAI; however, the relationship is species specific. Maximum biomass was reached well below the maximum LAI for *P. deltoides*, *Q. pagoda* and *P. occidentalis*. To determine how much light the canopy was capturing and the extent of which the treatments were influencing physiological mechanisms, photosynthesis data was collected for all three species. Leaves of which photosynthesis were measured were harvested, scanned, weighed, dried, and analyzed for nitrogen content. As expected, SLA, SLN, LAI, and A_{max} varied across the supplied resource gradient for all three species. Irrigation alone was

sufficient in *P. deltoides* and *P. occidentalis* to increase SLA whereas SLA responded to both irrigation and fertilization in *Q. pagoda*. A_{\max} reached peak rates for all species in the IRR+112 treatment. Finally, we wanted to determine the aboveground nutrient content and use efficiencies for these three species and understand the relationship between nitrogen, phosphorus, and potassium as it pertained to the resource gradient. We found that nutrient content, resorption efficiency and proficiency, leaf- and canopy-level nutrient use efficiency were not necessarily influenced by increased resource availability. While many plants have adaptations to conserve nutrients when nutrient levels are low, the available resources supplied by an abandoned agricultural field appear to be sufficient as to not alter the mechanism for nutrient conservation. Additionally, we found that maximum biomass production was not necessarily tied to maximum nutrient input. Understanding the interactions between the short-rotation woody species and intensive practices will assist development dedicated energy plantations.

CHAPTER 1 BACKGROUND

Introduction

Land managers have realized the need to balance the increasing demand for wood products with environmental and recreational benefits of forests (Steinbeck 1999, Stanosz 2000, Stanton et al., 2002, and Vogt et al., 2005). An increased need for hardwood pulp and short-rotation woody crops (SRWC) for biofuel have led to innovative ideas to increase productivity on tree plantations while decreasing the harvesting pressures on natural forests (Kelty 2006).

It has become apparent in recent years that management techniques such as fertilization and irrigation can increase biomass yields as much as four-fold compared to traditional forest management practices. For example, Cobb et al. (2008) found significant biomass increases for sweetgum (*Liquidambar styraciflua* L.) and American sycamore (*Platanus occidentalis* L.) using a combined fertilization and irrigation system, called fertigation, in Georgia. The economic and biological sustainability of a fertigation system depends on several factors such as species, fertilizer response, leaf area index (LAI), above- and belowground carbon allocation, and insect or disease attacks. The knowledge to manage such a system for maximum growth efficiency (GE), annual total tree biomass produced per unit leaf area) with the optimum level of resources (light, water, and nutrients) is just developing. For example, it is well known that productivity is closely correlated to leaf area (Waring 1983, Jose and Gillespie 1997. and Henderson and Jose 2005), and leaf area has been used for decades as a measure of forest productivity. However, growth models incorporating leaf area have yet to be developed for many of the commercially important hardwood species.

Tree leaf area regulates productivity through its influence on canopy light interception and resulting photosynthesis (Running et al. 1989, Will et al. 2005, Lhotka and Loewenstein 2009, and Motsinger et al. 2010). Variation in leaf area, light interception, and resulting productivity can be explained by site-specific resource (light, water, and nutrients) availability (Jose and Gillespie 1997 and Cobb et al 2008). However, the relationship between resource availability and resource use efficiency is seldom taken into account when making fertilizer or irrigation recommendations in intensively managed hardwood plantations. The timing and quantity of fertilization and irrigation will play a crucial role in determining the leaf area index and canopy nutrient content of a stand, which in turn, will determine the canopy photosynthetic efficiency and the production potential. There is a need to understand the temporal patterns of fertilizer and water requirements and resource use efficiencies of different hardwood species in order to estimate the proper rates and timing of application.

Fertilizing and irrigating a forest stand often results in greater aboveground biomass production (Coleman et al. 2006 and Cobb et al. 2008). However, how these practices influence belowground carbon allocation patterns is often overlooked. The belowground carbon allocation might also change in response to variations in resource availability. According to Axelsson and Axelsson (1986) and Albaugh et al. (1998) reduced resource investment in fine roots is one of the most important mechanisms by which improved nutrient availability increases aboveground biomass production.

Hence, the proposed study was undertaken to examine the temporal variation in aboveground carbon allocation patterns in relation to leaf area development and associated nutrient and water use in three selected fast growing hardwood species

cottonwood (*Populus deltoides* Bartr. ex Marsh.), cherrybark oak (*Quercus pagoda* Raf.), and American sycamore (*Platanus occidentalis* L.).

Literature Review

Environmental Limits on Productivity: An Overview

Primary productivity measurements are often described as the amount of carbon fixed minus respiration costs of maintenance and construction of new tissues (Pangle et al. 2009). Productivity can be measured by dry matter or biomass accumulation over time. Water and nutrient supply control canopy development and the relationship between above- and belowground productivity (Loustau et al. 2001 and Binkley et al. 2010). Several techniques have been developed for quantifying aboveground productivity. Allometric biomass equations, measurements of physical processes, and eddy covariance have been common among them. Allometric biomass equations require destructive measurements of individual components. Trees from several DBH (diameter at breast height) and height classes are harvested and weighed to develop components of the equations. Eddy covariance uses indirect measurements of climate and gas exchange within a forest stand to determine rates of productivity. Sensors at varying heights within the canopy collect the net uptake and release of CO₂ throughout the stand. Direct measurements of physical processes are nondestructive and are not subject to extreme extrapolation errors. Direct measurements of photosynthesis (A_{net} , P_{net} or A_{max}), specific leaf area (SLA), leaf area index (LAI), water, and nutrient use can be combined to give an entire portrayal of primary productivity. While direct measurements are subject to potential bias, a more precise extrapolation can be obtained from direct measurements of individual trees. Direct measurements give a

better understanding of the processes that can limit and alter primary productivity within a forest stand.

Forest productivity and the rate of biomass produced per unit of carbon fixed are determined by leaf area. Likewise, assimilation rates govern leaf initiation and expansion and thereby the rate of light interception. Light quality/quantity, CO₂, temperature, soil-water, and nutrient availability can control photosynthesis and the resulting carbohydrate production on a unit area basis (Foth 1984, Kramer and Kozlowski 1979, Barnes et al. 1998, Kull and Niinemets 1998, Lambers et al. 1998, and Loustau et al. 2001). The product of leaf photosynthetic rate and total canopy leaf area can determine net canopy photosynthesis. Leaf area measurements and photosynthetic rates from selected sun and shade leaves will give net photosynthetic rates per unit leaf area. These measurements can be extrapolated to whole canopy measurements by estimating the total leaf area in the canopy of multiple trees.

Supplying required components that regulate assimilation can enhance productivity. Temperature, CO₂, and light quality/quantity are not easily manipulated. While light quantity can be increased with thinning after canopy closure (Lhotka and Loewenstein 2008 and Motsinger et al. 2010), it is not always economically feasible. Light quality cannot reasonably be altered, while water and nutrients can. Fertilization experiments have shown how water and nutrients can control productivity of intensively managed tree plantations (Dalla-Tea and Jokela 1991, Kipp 1992, Albaugh et al. 1998, Leininger 2000, Loustau et al. 2001, Samuelson et al. 2001, Allen et al. 2002, Samuelson et al. 2007, and Cobb et al. 2008).

Poor quality sites produce less dry matter than good sites because foliage cannot function as efficiently if one or more required resources are lacking. On poor quality sites, carbohydrate production may be shifted belowground in response to decreased water and nutrient supply. Deficiencies in water and nutrients can slow photosynthesis and thus the creation of new tissues. For aboveground growth to occur, belowground and respiration requirements must be met first. When water supply is limited, photosynthesis is negatively affected as stomata close in response to water stress (Kull and Kruijt, 1999 and Warren and Adams, 2001). Stomata closure decreases CO₂ uptake resulting in reduced carbohydrate production (Lambers et al. 1998). Water deficiencies will ultimately limit growth, as canopy expansion becomes secondary to increased root growth in response to decreased water supply. The result of prolonged water stress can be decreased aboveground productivity (Tschaplinski et al. 2006) and eventual plant death (Lambers et al. 1998). Either soil-water holding capacity or soil-water supply must be increased to ensure adequate water supply for aboveground productivity.

Increasing water availability can increase productivity of plants (Kramer and Kozlowski 1979, Foth 1984, Barnes et al. 1998, Lambers et al. 1998, and Cobb et al. 2008). Barnes et al. (1998) reported that termination of shoot elongation occurred when soil-water stress was severe for many hardwood species. Soil-water replenishment through irrigation increases plant water balance, nutrient uptake Kreuzwieser and Gessler 2010) growth rates and net primary production (Birk 1997, Lambers et al. 1998, Tschaplinski et al., 2006, Karacic and Weih 2006, and Samuelson et al., 2007). Soil-water also facilitates the uptake of nutrients that regulate photosynthesis, stomatal

closure, turgidity, and cell enlargement (Kramer and Kozlowski 1979). In a recent study by Samuelson et al. (2007), conducted to determine long-term acclimation to irrigation and fertilization, irrigation was shown to increase aboveground biomass accrual. Their study suggested that while irrigation and fertilization necessarily increased aboveground biomass productivity, two- and three-fold, respectively, leaf area did not increase at the same rates suggesting the increased resources increased leaf-level photosynthetic efficiency. In a similar type study, Karacic and Weih (2006) found poplar clones increased two-fold with the application of irrigation and fertilization with no significant differences in leaf area ratio among treatments or clones. Cobb et al. (2008) found significantly greater leaf biomass with irrigation corresponding to an increase in aboveground biomass production for *L. styraciflua* and *P. occidentalis*.

Limited nutrient availability, especially nitrogen, can also decrease aboveground productivity (Dalla-Tea and Jokela 1991, Zhang et al. 1997 and Jokela and Martin 2000). Jokela and Martin (2000) found that total aboveground biomass for seven-year old loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englem.) grown in Florida was five- and two-fold higher respectively for fertilized trees over control treatments. The trend of higher aboveground biomass for fertilized plots over control plots continued through age 16 with increases of nearly two fold for both species. Zhang et al. (1997) found that 25-year old fertilized *P. taeda* had both increased volume and increased DBH over control treatments the first year after fertilizer applications. They also found increases for needle length, fascicle number, and leaf area for the fertilized treatment. Dalla-Tea and Jokela (1991) found increased productivity with fertilization for six-year

old *P. taeda* and *P. elliotii*. They also found that aboveground biomass was increased over five-fold for *P. taeda* and over two-fold for *P. elliotii* with fertilization.

In natural stands, nitrogen availability often depends on mineralization of nitrogen from decomposing litter by soil microorganisms. High rates of uptake and assimilation correspond to high rates of nitrogen mineralization. Without adequate nitrogen, foliage cannot function efficiently in capturing light. Nitrogen is necessary for the production of chlorophyll and other enzymatic reactions that occur during photosynthesis. When soil nitrogen content and mineralization rates are low, foliar uptake maybe reduced resulting in lower canopy photosynthesis and biomass production. The greater the amount of foliage, the greater the amount of light captured. High rates of light capture increase carbohydrate production available to meet and exceed respiratory demands.

Fertilizers help to promote the growth and productivity of plants by adding essential nutrients. Nitrogen (N), phosphorus (P), and potassium (K) are the major limiting elements in both agricultural and forest productivity (Lodhiyal and Lodhiyal 1997 and Johnson et al. 1998). Micronutrients such as iron, boron, manganese, zinc, copper, and molybdenum are also beneficial for plant growth (Lambers et al. 1998). Fertigation is the application of fertilizer introduced into an irrigation system. Fertigation can ameliorate nutrient and water deficiencies. Nutrients frequently applied through fertigation include nitrogen, potassium, and phosphorus (Kipp 1992). Fertigation optimizes nutrient availability at the root zone. Direct application decreases nutrient leaching and runoff while increasing productivity. Fertigation applications show higher rates of productivity than broadcast fertilization with irrigation or irrigation alone (Kipp 1992).

Paper and wood fiber industries and private landowners are beginning to implement fertigation on fast growing bottomland hardwood plantations (Leininger 2000). Several studies, (Nielsen et al. 1997, Stiles 1997, Samuelson 1998, Weinert et al. 2000, and Samuelson et al. 2001) have tested the effectiveness of fertigation on aboveground biomass production. One response of increased nutrient availability was a shift in biomass allocation to aboveground and a decrease in belowground productivity (Coyle and Coleman 2005). Because the nutrients are supplied directly at the base of the stem, root expansion required for nutrient and water uptake was decreased.

Resource Availability and Ecophysiology

Environmental variables such as water availability, which regulates leaf area, can influence forest productivity (Gholz 1982). Aboveground net primary productivity (ANPP) shows a positive correlation with increased site water balance (Coyle and Coleman 2005). Because plant water balance controls stomatal conductance, the formation of hydrogen ion gradients, and transporting photosynthate throughout the tree, measurements of water use efficiency can add to the understanding of plant productivity. Greater amounts of leaf area can affect the overall water balance by increasing transpiration rates, but can also increase photosynthesis. Lockaby et al. (1997) found increased aboveground productivity when water stress was minimized by irrigation for cottonwood (*Populus deltoides* Bartr. Ex Marsh.) grown in the upper Coastal Plain of Alabama. Santana et al. (2000) found that greater aboveground productivity was strongly correlated to soil-water availability for eucalypt plantations in Brazil. They also determined that nitrogen use efficiency (NUE), the amount of biomass produced per unit of nutrient) increased with increased water availability. In a similar study, Arp et

al. (1998) found that when soil-water was below optimal levels, NUE decreased as CO₂ uptake was reduced with stomatal closure. Because of decreased carbon assimilation, reduced growth rates were found to be well correlated with decreased soil-water. Santana et al. (2000) also reported that increased water availability increased leaf area, resulting in greater photosynthetic rates and net primary production.

Jose and Gillespie (1996) observed increases in SLA and LAI across an increasing moisture gradient in mixed hardwood stands located in the Midwest. A similar study by King et al. (1999) described increased leaf area with irrigated *P. taeda*. Along with increased leaf area, Albaugh et al. (1998) and King et al. (1999) found decreased fine root production with irrigation. Albaugh et al. (1998) also found decreased leaf area during dry years when water availability was low. Wright et al. (2001) suggested that the cost of new leaf construction, on dry sites or in drought conditions, resulted in smaller leaves and reduced leaf area.

Similarly, when water supply is limited canopy photosynthetic rates are presumably reduced due to decreased leaf area, reduced light captured per unit of leaf area, and rapid stomatal closure. A study by Samuelson (1998) found increased A_{net} with irrigation for *L. styraciflua* and *P. taeda*, which was attributed to decreased early stomatal closure. In times of drought, carbon allocation is shifted to root production, increasing the root:shoot ratio (Loustau et al. 2001). The study by Arp et al. (1998) also suggests reduced water supply will decrease photosynthesis and aboveground production for a variety of species. Kull and Kruit (1999) further support this theory with the model they developed using data collected from European aspen (*Populus tremula*

L.) and filbert (*Corylus avellana* L.). They estimated that both photosynthesis and positive carbon gain are slowed with water stress.

Hardwood trees typically have higher foliar nutrient concentrations than do coniferous species (Samuelson 1998) and are therefore more likely to grow on higher quality sites (Lockaby et al. 1997). Fertilization can increase soil-nutrient availability required for nutrient demanding hardwood trees (Samuelson 1998) allowing higher productivity levels in less than optimal environments. High soil-nutrient levels have been shown to be correlated with A_{net} and SLA for trees (Will et al. 2005), shrubs, C_3 , and C_4 grasses (Wright et al. 2001). Jose and Gillespie (1996) suggested that canopy nutrients in a mixed mesic forest were well correlated with SLA. Knops and Reinhart (2000) found increased SLA and LAI with fertilization for C_3 , and C_4 grasses in Minnesota. They also found increased foliar nitrogen levels and suggested higher rates of nitrogen cycling within their study site reduced the nitrogen cost for new leaf construction for some grass species. Allen et al. (2002) found that peak LAI for 15-year old *P. taeda* occurred with irrigation and fertilization treatments. Despite planting on a sandy soil, the LAI was over two-fold higher for the combination of water and nutrient applications over the control treatments. Studies by Albaugh et al. (1998) and Warren and Adams (2001) found that increased LAI was well correlated with increased nutrient and water availability as well as aboveground biomass production.

A study by Jose and Gillespie (1996) suggested that leaves with lower SLA (scaled to the canopy level) from high in the canopy (dominant and co-dominant species) would have higher photosynthetic rates than leaves growing in the shade. This idea was supported by the findings of Albaugh et al. (1996). They showed that

increased photosynthetic rates and increased foliar nitrogen levels were positively correlated to increased A_{net} . Warren and Adams (2001) also support this finding. They found a strong positive linear relationship between increased light interception and A_{net} . Their study also showed increased nitrogen concentration per unit leaf area positively correlated with A_{net} for maritime pine, (*Pinus pinaster* Aiton). Reich et al. (1998b) and Wright et al. (2001) also suggested that high rates of foliar nitrogen could be found in sun leaves owing to high photosynthetic rates. Anten et al. (1998) found increased photosynthetic nitrogen use efficiency with increased foliar nitrogen levels.

Reich et al. (1998b) suggested that leaf life span of several boreal tree species were shorter with high nutrient availability. Kaczmareck et al. (unpublished data) found a negative linear relationship with soil phosphorus availability and retranslocation and a positive relationship with foliar concentrations for white oak (*Quercus alba* L.) in the Central Hardwood Region of the Midwest. They found mixed results for soil nitrogen availability with foliar concentration and retranslocation. Their findings suggest rates of mineralization increases soil nutrient availability but may not decrease retranslocation due to high levels of competition for nitrogen in natural forests.

LAI - Productivity Relationships

Leaf production and the resulting leaf area are controlled by resource availability. In nutrient deficient soils, nutrients are allocated to root production for further nutrient capture. As resource allocation shifts to belowground, LAI is reduced. Limited leaf production results in reduced amounts of light capture and assimilation rates resulting in less stem and wood production.

Aboveground production is greater in fertile soils, or with fertilizer applications (Coyle and Coleman 2005). Jokela and Martin (2000) found increased LAI and

stemwood production for *P. taeda* and *P. elliotii* with fertilization. This increase was due to reduced resource allocation for root growth. The increase in resources at the leaf level results in greater amounts of leaf production and higher levels of light interception. High LAI values (high rates of intercepted light) indicate belowground resource needs are being met, allowing resources allocation to shift aboveground. Therefore, greater leaf area indicates a potential for greater amounts of light capture resulting in higher photosynthetic rates and more carbon allocation for stem and wood production. Dalla-Tea and Jokela (1991) also observed increased aboveground productivity with increasing LAI due to higher rates of light interception. They further suggested a strong linear relationship between growth and light interception. This relationship has been used to describe light use efficiency ((LUE) the amount of carbon gain per unit of light intercepted by the canopy). Reduced available water and nutrients can decrease the slope of the linear relationship. Samuelson (1998) suggested that leaf area was more responsive to fertilization than A_{net} .

Increased LAI may not translate into increased productivity above a threshold LAI. Jose and Gillespie (1997) found that although LAI increased across a moisture gradient, foliage biomass remained relatively constant. They also found that the ratio between wood:leaf production was not significantly different across the moisture gradient for mixed hardwood stands in the Midwest. Sampson and Allen (1995) suggested that increased self-shading occurred with increased LAI. They suggest that productivity may not increase as leaf area increases unless all leaves are receiving adequate light to promote positive carbon gain. Wright et al. (2001) suggested SLA and LAI are at their highest when water and nutrient levels are optimal for a variety of trees,

shrubs, and subshrubs in New South Wales. This study indicates that variability in resource use efficiency across an ecosystem will depend on the species within the site.

Much of the notable literature regarding tree productivity is centered on pine plantations. It is well known that increasing aboveground biomass of pine plantations with fertilization and herbicide applications reduces harvest rotations and enhances profit. One area of research that needs more complete development is that of fast growing hardwood plantations. While there is some information available on this subject, it is limited in nature and not as extensive or well developed as that of pine plantations. Recently research has focused production of coppiced (Tharakan et al. 2003) and planted (Tharakan et al. 2005) willow (*Salix* spp.) and poplar (*Populus*) clones in fertilized (Updegraff et al. 2004) and unfertilized, (Rytter and Stener 2005, Devine et al. 2010) studies to determine woody biomass production in SRWC systems. Tharakan et al. (2003) suggested variability among *Salix* and *Populus* clones with respect to wood quality and energy production for bioenergy sources. However, both Tharakan et al. (2003) and Devine et al (2010) suggest greater energy potential with multi-clonal rather than single clonal tree crops. While previous research has suggested increased woody biomass production of some single clonal *Populus* plantations, Rytter and Stener (2005) suggest periodic thinning operations may further increase woody biomass production and thereby energy production. Upon investigating the economic feasibility of co-firing woody biomass with coal, Tharakan et al. (2005) suggested increased subsidies, tax-breaks, and methods to maximize production may be needed to further interest in SRWC systems. Understanding the requirements of resource additions and clonal selection for SRWC systems will be necessary for

obtaining maximum biomass production for bioenergy and bioproducts purposes. As the amount of land available for hardwood harvesting decreases and the commercial need for hardwood for pulp and biomass/biofuel increases, improving productivity of short-rotation hardwood plantations becomes more relevant. The following three chapters discuss the production ecology and ecophysiology of three commonly used short-rotation hardwood plantation species in the U.S.

CHAPTER 2

BIOMASS PRODUCTION POTENTIAL OF THREE SHORT-ROTATION WOODY CROP SPECIES UNDER VARYING NITROGEN AND WATER AVAILABILITY

Fast growing trees in short-rotation woody crop (SRWC) systems may increasingly meet societal needs ranging from renewable energy to ecosystem services such as environmental mitigation and remediation (Rockwood et al. 2004 and Jose 2009). Trees have been identified as part of the bioenergy solution in the “Billion Ton Report” (Perlack et al. 2005) that investigated the feasibility of producing the estimated one billion dry tons of lignocellulosic biomass needed annually to meet the “30×30” goal for a 30% replacement of the U.S. petroleum consumption with biofuels by 2030. Demand for woody biomass for fuel or fiber combined with reduced land availability has forced land managers to increase productivity of SRWC systems.

While some genetically improved pine species have shown superior growth rates, (Jayawickrama 2001, South and Rakestraw 2002, and Xiao et al. 2003), production potential remains low without additional soil nutrient amendments. Fertilization has long been an answer to poor site quality and has become a readily employed silvicultural tool for increasing productivity, especially in the southeastern U. S. (Allen 1987, Jokela et al. 1989, Zhang et al. 1997, and Scott et al. 2004). Much of the current research regarding fertilization rates and applications has focused on commercially important pine species such as loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englem.). Current research has focused primarily on growth response of pines to a single, early application; split application; and mid-rotation application of various fertilizers (Jokela and Stearns-Smith 1993, Jokela and Martin 2000, Will et al. 2002, Bekele et al. 2003, and Scott et al. 2004).

Despite positive results reported from extensive fertilization research of pine plantations (Fox et al. 2007), few studies in the U.S. have focused on short-rotation hardwood plantations with potential for bioenergy and biofuel applications. Recently, concerns about national energy security have spurred incentives and policies encouraging renewable energy production (Abt et al. 2010, Shivan and Mehmood 2010, and Benjamin et al. 2009). New-found interest in co-firing wood in coal plants has led some states to enact a plant to generate electrical power with renewable energy sources (North Carolina General Assembly 2007). Much of the research regarding hardwood plantation production, specifically in the southeastern U.S., has focused mainly on the production response of hardwood coppice systems or to varying planting densities (Schlaegel 1981, Schlaegel and Wilson 1983, Schlaegel 1984a, b, c, Clatterbuck and Hodges 1987, Oliver et al. 1990, Steinbeck 1999, and Lockhart et al., 2003). More recent studies have concentrated on single fertilizer rates or the combined application of fertilizer with herbicide (Samuelson 1998 and Samuelson et al. 2001). Several studies have focused on the relationship between nutrient availability and mechanisms that influence biomass production in natural stands (Monteith 1972, Crow 1978, Nadelhoffer et al. 1983, Wang et al. 1995, Fassnacht and Gower 1997, Jose and Gillespie 1997, Reich et al. 1997, and Wright et al. 2001) and in plantations (Coleman et al. 1998, Samuelson 1998, and Green et al. 2001).

For the best management of hardwood plantations as SRWC, it is not only useful to know production potential of the species, but also know the best combination and level of resources needed for the greatest return on investment. While it has been shown that increasing LAI increases light capture and is linked to improved

aboveground biomass production (Nadelhoffer et al. 1983, McCrady and Jokela 1996, Jose and Gillespie 1997, and Bolstad et al. 2001), the aboveground response in LAI and biomass is intrinsically linked to belowground resource availability (Rhodenbaugh and Pallardy 1993, Reich et al. 1998a, Samuelson 1998, Chang 2003, and Albaugh et al. 2004). Many of the fast growing hardwood species that would be desirable for short-rotation plantations such as sweetgum (*Liquidambar styraciflua* L.; (Clatterbuck and Hodges 1987), green ash (*Fraxinus pennsylvanica* Marsh.); (Kennedy 1988), nuttall oak (*Quercus nuttallii* Palmer); (Krinard and Kennedy 1981) are native to alluvial soils where water and where nutrients are readily accessible suggesting a greater demand for belowground resources may be required to attain their maximum production potential.

In the present study, we investigated the effect of water and nutrient availability, on survival, basal area ($\text{m}^2 \text{ha}^{-1}$), volume ($\text{m}^3 \text{ha}^{-1}$), standing biomass (Mg ha^{-1}), aboveground net primary productivity (ANPP, $\text{Mg ha}^{-1} \text{yr}^{-1}$, where herbivory and litter from bark and branches were not calculated), leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$), and growth efficiency (GE, $\text{Mg (ANPP) ha}^{-1} \text{yr}^{-1} \text{LAI}^{-1}$), for three economically important hardwood species *Populus deltoides* Bartr. (cottonwood), *Quercus pagoda* Raf. (cherrybark oak, previously *Quercus falcata* var. *pagodafolia* Ell.) and *Platanus occidentalis* L. (sycamore), (nomenclature follows USDA, NRCS Plants Database 2009) Our objectives were to: 1) determine the level of resources needed for attaining the highest biomass production for each species, and 2) quantify the leaf area-biomass relationship across the treatments. We hypothesized that aboveground production would peak well below the maximum level of nutrient supply.

Methods

Study Site

Our study was conducted in a fertigation trial established on an abandoned agricultural field (30.50'N, 87.11'W) in Santa Rosa County, Florida, USA. The climate is temperate with mild winters and hot, humid summers. Average rainfall is 1700mm, with average minimum and maximum temperatures of 10 and 27 °C respectively (NOAA, 2003). The soil is characterized as a well-drained, Redbay sandy loam (a fine-loamy, siliceous, thermic, Rhodic Paleudult) formed in thick beds of loamy marine deposits with an average water table depth of 1.8m (Lee and Jose 2003).

Treatment plots of *P. deltoides* and *P. occidentalis* consisted of 40 trees plot⁻¹ and *Q. pagoda* *Q. pagoda* contained 16 trees plot⁻¹; (although the *Q. pagoda* plots were the smallest of the three species, and found for this study should be treated with caution, the results reflect data collected within the study). All treatment plots were planted at 2.13m X 3.35m spacing (1400 trees ha⁻¹). The study design was a randomized complete block (RCB) with four replications of each treatment. Site preparation included disking and subsoiling to facilitate planting. Fertilization at the time of planting included broadcast application of diammonium phosphate, dolomitic lime, potash, and a micronutrient mixture. These treatments added elemental calcium, nitrogen, phosphorus, magnesium, zinc, copper, and manganese (1009, 50, 56, 126, 3, 3, and 2 kg ha⁻¹ respectively, Greg Leach, personal communication). Soil pH was adjusted to 6.0, with 3363 kg ha⁻¹ of dolomitic lime, based on recommendations from a similar trial at North Carolina State University Research Cooperative (Coleman et al. 2004, Samuelson et al. 2004a, and Samuelson et al. 2004b). A combination of chemical (sulfometuron methyl and glyphosate) and mechanical (mowing and manual

pulling) treatments were used for weed control during the first and second growing seasons, (Greg Leach, personal communication). Installation of the nutrient supply system and planting of trees occurred during spring 1995. The irrigation system operated for approximately two hours each day during the growing season (May-Sep.) with nitrogen application occurring two to eight minutes each day (on average 390mm water, Greg Leach, personal communication) creating the nitrogen gradient across the treatments (Lee and Jose 2003; 2006). The five treatments created by the irrigation and fertigation system included a control (CON), irrigation only (IRR), and three nutrient supplements supplied through irrigation including 56, 112, and 224 kg N ha⁻¹ yr⁻¹ (referred to as IRR+56, IRR+112, and IRR+224, respectively).

Data Collection

Diameter at breast height (DBH) and height of all trees in each plot within each treatment were measured yearly. Basal area (m² ha⁻¹), survival, and volume (m³ ha⁻¹) were calculated on a yearly basis, whereas standing biomass (Mg ha⁻¹), ANPP (Mg ha⁻¹ yr⁻¹, excluding herbivory or litter of branches, bark, or fruits, as defined on page 9), LAI (m² m⁻², calculated by multiplying weight (g) and area (m²) of leaf litter collected in litter trays by SLA (m² g⁻¹) of randomly selected canopy leaves, as defined on page 9), and total aboveground growth efficiency (Mg ha⁻¹ yr⁻¹ LAI⁻¹, ANPP per year per LAI, as defined on page 9) were calculated for years six through eight. Whole-tree allometric equations developed by Shelton et al. (1982) were used to calculate volume and aboveground woody biomass for *P. deltooides*. Their equations for *P. deltooides* were developed from trees of comparable age range, and soil type, grown in areas with similar longitude, latitude, and climate as this study. Standing woody biomass consisted of all woody components (bark, branches, and trunk/bole). Foliage biomass was

determined by summing the weight of annual litter fall collected monthly (May to January) from five litter traps (0.5 m²) for *P. deltooides*.

Biomass equations developed by Schlaegel and Kennedy (1986) were used to calculate volume and aboveground woody biomass for both *Q. pagoda* and *P. occidentalis*. The original Schlaegel and Kennedy (1986) equations used diameter measured at approximately 15 cm above ground level. All *Q. pagoda* and *P. occidentalis* DBH data were corrected to reflect the dbh measurements of the equations at 15 cm height above ground level, by using regression equations developed from sampling 100 trees per species measured at the appropriate height (data not shown, R² = 0.97 and 0.93 respectively for *Q. pagoda* and *P. occidentalis*). Foliage biomass was determined by summing the weight of annual litter fall collected from five and two litter traps (0.5 m²), for *P. occidentalis* and *Q. pagoda* respectively in each plot.

Projected LAI was calculated from the weight (g) and area (m²) of the leaf litter trays and SLA (scaled to the canopy level – m² g⁻¹) for each species within each treatment. Care was taken to ensure only leaf litter from the species within the plot was processed. If litter from other species fell or were blown into the tray, it was removed prior to collection. Leaf litter was dried for 48 hours at 70 °C and weighed to the nearest 0.01g.

Statistical Analysis

All the measured and calculated variables were compared among treatments using a repeated measure analysis of variance (ANOVA) (SAS Institute Inc. 2001) with treatment assigned as a random effect in the model. If significant differences ($\alpha = 0.05$) among treatments were revealed, multiple pairwise comparisons of means were

performed using Tukey's multiple mean test for mean separation and determining significance. Linear regression was used to analyze the relationships between LAI and ANPP and LAI and GE. Where no strong linear pattern emerged, appropriate curvilinear functions, using second order polynomial equations were fit to the data. It has been suggested that as soil nitrogen levels increase, uptake of nitrogen can be limited by the availability of other nutrients (Aber et al. 1989). Additionally, because of results from studies like Pastor and Bridgham (1999) and Bridgham et al. (1995) we hypothesized that the highest rate of nitrogen application would be far greater than the trees could utilize. As such, curvilinear functions were chosen *a priori* to ANOVA analysis and in accordance with our hypothesis that aboveground production variable responses were likely to plateau well below the maximum level of nutrients supplied by the treatments.

Results

Survival

Among all three species, *P. deltoides* had the lowest survival rates throughout the study period (Fig. 2-1), with the lowest rate occurring in the CON treatment. Survival for *P. deltoides* CON treatment decreased from 73 to 63 % from the beginning of the study through year eight. *P. deltoides* survival was greatest in the IRR treatment for all eight years ranging from 93 to 88 %. *P. occidentalis* survival changed little until year four then decreased considerably in each treatment (Fig. 2-1). Like *P. deltoides*, *P. occidentalis* survival was lowest in the CON treatment and highest in the IRR treatment (Fig. 2-1). By year eight, *P. occidentalis*, survival was 66, 85, 77, 74, and 76 % (CON, IRR, IRR+56, IRR+112, and IRR+224, respectively). *Q. pagoda* survival rates were the highest of all three species during all eight years, with the lowest survival rate occurring

in the IRR+56 treatment (83 % after year eight). Survival in the CON and IRR and IRR+112 and IRR+224 treatments for *Q. pagoda* reached 91 and 89 % respectively (Fig. 2-1).

Basal Area and Volume

Basal area for *P. deltooides* increased sharply through year five and then exhibited a slower rate of increase through year eight (Fig. 2-2). Although the *P. deltooides*, basal area in the CON treatment increased to 13.6 m² ha⁻¹ in year five a slower rate of increase occurred in year eight (17.5 m² ha⁻¹). *P. deltooides* basal area for IRR, IRR+56, IRR+112, and IRR+224, reached a maximum at 24.6, 27.3, 25.7, and 25.6 m² ha⁻¹, respectively). Basal area for *Q. pagoda* was minimal through year four, but increased substantially in all the treatments thereafter. Maximum basal area in year eight for *Q. pagoda* was 4.4, 7.4, 8.4, 9.8, and 12.9 m² ha⁻¹ for CON, IRR, IRR+56, IRR+112, and IRR+224 respectively (Fig. 2-2). Basal area in the CON treatment was always lower than other treatments for all three species throughout the study. Similarly to *P. deltooides*, *P. occidentalis* basal area increased sharply between years four and five, then more slowly through year eight. Year eight basal area for *P. occidentalis* was 11.2, 12.4, 13.8, 13.2, and 13.7 m² ha⁻¹ for CON, IRR, IRR+56, IRR+112, and IRR+224 respectively (Fig. 2-2).

Volume for each species (Table 2-1) during all three years followed the same trends as basal area. Volume was calculated as inside bark with equations developed by Shelton et al (1982) and Schlaegel and Kennedy (1986) for *P. deltooides*, *P. occidentalis*, and *Q. pagoda*, respectively). Maximum volume was obtained during year eight for all three species (219.6, 138.7, and 123.6 m³ ha⁻¹ respectively for *P. deltooides*,

P. occidentalis, and *Q. pagoda*). CON treatment volume remained consistently and significantly lower than either the IRR or the N treatments throughout the entire study.

Foliar Biomass

Foliar biomass production in the CON treatment was reduced for all species during the entire study period (Table 2-1) compared to the other treatments. Production of foliar biomass for *P. deltooides* peaked during years six and seven in the IRR+56 treatment and in the IRR treatment during year eight (3.2, 3.8, and 4.7 Mg ha⁻¹, respectively). *Q. pagoda* foliar production peaked during years six and seven in the IRR+224 treatment (2.6 and 3.1 Mg ha⁻¹, respectively) and in the IRR+112 treatment (3.6 Mg ha⁻¹) during year eight, but was not significantly different from foliar production in the IRR or other fertigation treatments (Table 2-1). Peak foliar production for *P. occidentalis* was observed in either the IRR or IRR+224 treatments for years six, seven, and eight (3.59, 4.86, and 5.48 Mg ha⁻¹, respectively).

Woody Biomass

Woody biomass (bole, branches, and bark) for *P. deltooides* and *P. occidentalis* increased significantly between the CON and the IRR treatments during all three years (Table 2-1). However, the addition of N did not result in any further significantly different increases in woody biomass for *P. deltooides*. Peak woody biomass for this species was found in the IRR+56 treatment for years six and seven (9.1 and 10.7 Mg ha⁻¹, respectively) and in the IRR treatment (12.9 Mg ha⁻¹) in year eight. For *Q. pagoda*, the fertigation treatments increased woody biomass each year successively across the nutrient gradient (Table 2-1). Peak woody biomass for this species was found in the IRR+224 for all three years (0.9, 1.5, and 2.4 Mg ha⁻¹ for years six, seven and eight, respectively). Woody biomass for *P. occidentalis* showed significantly different woody

biomass production between the IRR+56 and IRR+112 treatments with peak production occurring in the IRR+56 treatment for all three years (4.2, 4.5, and 5.0 Mg ha⁻¹ for years six, seven and eight, respectively).

Total Standing Biomass

As expected, throughout the study, total standing biomass (woody + foliage) was consistently and significantly lower in the CON treatment compared to the IRR and N treatments for all three species (). Total standing biomass for all three species in all three years showed the largest production values occurred during year eight (17.6, 5.4, and 10.4 Mg ha⁻¹, Fig. 2-3A, B, and C for *P. deltooides*, *Q. pagoda*, and *P. occidentalis*, respectively). *P. deltooides* total standing biomass reached a plateau in the IRR+56 treatment during years six and seven (12.4 and 14.5 Mg ha⁻¹, respectively, Fig. 2-3A) and in the IRR treatment in year eight (17.6 Mg ha⁻¹). Total standing biomass for *Q. pagoda* in the IRR+112 and IRR+224 treatments was significantly greater than the IRR and CON treatments in years six and seven (Table 2-1). During the eighth growing season, *Q. pagoda* total standing biomass reached a maximum (5.4 Mg ha⁻¹) in the IRR+112 treatment (Fig. 2-3B). *P. occidentalis* total standing biomass (Fig. 2-3C) peaked in the IRR treatment during years six and eight (7.4 and 10.4 Mg ha⁻¹ respectively) and in the IRR+224 treatment during year seven (9.0 Mg ha⁻¹). However, the peaks in total standing biomass for years six and seven were not significantly greater across the IRR or N treatments. For year eight, *P. occidentalis* total standing biomass in the IRR treatment was only significantly greater than the IRR+112 and IRR+224 treatments (Fig. 2-3C).

LAI

No significant differences in one-sided projected LAI for any of the three species were found between years seven and eight (Table 2-2). *P. deltooides* LAI was significantly lower in the CON treatment than in either the IRR or the N treatments in both years. However, during year eight, LAI in the IRR treatment was significantly higher than the N treatments. *Q. pagoda* LAI for year seven peaked in the highest (IRR+224) fertigation treatment ($6.0 \text{ m}^2 \text{ m}^{-2}$) and during year eight, peaked in the IRR+56 treatment ($6.3 \text{ m}^2 \text{ m}^{-2}$ Table 2-2). During year seven, *Q. pagoda* LAI in the CON and IRR treatment were not significantly different and no significant increase in LAI was detected among the N treatments. In year eight, significant differences were found only for CON, IRR+56 and IRR+224 treatments (2.5 , 6.3 , and $3.5 \text{ m}^2 \text{ m}^{-2}$, respectively). Peak LAI for *P. occidentalis* ($9.4 \text{ m}^2 \text{ m}^{-2}$) occurred in the IRR+224 treatment during year seven but was not significantly higher than LAI found in the IRR treatment. During year eight, no significant differences were found between the IRR and all of the N treatments, with peak LAI occurring in the IRR+112 treatment ($9.7 \text{ m}^2 \text{ m}^{-2}$, Table 2-2).

ANPP

The ANPP was significantly higher during year eight than year seven for all species and all treatments (Table 2-2). The CON treatment for all three species consistently had the lowest ANPP (2.3 , 1.5 , $3.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in year seven and 3.1 , 2.1 , $2.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in year eight for *P. deltooides*, *Q. pagoda*, and *P. occidentalis*, respectively, Table 2-2). For *P. deltooides*, peak ANPP during year seven occurred in the IRR+56 treatment ($5.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), but was not significantly greater than the IRR or other N treatments. During year eight *P. deltooides*, ANPP in the IRR treatment was

significantly higher than that observed in the N treatments (6.7 vs. 5.8, 5.5, and 5.4 Mg ha⁻¹ yr⁻¹, respectively). During year seven, *Q. pagoda* ANPP peaked in the IRR+224 treatment (3.8 Mg ha⁻¹ yr⁻¹) and was significantly higher than the IRR and IRR+56 treatments (2.5 and 2.6 Mg ha⁻¹ yr⁻¹ respectively). *Q. pagoda* ANPP during year eight peaked in the IRR+112 treatment but was not significantly greater than the IRR or N treatments. *P. occidentalis* ANPP peaked in the IRR+224 treatment (5.2 Mg ha⁻¹ yr⁻¹) but was not significantly different from the IRR or other N treatments (Table 2-2). For year eight, *P. occidentalis* ANPP peaked in the IRR treatment (6.38 Mg ha⁻¹ yr⁻¹) and was only moderately, but not significantly higher than the N treatments (5.8, 5.2, and 5.4 Mg ha⁻¹ yr⁻¹ for IRR+56, IRR+112, and IRR+224 treatments respectively).

Regression analysis indicated a significant relationship between ANPP and LAI for all three species (Fig. 2-4A, B, and C). For *P. deltooides*, the relationship peaked near peak LAI values found in the IRR treatment ($R^2 = 0.69$ $p \leq 0.0001$). For *Q. pagoda* and *P. occidentalis*, ANPP peaked at LAI values well below the maximum calculated LAI values (Fig. 2-4B and C, $R^2 = 0.77$ $p \leq 0.0001$ and $R^2 = 0.75$ $p \leq 0.0001$ respectively)

Growth Efficiency

Growth efficiency increased significantly between years seven and eight for *P. deltooides* and *P. occidentalis* (Table 2-2). However, no significant differences were found in growth efficiency across all treatments for both species within each year (Table 2-2). For *P. deltooides*, GE ranged from 0.7 Mg ha⁻¹ yr⁻¹ LAI⁻¹ (IRR+224) to 0.9 Mg ha⁻¹ yr⁻¹ LAI⁻¹ (IRR+56) for year seven. During year eight, GE increased for each treatment and ranged from 0.9 Mg ha⁻¹ yr⁻¹ LAI⁻¹ (IRR and IRR+224) to 1.1 Mg ha⁻¹ yr⁻¹ LAI⁻¹ (CON) but showed no significant differences among all treatments. For, *P. occidentalis* GE

ranged from 0.5 Mg ha⁻¹ yr⁻¹ to 0.6 Mg ha⁻¹ yr⁻¹ (IRR and CON) in year seven and from 0.5 Mg ha⁻¹ yr⁻¹ to 0.71 Mg ha⁻¹ yr⁻¹ (CON and IRR) in year eight, indicating a reduction in GE in both the CON and IRR+112 treatments between the two years, likely due to increased mortality and crown breakage. *Q. pagoda* growth efficiency was lower in the N treatments compared to the CON and IRR treatments in year seven. However, during year eight, *Q. pagoda* GE was significantly higher in IRR+224 treatment (1.1 Mg ha⁻¹ yr⁻¹ LAI⁻¹).

GE decreased with increasing LAI for all three species (Fig. 2-5). *P. deltooides* growth efficiency decreased linearly with increasing LAI and showed a weakly significant relationship between the two variables (R^2 0.20, $p = 0.04$). Both *Q. pagoda* and *P. occidentalis* exhibited a curvilinear relationship with a more highly correlated association between the two variables ($R^2 = 0.53$, $p = 0.001$ and $R^2 = 0.47$, $p = 0.006$, respectively). For example, maximum growth efficiency for *Q. pagoda* and *P. occidentalis* was observed at average LAI values of 4 m² m⁻² and 9 m² m⁻², respectively whereas individual species LAI reached a maximum near 8 m² m⁻² and 12 m² m⁻². It is likely that at the highest LAI values self-shading occurred resulting in less efficient light capture and therefore reduced biomass accumulation.

Discussion

Basal area and survival for all three species suggests that stand development followed an expected, but distinct pattern for each species. Although *P. deltooides* mortality was the highest among all three species (Fig. 2-1), basal area was much greater than that of *Q. pagoda* or *P. occidentalis* (Fig. 2-2). Sulfometuron methyl was applied to inhibit herbaceous and woody competition. It has been suggested that sulfometuron methyl presence in water and soil can range from 14 to 60 days and five

to 33 days, respectively (Buckwalter et al. 1996). We do not feel that mortality rates in this study were increased by the herbicide application, and possible presence in the soil and water, given that the highest mortality rates found in this study were in the CON treatment which did not have IRR or fertigation treatments. A study conducted by Netzer (1995) suggests that hybrid poplar response to sulfometuron methyl application ranged from slight decreases in growth to foliar damage. Additionally, survival rates remained high throughout the study for *Q. pagoda*, which had been subjected to the same herbicide applications as *P. deltoides* and *P. occidentalis* (Fig. 2-1). *P. occidentalis* mortality remained low during early stand development. Nevertheless, as basal area increased (Fig. 2-2) mortality remained relatively steady through year five. Lastly, because year eight woody biomass produced for *P. deltoides* in the CON treatment was comparable to *P. occidentalis* (Table 2-1) in the IRR and fertigation treatments we feel no deleterious effects of sulfometuron methyl on any of the three species. Although canopy differentiation between crown classes was not measured, observations within the stands suggested the canopy was stratifying into dominate, co-dominant, intermediate, and over-topped individuals. Mortality rates seen in *P. deltoides* toward the end of the study were likely caused by death of intermediate and overtopped trees.

Following a rapid increase in basal area through age five, basal area growth for both *P. deltoides* and *P. occidentalis* slowed and appeared to reach a plateau (Fig. 2-2). Despite reduced mortality for *Q. pagoda*, basal area remained low suggesting a slower growth pattern, which was confirmed by the low ANPP values observed in our study (Table 2-2). The ANPP values suggest available growing space was more limiting for

P. deltoides and *P. occidentalis* than for *Q. pagoda*, despite the increase in *Q. pagoda* standing biomass each year and across successive treatments (Fig. 2-3). In a study designed to determine growth rates of various clonal *Populus* species, Devine et al. (2010) found that mortality was higher for more closely spaced individuals, but failure of an irrigation system may have confounded their results.

Although, a study by Jokela et al. (2004) suggested that silvicultural treatments such as fertilization did not necessarily alter size-density relationships and competition related mortality, growing space is likely to become limited much earlier in stand development when fertilization is used. This can be substantiated by higher mortality rates in the N treatments versus IRR treatments for all three species (Fig. 2-1). High mortality rates in the CON treatments for *P. deltoides* and *P. occidentalis* might be explained by inadequate water and nutrient supplies (Henderson and Jose, 2005). The below normal rainfall (Fig. 2-6) experienced during this study likely altered mortality more so in the CON plots than in the IRR or N treatments. The IRR and N treatments likely supplemented yearly precipitation levels providing sufficient water resources to decrease mortality levels for *P. deltoides* and *P. occidentalis* which would be expected to require greater resources due to increased biomass production. However, DeBell and Whitesell (1988) suggested that self-thinning and therefore mortality occurred at higher rates of planting densities for *Eucalyptus saligna* SM. (Sydney bluegum) regardless of stand age, site quality, or soil fertility levels. Their study further suggests spacing standards to reduce mortality for this species given selected target diameters for harvesting. To expand on this idea, Goelz and Meadows (1997) suggested specific relationships between planting densities and mortality rates depending on stand

management, length of rotation, production goals, and thinning schedules for various southern bottomland hardwood plantation systems.

A study by Lockaby et al. (1997) found that IRR was not as beneficial for increasing *P. deltoides* biomass, as was the combination of IRR and fertilization treatments. In our study, *P. deltoides* height increased more than one meter and DBH increased more than 15 % with IRR and fertilization over the CON treatment (data not shown). In years six and seven of our study, *P. deltoides* woody biomass (Table 2-1) in the IRR+56 treatment was slightly less than three-fold of that found in the CON treatment. By year eight, woody biomass was greatest in the IRR treatment, slightly greater than threefold, but no significant differences were found between the IRR and N treatments. Production for natural stands, of similarly aged quaking aspen (*Populus tremuloides*) in northern Wisconsin, peaked at 25.0 Mg ha⁻¹ (Ruark and Bockheim, 1988), which is comparable to the maximum found in one plot of the IRR treatment (24.3 Mg ha⁻¹, individual data points not shown) in our study. In another study, involving quaking aspen, production varied from 0.8 to 4.2 Mg ha⁻¹ for second growth natural stand of varying ages (Crow, 1978). Although stem density was greater in the Crow (1978) study versus our study, production values for *P. deltoides* in the CON treatments (2.8 to 7.2 Mg ha⁻¹) were on the upper range of values reported by Crow (1978). In British Columbia, production for slightly younger stands of quaking aspen, on mildly fertile soils growing in mixed stand of black and white spruce, reported by Wang et al. (1995), were similar to those we calculated during year six for the IRR treatment (7.1 to 16.6 Mg ha⁻¹) in our study.

Lockaby et al. (1997) also found 80 % increase in DBH and height in response to the combination of irrigation and fertilization over the control treatment for *P. occidentalis*. Our year six and seven woody biomass for *P. occidentalis* indicated a 50 and 60 % increase, respectively, in the IRR+56 treatment. While standing biomass for *P. occidentalis* was similar to Saucier et al. (1972), decreased survival (85 to 77% year seven and eight, respectively), likely kept production from reaching its potential. Additionally, biomass was lost for this species between years seven and eight when top dieback occurred in several trees, further reducing production potential. The loss of height can account for the small differences found among treatments, as allometric equations used in this study to determine standing crop, integrate height into the calculations for biomass (Schlaegel and Kennedy 1986). While we did not thoroughly investigate the cause of the dieback, Burns and Honkala (1990) indicate plantation grown *P. occidentalis* are susceptible to a host of diseases and insect infestations such as *Xylella fastidiosa*, which may increase susceptibility to other opportunistic infestations. *X. fastidiosa* causes xylem vessels to become blocked stopping water transport through branches to leaves. This bacterium was considered the likely cause for the top dieback in *P. occidentalis* in our study. Additionally, Fiddler et al. (1989) suggested that for some species such as *Pinus ponderosa* Laws. (ponderosa pine) thinning of densely stocked stands not only reduces mortality rates, but likely reduces the rate of infestation from insects and pathogens.

Unlike *P. deltooides* and *P. occidentalis*, *Q. pagoda* production increased linearly with increased resource availability (Fig. 2-1B). The different production responses between *P. deltooides*, *P. occidentalis*, and *Q. pagoda* can be explained in part by the

silvical characteristics of the three species. *P. deltooides* and *P. occidentalis* are fast growing early successional species, both are described as intolerant of competition, are typically found in low-lying areas, and often dominate floodplains because of profuse seed crops (Burns and Honkala, 1990). *Q. pagoda* is a much slower growing longer-lived species and while it can be found in fertile bottomlands, it is generally found on the drier areas or ridges along floodplains, and is slightly more tolerant of competition than *P. deltooides* or *P. occidentalis* (Burns and Honkala, 1990).

According to our original hypothesis, peak biomass production for all three species was expected along the resource gradient at a point below the highest level of supplied nutrients. Standing biomass (Fig. 2-3) and ANPP (Table 2-2) of both *P. deltooides* and *P. occidentalis* reached peak biomass values in the IRR treatment during the last year of the study period. Additional N did not result in increased production for either of these species. *Q. pagoda* standing biomass (Fig. 2-3), on the other hand, showed positive response to both IRR and across successive N treatments. In general, both standing biomass and ANPP for *Q. pagoda* increased with increasing resources. Maximum standing biomass was observed in the IRR+224 treatment and maximum ANPP in the IRR+112 and IRR+224 treatments. Other measured variables for *Q. pagoda* such as basal area and volume followed similar trends (Fig. 2-2 and Table 2-1, respectively).

ANPP and LAI were significantly correlated for all three species (Fig. 2-4, $R^2 = 0.69, 0.77, \text{ and } 0.75, p < 0.0001$ for *P. deltooides*, *Q. pagoda* and *P. occidentalis* respectively). The observed relationships are similar to findings from other studies from both natural stands and plantations (Fassnacht and Gower, 1997, Albaugh et al., 1998

and Bolstad et al., 2001). The curvilinear relationship for all three species indicates that maximum ANPP is often reached at an optimum LAI and not at maximum LAI. This relationship also suggests that additional resources, beyond those affecting optimum LAI will likely not result in increased aboveground biomass production. Other studies have also shown a curvilinear relationship between ANPP and LAI (Waring 1983, Jose and Gillespie 1997, and Fang et al. 1998). Increased LAI beyond this threshold can result in self-shading and decreased canopy photosynthetic efficiency (Henderson and Jose, 2005). This was also revealed while examining the relationship between growth efficiency and LAI (Fig. 2-5). A negative linear relationship was found for *P. deltooides* and curvilinear relationships were observed for *Q. pagoda* and *P. occidentalis* with increasing LAI. This suggests that increased light capture allowed by increased foliar biomass+ does not necessarily translate into higher carbon allocation aboveground. A companion study by Henderson and Jose (2005) also revealed canopy photosynthetic thresholds suggesting no further increase in aboveground biomass production was observed for the same species.

The lack of response of LAI and ANPP to increasing levels of N is perhaps an indication of sufficient mineralized N in the soil. For *P. deltooides* and *P. occidentalis*, IRR alone was sufficient to increase LAI and ANPP to the peak values. In fact, *P. deltooides* ANPP and LAI exhibited significant decreases with the addition of N. ANPP and LAI of *Q. pagoda* also decreased in the IRR+224 treatment compared to the other N treatments.

P. deltooides and *P. occidentalis* ANPP followed the same trend as standing biomass with ANPP reaching a plateau in the IRR treatment. The ANPP values in our

study are within the range reported in other studies (Table 2-3). For example, a study by Singh (1998) estimated average ANPP, for a 10-year-old *P. deltoides* plantation, ranged from 1.5 to 4.9 Mg ha⁻¹ yr⁻¹ with a much higher planting density (Table 2-3) than our study. In our study, we found ANPP rates for the same species to be much higher at 6.8 Mg ha⁻¹ yr⁻¹ with a stocking density of 1400 trees ha⁻¹. A study by Netzer et al. (2002) of hybrid *Poplar* clones reported ANPP values ranging from 3.5 to 9.5 Mg ha⁻¹ yr⁻¹ for eight-year-old plantations, planted at approximately 25 % greater density than our study. Ruark and Bockheim (1988) reported ANPP values of 5.9 Mg ha⁻¹ yr⁻¹ for eight-year-old *P. tremuloides* grown in the north central USA that are comparable to our findings. ANPP found in other studies (see Table 2-3; Bowersox and Ward 1976, Dawson et al. 1976, and Hopmans et al. 1990) were similar to our findings but with greater stocking densities. In a similar study, Strong and Hansen (1993) reported ANPP values for *Populus* clone NE-41, ranged from 4.9 to 6.3 Mg ha⁻¹ yr⁻¹ for an eight-year-old plantation. A few studies (see Table 2-3; Hopmans et al. 1990, Strong and Hansen 1993, and De Bell and Harrington 1997) reported higher ANPP rates with greater stocking densities.

P. occidentalis had ANPP values similar to those found in plantations or natural stand of similarly aged hardwoods (Table 2-3). For example, Saucier et al. (1972) found ANPP for four-year-old *P. occidentalis* ranging from 1.8 to 4.0 Mg ha⁻¹ yr⁻¹. In our study, maximum ANPP of eight-year-old *P. occidentalis* reached a maximum of 6.31 Mg ha⁻¹ yr⁻¹. Several studies found comparable (see Table 2-3; Coyle and Coleman 2005) or lower (see Table 2-3; Krinard and Kennedy 1981, Tuskan and de la Cruz 1982, and Francis 1984,) rates of ANPP for younger *P. occidentalis* planted at a lower rate of

stocking density. Other studies with greater stocking densities found lower (see Table 2-3; Wood et al, 1976, Wittwer et al. 1978, Dickman et al. 1985, Tschaplinski et al. 1991, and Steinbeck 1999), comparable (see Table 2-3; Wittwer 1980 and Tang and Land 1996), or higher (see Table 2-3; Steinbeck et al. 1972 and van Miegroet et al. 1994) rates of ANPP. These comparisons suggest the application of IRR and N treatments can increase site nutrient availability, resulting in increased biomass with lower stocking density. Fewer trees ha⁻¹ would suggest increased growing space and a delay in competition both above- and below-ground.

ANPP values for *Q. pagoda* also followed the same trend found for standing biomass, with peak values observed in either the IRR+112 (year seven) or the IRR+224 (year eight) treatments. Although no comparable studies on *Q. pagoda* ANPP were found in the literature, values observed in this study were within the range reported for oak dominated natural stands. A study by Fassnacht and Gower (1997) reported ANPP values ranging from 3.3 to 4.0 Mg ha⁻¹ yr⁻¹ for natural stands dominated by *Quercus* species in the upper Midwest. Additionally, Jose and Gillespie (1997) found ANPP for mature mixed hardwood stands that ranged from approximately 1.0 to 6.0 Mg ha⁻¹ yr⁻¹.

Few studies have looked at simultaneous application of irrigation with fertilizer for growing SRWC on agricultural fields. While fertigation techniques are relatively infrequent, the resource gradient allows an opportunity to study resource requirements and mechanisms necessary for maximum aboveground biomass production. Given the data collected during our study and the current literature available for these three species, several generalizations regarding the use of *P. deltoides*, *Q. pagoda*, and *P. occidentalis* in short-rotation plantations can be made. Our data indicate that plantation

establishment for *P. deltooides* may not have to be restricted to bottomland sites for maximum production. The significant production response of *P. deltooides* to the IRR treatment and the lack of significant differences for the N treatments suggest that IRR alone may be sufficient to obtain maximum growth on good quality sites such as agricultural fields. *P. deltooides* may benefit from low levels of fertilization on low quality sites. *Q. pagoda*'s positive linear response to treatments applied in this study may prove beneficial for accelerating production in plantations. Its slow growth rate, compared to *P. deltooides* and *P. occidentalis*, would otherwise preclude it from short-rotation operations. Despite increased production in response to the IRR treatment, standing biomass for *P. occidentalis* was considerably lower than *P. deltooides*. Disease, crown breakage, and mortality may have confounded the production response of *P. occidentalis* to cultural treatments. Overall, our results suggest that ANPP is highly correlated with LAI; however, the relationship is species specific given the differing growth rates among the three species. Maximum ANPP was reached well below the maximum LAI for *Q. pagoda* and *P. occidentalis*. *P. deltooides* ANPP was highest at the maximum LAI, which was achieved with IRR alone.

These results suggest that species-specific cultural practices that produce the optimum LAI and maximum ANPP need to be identified before fertigation techniques can be widely adopted for increasing biomass production potential of SRWC. The high biomass production potential of SRWC such as those tested in our study will play a significant role in helping to meet renewable energy standards.

Table 2-1. Volume, woody, and foliar biomass for all three species for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* and all five treatments control (CON), irrigation (IRR), 56 kg N ha⁻¹ yr⁻¹ (IRR+56), 112 kg N ha⁻¹ yr⁻¹ (IRR+112), and 224 kg N ha⁻¹ yr⁻¹ (IRR+224). Upper case letters indicate significant differences between years ($p \leq 0.05$) and lower case letters indicate significant differences among treatments within a year for each species.

	Volume (m ³ ha ⁻¹)		Woody Biomass (Mg ha ⁻¹)				Foliar Biomass (Mg ha ⁻¹)			
	<i>P.</i> <i>deltooides</i>	<i>Q. pagoda</i>	<i>P.</i> <i>occidentalis</i>	<i>P.</i> <i>deltooides</i>	<i>Q. pagoda</i>	<i>P.</i> <i>occidentalis</i>	<i>P.</i> <i>deltooides</i>	<i>Q. pagoda</i>	<i>P.</i> <i>occidentalis</i>	
Year 6										
CON	90.63 Ab	12.34 Ad	65.26 Ac	3.25 Ab	0.08 Ad	2.81 Ac	1.61 Ac	1.36 Ac	2.66 Ad	
IRR	142.04 Aa	26.03 Ac	85.81 Ab	8.53 Aa	0.36 Ac	3.77 Aab	2.95 Aab	1.86 Abc	3.59 Aa	
IRR+56	163.30 Aa	33.10 Abc	97.85 Aa	9.14 Aa	0.50 Abc	4.18 Aa	3.21 Aa	1.95 Ab	2.82 Acd	
IRR+112	153.56 Aa	37.85 Ab	87.25 Ab	8.25 Aa	0.59 Ab	3.62 Ab	2.57 Aab	2.18 Aab	3.14 Abc	
IRR+224	150.29 Aa	52.97 Aa	96.95 Aa	9.09 Aa	0.88 Aa	3.90 Aab	2.36 Ab	2.62 Aa	3.29 Aab	
Year 7										
CON	98.94 Bb	18.01 Bd	67.93 Bd	3.64 Bb	0.14 Bc	2.78 Bc	1.86 Bb	1.40 Ac	3.42 Bc	
IRR	155.19 Ba	40.07 Bc	96.82 Bbc	9.51 Ba	0.68 Bb	4.05 Bab	3.51 Ba	2.12 Ab	4.44 Bab	
IRR+56	188.32 Ba	50.66 Bbc	111.89 Ba	10.73 Ba	0.89 Bb	4.49 Ba	3.78 Ba	2.15 Ab	4.17 Bb	
IRR+112	167.70 Ba	55.75 Bb	95.65 Bc	9.13 Ba	0.99 Bb	3.65 Bb	3.46 Ba	2.57 Aab	4.36 Bab	
IRR+224	168.75 Ba	80.92 Ba	108.60 Bab	10.28 Ba	1.48 Ba	4.15 Bab	3.29 Ba	3.14 Aa	4.86 Ba	
Year 8										
CON	111.72 Cb	30.98 Cc	82.18 Cc	4.22 Cb	0.51 Cc	2.42 Cc	2.52 Cb	1.77 Bb	3.16 Cc	
IRR	199.26 Ca	65.98 Cb	123.82 Cb	12.87 Ca	1.28 Cb	4.88 Ca	4.68 Ca	2.80 Bab	5.48 Ca	
IRR+56	219.61 Ca	77.11 Cb	142.02 Ca	12.60 Ca	1.41 Cb	4.97 Ca	3.89 Ca	3.09 Bab	5.22 Cab	
IRR+112	194.44 Ca	89.80 Cb	124.82 Cb	10.63 Ca	1.78 Cab	4.12 Cb	3.91 Ca	3.64 Ba	4.64 Cb	
IRR+224	195.67 Ca	123.56 Ca	138.71 Cab	11.69 Ca	2.38 Ca	4.55 Cab	3.99 Ca	2.84 Bab	4.92 Cab	

Table 2-2. ANPP, LAI, and growth efficiency (GE) for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* and all five treatments control (CON), irrigation (IRR), 56 kg N ha⁻¹ yr⁻¹ (IRR+56), 112 kg N ha⁻¹ yr⁻¹ (IRR+112), and kg N ha⁻¹ yr⁻¹ (IRR+224). Upper case letters indicate significant differences between years ($p \leq 0.05$) for each species. Lower case letters indicate significant differences among treatments within a year ($p \leq 0.05$) for each species.

Year	ANPP (Mg ha ⁻¹ yr ⁻¹)			LAI (m ² m ⁻²)			GE (Mg ha ⁻¹ yr ⁻¹ LAI ⁻¹)		
	<i>P. deltooides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>	<i>P. deltooides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>	<i>P. deltooides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>
Year 7									
CON	2.25 Ab	1.47 Ac	3.39 Ab	2.85 Ab	1.50 Ab	5.48 Ac	0.79 Aa	0.98 Aa	0.62 Aa
IRR	4.48 Aa	2.44 Ab	4.73 Aa	6.37 Aa	3.05 Ab	9.08 Aab	0.70 Aa	0.80 Aa	0.53 Aa
IRR+56	5.37 Aa	2.54 Ab	4.48 Aa	6.26 Aa	5.48 Aa	8.01 Ab	0.86 Aa	0.46 Ab	0.56 Aa
IRR+112	4.34 Aa	2.97 Aab	4.39 Aa	5.62 Aa	5.58 Aa	7.49 Ab	0.77 Aa	0.53 Ab	0.59 Aa
IRR+224	4.46 Aa	3.75 Aa	5.11 Aa	6.62 Aa	5.93 Aa	9.39 Aa	0.67 Aa	0.63 Aab	0.55 Aa
Year 8									
CON	3.10 Bc	2.14 Bb	2.81 Bc	2.76 Ac	2.46 Ac	5.46 Ab	1.12 Ba	0.87 Abc	0.51 Ba
IRR	6.66 Ba	3.40 Bab	6.31 Ba	7.41 Ab	4.09 Aab	8.87 Aa	0.90 Ba	0.83 Aabc	0.71 Ba
IRR+56	5.76 Bb	3.62 Bab	5.71 Bab	5.84 Aa	6.26 Ab	9.18 Aa	0.99 Ba	0.58 Ac	0.62 Ba
IRR+112	5.41 Bb	4.43 Ba	5.11 Bb	5.94 Aa	4.71 Aab	9.68 Aa	0.91 Ba	0.94 Aab	0.53 Ba
IRR+224	5.39 Bb	3.74 Bab	5.31 Bb	5.98 Aa	3.51 Aa	9.38 Aa	0.90 Ba	1.07 Aa	0.57 Ba

Table 2-3. Aboveground net primary productivity (ANPP) of plantations and naturally occurring stands of *P. deltoides*, *Q. pagoda* and *P. occidentalis* from published literature.

Species	Location	ANPP (Mg ha ⁻¹ yr ⁻¹)	Stocking (trees ha ⁻¹)	Age (years)	Reference
<i>P. deltoides</i> ¥	Florida , USA	6.7	1400	8	This study
<i>P. deltoides</i> †	Pennsylvania, USA	5.1	>21,739	4	Bowersox and Ward (1976)
Populus clone (<i>Tristis</i> #1) ‡	Wisconsin, USA	2.5	31,338	1	Dawson et al. (1976)
<i>P. deltoides</i> §	Washington, USA	16	20,000	3	De Bell and Harrington (1997)
<i>P. deltoides</i> *	Wodonga, Australia	11.7	620	4	Hopmans et al. (1990)
<i>P. deltoides</i> *	Wodonga, Australia	6.8	6,620	4	Hopmans et al. (1990)
<i>P. deltoides</i>	Banthra, India	4.9	1,666	10	Singh (1998)
Populus clone NE-41	Wisconsin, USA	12.8	10,000	16	Strong and Hansen (1993)
<i>Q. pagoda</i> ¥	Florida, USA	4.4	1,400	8	This study
<i>P. occidentalis</i> ¥	Florida, USA	6.3	1,400	8	This study
<i>P. occidentalis</i>	South Carolina, USA	6.3	1,333	3	Coyle and Coleman (2005)
<i>P. occidentalis</i>	Georgia, USA	4.6	3,472	4	Dickmann et al. (1985)
<i>P. occidentalis</i>	Arkansas, USA	2.5	883	5	Francis (1984)
<i>P. occidentalis</i>	Mississippi, USA	2.4	1,076	5	Krinard and Kennedy (1981)
<i>P. occidentalis</i>	Georgia, USA	9.2	26,898	4	Steinbeck et al. (1972)
<i>P. occidentalis</i>	Georgia, USA	5.8	3,363	4	Steinbeck (1999)
<i>P. occidentalis</i>	Mississippi, USA	6.8	2,252	3	Tang and Land (1996)
<i>P. occidentalis</i>	Tennessee, USA	4.0	4,000	1	Tschaplinski et al. (1991)
<i>P. occidentalis</i>	Mississippi, USA	4.3	1,200	5	Tuskan and de la Cruz (1982)
<i>P. occidentalis</i>	Tennessee, USA	14.5	3,333	3	van Miegroet et al. (1994)
<i>P. occidentalis</i>	Kentucky, USA	4.1	37,037	3	Wood et al. (1976)
<i>P. occidentalis</i>	Kentucky, USA	3.4	5,978	5	Wittwer et al. (1978)
<i>P. occidentalis</i>	Kentucky, USA	6.5	6,050	5	Wittwer et al. (1980)

¥Calculated average from this study, *calculated average from Hopmans et al. (1990), †calculated average from Bowersox and Ward (1976), ‡calculated average from Dawson et al. (1976), §calculated average from de Bell and Harrington (1997).

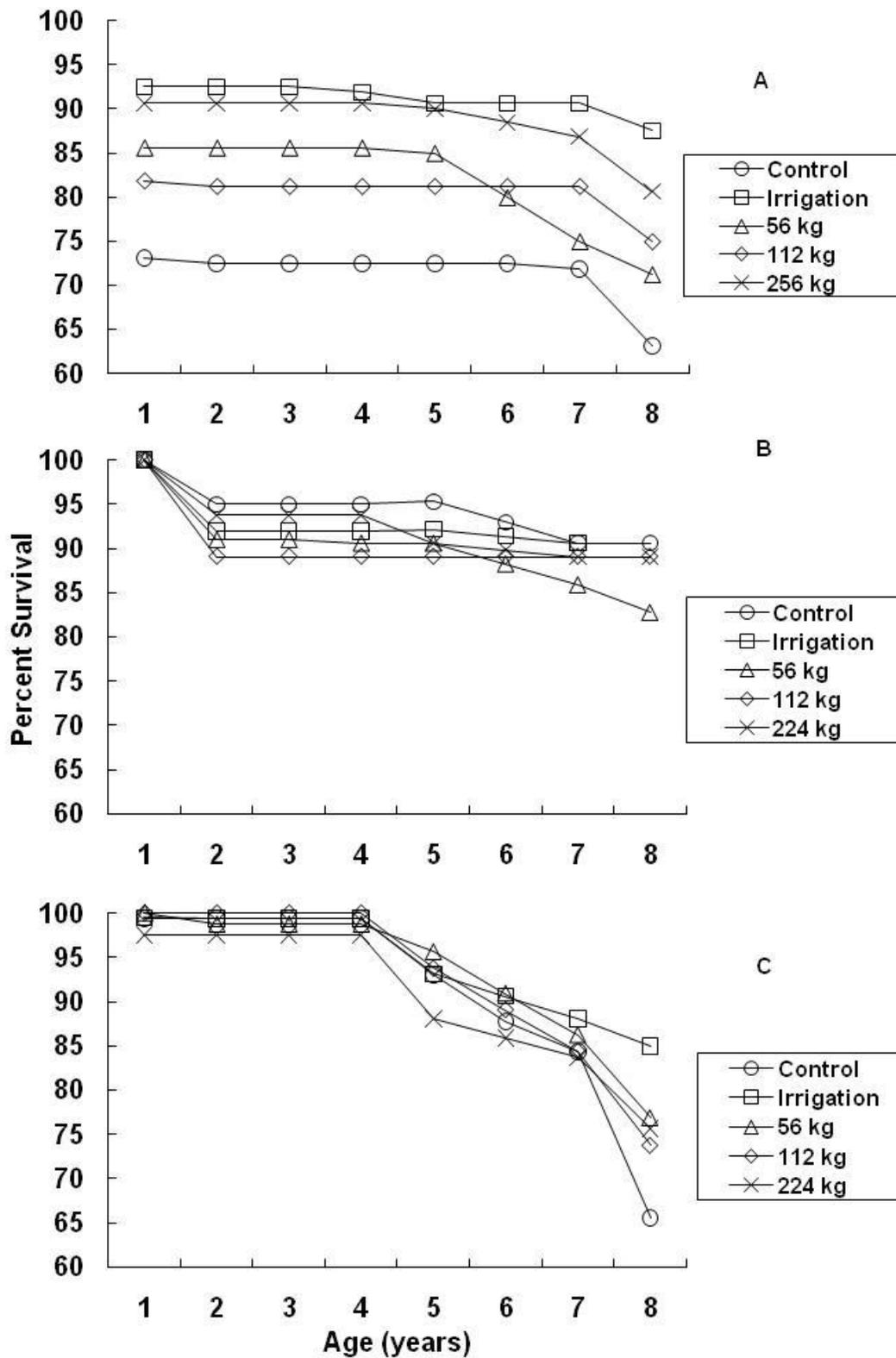


Figure 2-1. Percent survival for, *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) within each treatment.

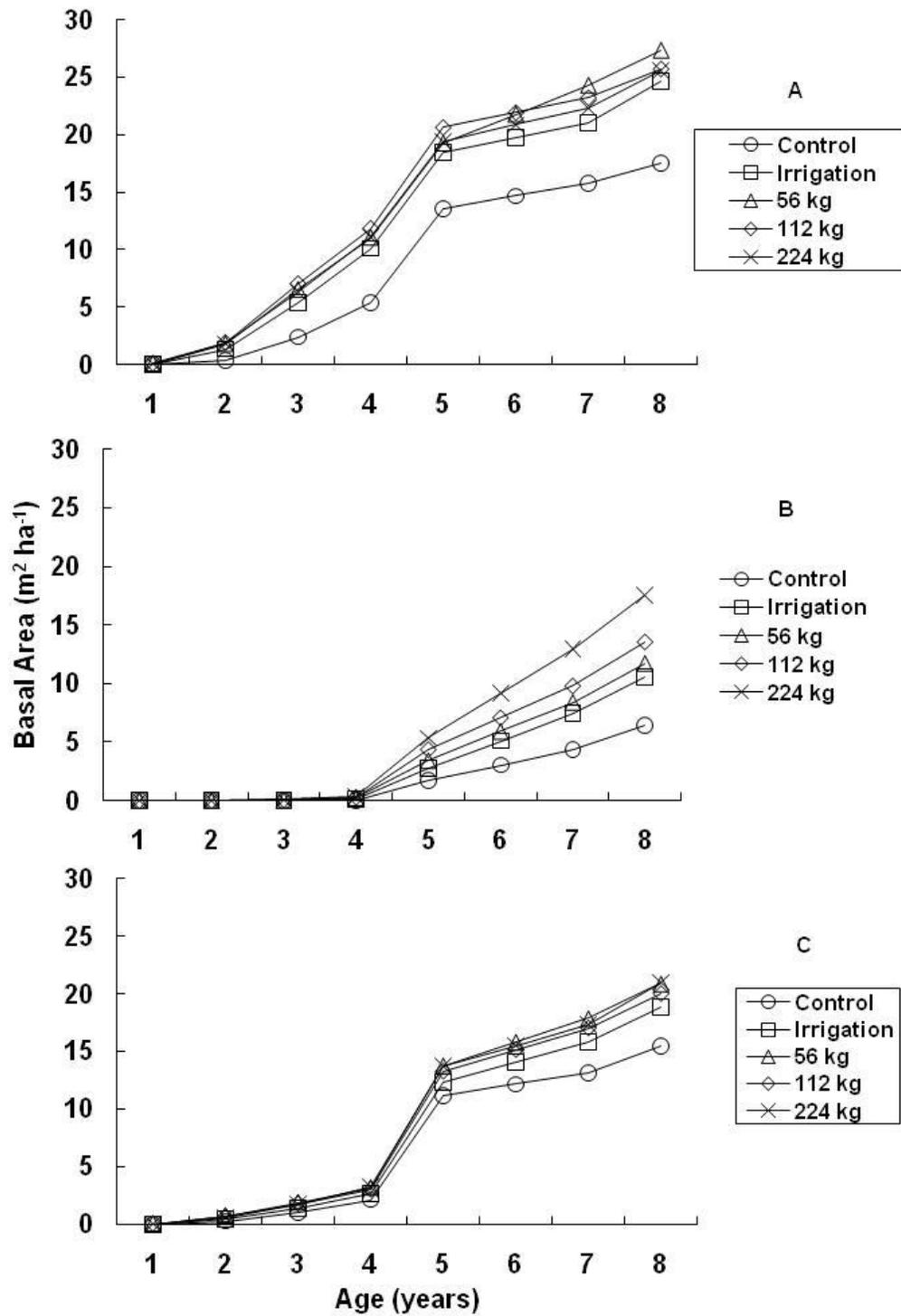


Figure 2-2. Annual basal area accretion (m² ha⁻¹) species, *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) within each treatment for each.

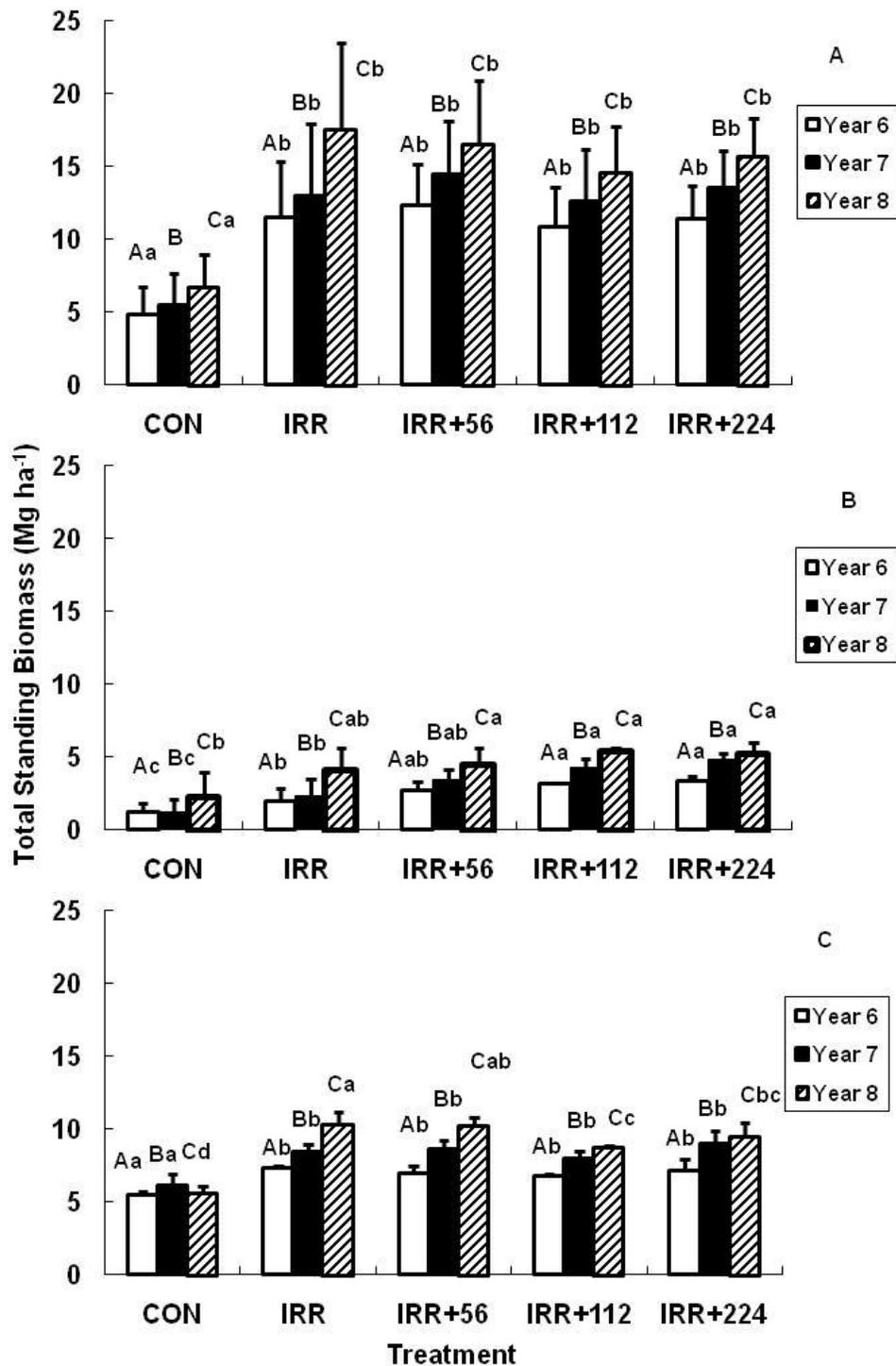


Figure 2-3. Total (woody + foliar) standing biomass (Mg ha⁻¹) for years six, seven, and eight for *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C). Capital letters indicate significant differences between years ($p \leq 0.05$). Lower case letters indicate significant differences among treatments within a year ($p \leq 0.05$).

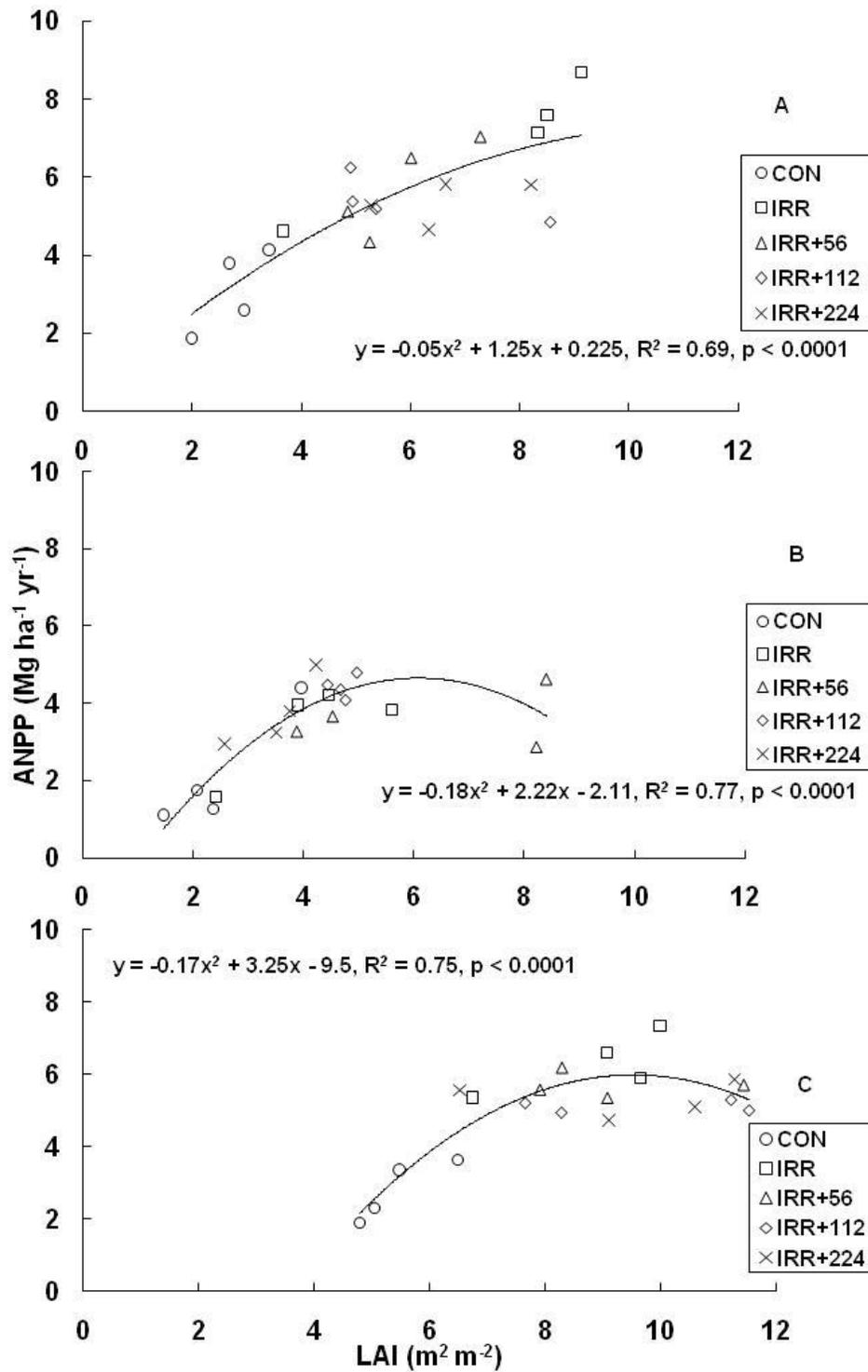


Figure 2-4. Relationship between ANPP (Mg ha⁻¹ yr⁻¹) and LAI for *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C).

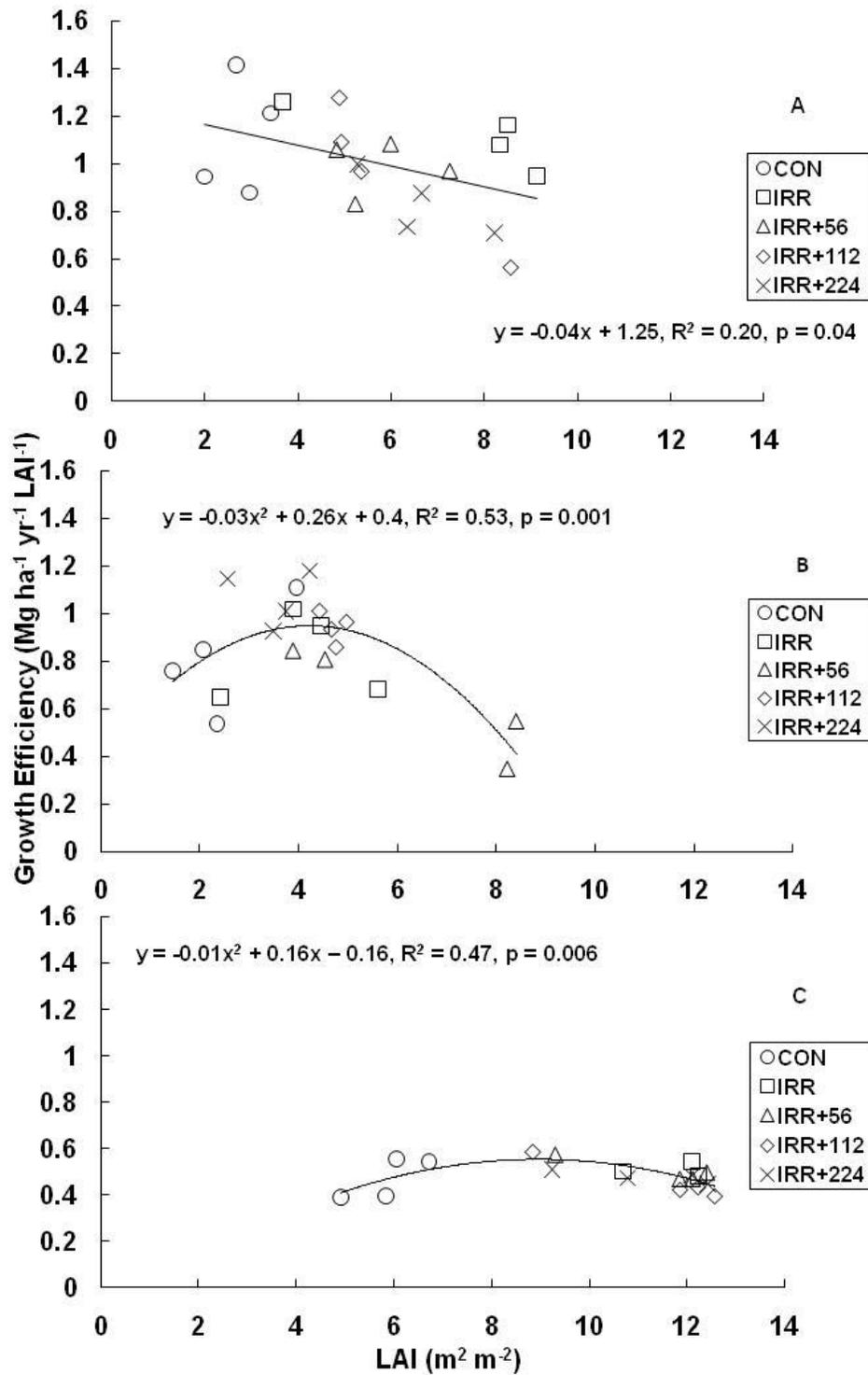


Figure 2-5. Growth Efficiency ($\text{Mg ha}^{-1} \text{ yr}^{-1} \text{ LAI}^{-1}$) and mean LAI (per species per treatment) for *P. deltoides* (A), *Q. pagoda* (B), and *P. occidentalis* (C).

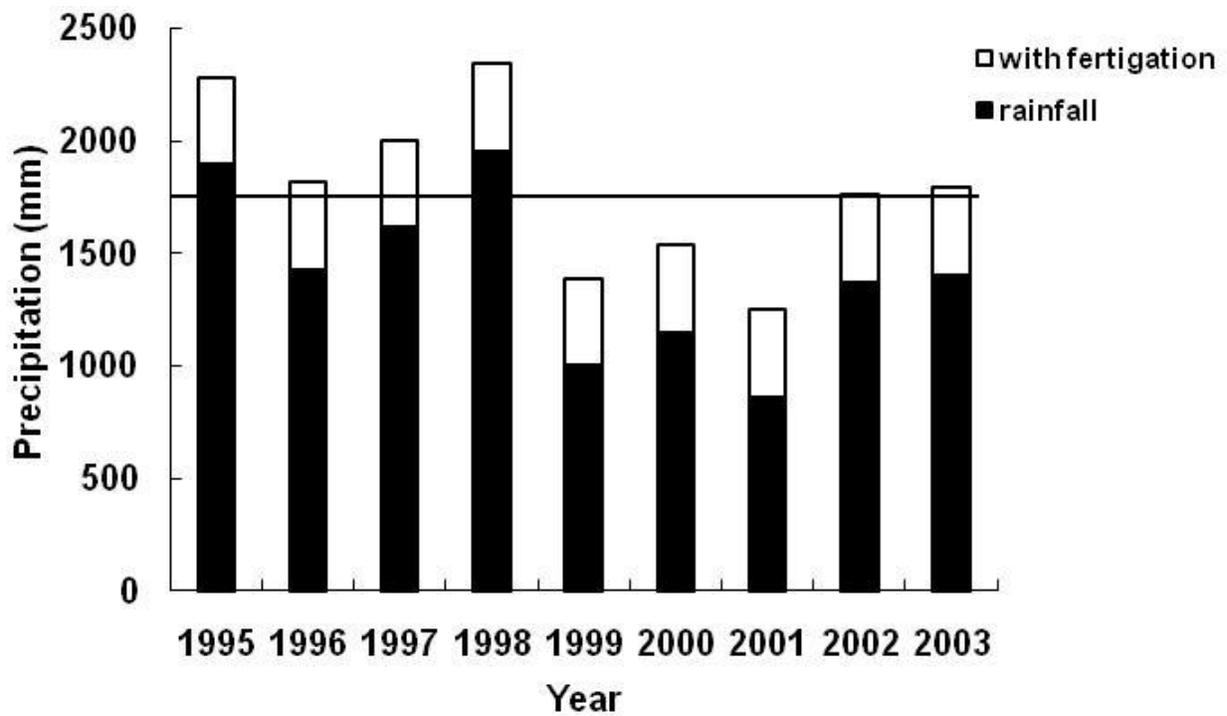


Figure 2-6. Yearly rainfall averages during the study, 1995 (year 0) through 2003 (year 8). Dark bars indicate the annual rainfall and light bars indicate the addition of moisture from the fertigation system. Historic annual rainfall averages near 1700 mm represented by the solid line.

CHAPTER 3

PRODUCTION PHYSIOLOGY OF THREE FAST GROWING HARDWOOD SPECIES UNDER VARYING NITROGEN AND WATER AVAILABILITY

It is well known that a suite of canopy level mechanisms influence potential aboveground production and that each mechanism can influence the functionality of others. The highly correlated relationships between leaf area (LA), net photosynthesis (P_{net} , P_{max} , A_{net} , or A_{max}), and foliar nitrogen (N) content can be characterized mechanistically, either singly or in combination, to describe limitations placed on aboveground biomass accumulation. These mechanisms have been studied extensively, (Wang et al. 1991, Ellsworth and Reich 1992, Jose and Gillespie, 1997, Jokela and Martin 2000, and Samuelson et al. 2001) and found to be the main constraints operating within tree canopies, influencing carbon fixation and allocation patterns (Tan and Hogan 1997, Albaugh et al., 1998, and King et al. 1999).

The amount of LA available for light capture is controlled by both resource availability and growing space (Rhodenbaugh and Pallardy 1993, Samuelson 1998, Reich et al. 1998a, Chang 2003, and Allen et al. 2004). Studies have shown a positive correlation between leaf area and water availability in both plantations and natural stands (Jose and Gillespie 1997, Albaugh 1998, and Stape et al. 2004). Decreased water availability can also restrict P_{net} on a leaf area and weight basis, which often translates into reduced aboveground biomass (Pereire et al. 1992, Davis et al. 1999, and Samuelson 2000). It is well known that leaf gas exchange, and therefore intake of CO_2 decreases as water availability decreases (Rhodenbaugh and Pallardy 1993, Reich et al. 1999, and Gunderson et al. 2002). However, if LA can be increased by increasing water availability, even without simultaneous increases in photosynthetic rates, the net result is an overall increase in the rate of canopy P_{net} (Binkley et al. 2004). For

instance, a study of *Eucalyptus* spp. plantations conducted by Stape (2002) found that irrigation increased LA and thereby light capture resulting in a two-fold increase in woody biomass increment over the control treatment, while P_{net} changed very little. Conversely, in a study of 4-year-old sweetgum, (*Liquidambar styraciflua* L.), *Populus deltoides* Bartr. and *Platanus occidentalis* L., Lockaby et al. (1997) found that irrigation alone did not translate into increased woody biomass. While specific site characteristics, species, and stage of tree development can make comparisons between studies difficult, the above examples and other studies suggest that water may be limiting potential gains in aboveground biomass.

Regardless of the amount of LA displayed, low photosynthetic rates, especially for slower growing species, may only be sufficient to fulfill energy demands of respiration and cell maintenance, which will inherently restrict potential aboveground growth (Lambers et al. 1998). When nutrients such as nitrogen are limiting for photosynthetic processes, feedback mechanisms can function to increase belowground biomass enhancing resource capture (Lambers et al. 1998). Studies have shown that increased foliar N content is positively correlated with P_{net} and subsequent increases in aboveground biomass (Monteith 1972, Coleman et al. 1998, Samuelson 1998, Green et al. 2001, and Wright et al. 2001). However, a study by King et al. (1999) indicated an increase in belowground biomass for 8-year-old fertilized and irrigated loblolly pine (*Pinus taeda* L.) over the control treatment, indicating for some species, shifts in biomass partitioning may be constrained by ontogeny as well as environmental conditions. Samuelson et al. (2001) found that the combination of irrigation and fertilization resulted in increased growth, but not increased net photosynthesis or

production efficiency for loblolly pine, suggesting belowground biomass may have increased with irrigation and fertilization. Given the above findings, further research is needed to understand the link between canopy processes and the interactions between leaf area, P_{net} , and foliar N concentration in regulating aboveground biomass production.

Our study was designed to investigate the canopy processes regulating aboveground biomass production across a broad soil resource gradient. We wanted to determine how photosynthesis, SLA (specific leaf area $\text{cm}^2 \text{g}^{-1}$ or $\text{m}^2 \text{kg}^{-1}$), SLN (g N m^{-2}), and projected LAI ($\text{m}^2 \text{m}^{-2}$) would respond to increased resources. We hypothesized that by increasing water and nitrogen availability we would see a corresponding increase in SLA and SLN, which, in turn, would increase A_{max} on a leaf area basis. Increased A_{max} in combination with an increase in LAI would result in greater aboveground biomass production along the increasing resource gradient.

Methods and Materials

Study Site

Our study was conducted in a fertigation trial established on an abandoned agricultural field (30.50'N, 87.11'W) in Santa Rosa County, Florida, USA. The climate is temperate with mild winters and hot, humid summers. Average rainfall is 1700mm, with average minimum and maximum temperatures of 10 and 27 °C respectively (NOAA, 2003). The soil is characterized as a well-drained, Redbay sandy loam (a fine-loamy, siliceous, thermic, Rhodic Paleudult) formed in thick beds of loamy marine deposits with an average water table depth of 1.8m (Lee and Jose 2003).

Treatment plots of *P. deltoides* (cottonwood) and *P. occidentalis* (sycamore) consisted of 40 trees plot^{-1} and *Quercus pagoda* Raf., (cherrybark oak). *Q. pagoda*

contained 16 trees plot⁻¹; (although the *Q. pagoda* plots were the smallest of the three species, and found for this study should be treated with caution, the results reflect data collected within the study). All treatment plots were planted at 2.13m X 3.35m spacing (1400 trees ha⁻¹). The study design was a randomized complete block (RCB) with four replications of each treatment. Site preparation included disking and subsoiling to facilitate planting. Fertilization at the time of planting included broadcast application of diammonium phosphate, dolomitic lime, potash, and a micronutrient mixture. These treatments added elemental calcium, nitrogen, phosphorus, magnesium, zinc, copper, and manganese (1009, 50, 56, 126, 3, 3, and 2 kg ha⁻¹ respectively, Greg Leach, personal communication). Soil pH was adjusted to 6.0, with 3363 kg ha⁻¹ of dolomitic lime, based on recommendations from a similar trial at North Carolina State University Research Cooperative (Coleman et al. 2004, Samuelson et al. 2004a, and Samuelson et al. 2004b), and remained near that pH level throughout the study (Lee and Jose 2003). Herbaceous weed control was attained with combinations of chemical (sulfometuron methyl and glyphosate) and mechanical (mowing and manual pulling) treatments during the first and second growing seasons. Installation of the nutrient supply system and planting of trees occurred during spring 1995. The irrigation system operated for approximately two hours each day (on average 390mm water Greg Leach, personal communication) during the growing season (May-Sep.) with nitrogen application occurring two to eight minutes each day creating the nitrogen gradient across the treatments (Lee and Jose 2003; 2006).

The study design was a Randomized Block Design with four replications of each treatment. Five treatments were established including control (CON), irrigated only

(IRR), and three nitrogen supplements, (56, 112, and 224 kg N ha⁻¹ yr⁻¹, referred to as IRR+56, IRR+112, and IRR+224), supplied through irrigation. Treatment plots of *P. deltoides* (*Populus deltoides* Bartr.) and *P. occidentalis* (*Platanus occidentalis* L.) consisted of 40 trees per plot and *Q. pagoda* (*Quercus falcata* var. *pagodafolia*) had only 16 trees per plot due to space constraints. All treatment plots were planted at 2.13m X 3.35m spacing (1400 trees per ha).

Data Collection

Light saturated photosynthesis, A_{\max} ($\mu\text{mol m}^2 \text{s}^{-1}$), was measured with a Li-Cor 6400 portable infrared gas analyzer (Li-Cor, Lincoln, NE, USA) during mid-summer and peak foliar production, (June 26 through July 2, 2002; 6-year-old trees). Relative humidity, temperature, and CO₂ were maintained at ambient levels with irradiance kept constant at 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ by a red/blue LED light source. Samples were collected between the hours of 0800 and 1500. Measurements were made on five randomly chosen sun (upper one third of the canopy and exterior position), and shade (lower one third of the canopy), leaves on two representative trees within each plot for each species and each treatment. All leaves sampled for photosynthesis were labeled, stored on dry ice in the field and then refrigerated at the lab for not more than three days before analysis. Leaf area (cm²) was determined by passing each leaf through a Li-Cor LI-3100 Leaf Area Meter and then weighed to the nearest 0.01g. SLA was calculated by dividing the foliar area by weight. The foliar samples were dried at 70 °C for 48 hours, ground to a fine powder and analyzed for total nitrogen (Kjeldahl), at the University of Florida Analytical Research Laboratory. Specific leaf nitrogen (SLN g N m⁻²)

²) was calculated using specific leaf weight (SLW g m^{-2}) and leaf nitrogen concentration (mg N g^{-1} leaf weight).

Canopy photosynthesis was calculated by slightly modifying the protocol of Herrick and Thomas (2003). Rather than multiplying the mean sun and shade leaf A_{max} by total leaf area, we multiplied mean sun and shade A_{max} by LAI. This is different from calculating the whole canopy photosynthesis of individual trees; however, it gives a measure of canopy photosynthesis per square meter of ground area.

For biomass calculations, diameter at breast height (DBH) and height of all trees in each plot within each treatment were measured yearly. Standing biomass (Mg ha^{-1}), ANPP ($\text{Mg ha}^{-1} \text{ yr}^{-1}$, excluding herbivory or litter of branches, bark, or fruits, as defined on page 9), LAI ($\text{m}^2 \text{ m}^{-2}$, calculated by multiplying weight (g) and area (m^2) of leaf litter collected in litter trays by SLA ($\text{m}^2 \text{ g}^{-1}$) of randomly selected canopy leaves, as defined on page 9), were calculated for year six. Whole-tree allometric equations developed by Shelton et al. (1982) were used to calculate volume and aboveground woody biomass for *P. deltoides*. Their equations for *P. deltoides* were developed from trees of comparable age range, and soil type, grown in areas with similar longitude, latitude, and climate as this study. Standing woody biomass consisted of all woody components (bark, branches, and trunk/bole). Foliage biomass was determined by summing the weight of annual litter fall collected monthly (May to January) from five litter traps (0.5 m^2) for *P. deltoides*.

Biomass equations developed by Schlaegel and Kennedy (1986) were used to calculate volume and aboveground woody biomass for both *Q. pagoda* and *P. occidentalis*. The original Schlaegel and Kennedy (1986) equations used diameter

measured at approximately 15 cm above ground level. All *Q. pagoda* and *P. occidentalis* DBH data were corrected to reflect the dbh measurements of the equations at 15 cm height above ground level, by using regression equations developed from sampling 100 trees per species measured at the appropriate height (data not shown, $R^2 = 0.97$ and 0.93 respectively for *Q. pagoda* and *P. occidentalis*). Foliage biomass was determined by summing the weight of annual litter fall collected from five and two litter traps (0.5 m^2), for *P. occidentalis* and *Q. pagoda* respectively in each plot.

Projected LAI was calculated from the weight (g) and area (m^2) of the leaf litter trays and SLA (scaled to the canopy level – $\text{m}^2 \text{ g}^{-1}$) for each species within each treatment. Care was taken to ensure only leaf litter from the species within the plot was processed. If litter from other species fell or were blown into the tray, it was removed prior to collection. Leaf litter was dried for 48 hours at $70 \text{ }^\circ\text{C}$ and weighed to the nearest 0.01g.

Statistical Analysis

All the measured and calculated variables were compared among treatments using analysis of variance (ANOVA) for a randomized block design (SAS Institute Inc. 1999) for each species. If significant differences ($\alpha = 0.05$) among treatments were revealed, multiple pairwise comparisons of means were performed using Duncan's multiple range test for mean separation. Linear regression was used to analyze the relationships between A_{max} and SLN. It has been suggested that as soil nitrogen levels increase, uptake of nitrogen can be limited by the availability of other nutrients (Aber et al. 1989). Additionally, because of results from studies like Pastor and Bridgham (1999) and Bridgham et al. (1995) we hypothesized that the highest rate of nitrogen application

would be far greater than the trees could utilize. As such, curvilinear functions were chosen *a priori* to ANOVA analysis and in accordance with our hypothesis that physiological responses and the relationships with growth parameters would likely to plateau, well below the maximum level of nutrients supplied by the treatments, specifically, the relationship between canopy A_{\max} and ANPP.

Results

A_{\max}

A_{\max} reached peak rates for all three species in the IRR+112 treatment for both sun and shade leaves (Fig. 3-1). Overall, *P. deltooides* had the highest rate of photosynthesis for sun leaves ($34.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ Fig. 3-1A) with *Q. pagoda* and *P. occidentalis* having slightly lower photosynthetic rates (31.6 and $28.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively, Fig. 3-1B and 3-1C). The same trend was observed for photosynthetic rates of shade leaves. The lowest photosynthetic rates for shade leaves were observed in the CON treatment for all three species, except for *P. deltooides* where CON and IRR only treatment had similar levels of A_{\max} .

SLA

Shade leaves had higher SLA than sun leaves for all species in all the treatments, as expected (Table 3-1). The response of sun or shade leaf SLA to individual treatments, however, differed significantly. For example, *P. deltooides* SLA, for sun leaves, was greatest in the IRR only treatment ($19.1 \text{ m}^2 \text{ kg}^{-1}$, scaled to canopy level from $\text{cm}^{-2} \text{ g}^{-1}$). Although the N treatments increased SLA of sun leaves compared to CON, the values were significantly lower than the SLA of the IRR only treatment. *P. occidentalis* followed similar trends with both IRR and fertilization having a major influence on sun and shade leaf SLA. Sun leaf SLA of *Q. pagoda*, however, did not

show any response to the IRR only treatment. Rather, a significant increase (32%) was observed only in the IRR+56 treatment compared to the CON. For shade leaves, SLA was higher for the three N treatments compared to the CON and IRR only treatments.

SLN

The trend for sun and shade leaf SLN, for all three species, was similar with shade leaves consistently exhibiting lower SLN irrespective of the treatments (Fig. 3-2). *P. deltooides* SLN for sun and shade leaves (1.7 and 0.7 g N m⁻², respectively) peaked in the IRR+112 treatment, with no significant differences found among the CON, IRR, IRR+56, or IRR+224 treatments. However, SLN for *Q. pagoda* and *P. occidentalis* (1.9 and 1.1 g N m⁻² for *Q. pagoda*, and 1.5 and 0.9 g N m⁻² for *P. occidentalis* sun and shade leaves, respectively) attained a plateau in the IRR+56 treatment. Apparently, addition of N beyond 56 kg ha⁻¹ did not result in any appreciable increase in SLN in both sun and shade leaves of both species suggesting N demand may have been met by the residual fertility within this abandoned agriculture field.

SLN vs. A_{\max}

A_{\max} was positively correlated to SLN in all species and for both sun and shade leaves (Fig. 3-3). The linear relationships clearly indicate that nitrogen limitation to photosynthesis was occurring in the CON treatment, but N fertilization helped to alleviate this with an increase in SLN. For example, an increase in sun leaf SLN from 0.5 to 1.5 g N m⁻² in *P. deltooides* resulted in 84.4% increase in A_{\max} . Similar increases were observed in both *Q. pagoda* and *P. occidentalis*.

LAI

Both *P. deltooides* and *P. occidentalis* LAI reached a plateau in the IRR only treatment, with no significant differences found between the IRR and fertilization

treatments (Fig. 3-4). In other words, addition of N did not result in any increase in LAI in these species. However, *Q. pagoda* LAI responded to both IRR and fertilization. The N treatments resulted in significantly higher LAI in *Q. pagoda* compared to the CON and IRR treatments. Addition of N beyond 56 kg, however, did not result in any further increase in LAI.

ANPP and Canopy A_{max}

ANPP for both *P. deltooides* and *P. occidentalis* was significantly higher in the IRR and fertigation treatments compared to the CON. However, a plateau in ANPP was reached in the IRR only treatments for *P. deltooides* and *P. occidentalis* respectively (Table 3-2). The intermediate and highest levels of fertilization yielded the highest ANPP for *Q. pagoda* with no significant differences among them. CON treatment had the lowest canopy A_{max} for all three species and showed an increasing trend with increasing resources (Fig. 3-5). Canopy level photosynthesis and ANPP exhibited significant curvilinear relationships for all three species. As is evident from Fig. 3-5, ANPP reached a plateau at about 60% of the maximum canopy A_{max} for all three species.

Discussion

One of the mechanisms studied extensively, to explain production differences in forest stands, is the relationship between foliar biomass or area and light capture (Dalla-Tea and Jokela 1991, Pereira et al. 1992, Samuelson 1998, King et al. 1999, Stape et al. 2004, and Wilson and Maguire 2009). Increased leaf area with increased resource availability, either natural or created with irrigation and fertilization, has been shown to increase light capture and thereby production (Chang 2003, Jose et al. 2003, and Allen et al. 2004). The underlying physiological basis for this observation is an increase in

leaf level and/or canopy level photosynthesis in response to resources. Increased resource availability, especially nitrogen, has been shown to increase leaf level P_{net} in a number of forest species (Coleman et al. 1998, Wright et al. 2001, Jose et al. 2003, and van Kuijk and Anten 2009).

The functional interpretation of this relationship is that by increasing nitrogen availability, production of photosynthetic enzymes and proteins will increase, allowing a higher rate of photosynthesis to occur (Evans 1989, Reich et al. 1991, and Warren and Adams 2001). For our study, the significant differences for all three species between the CON and fertigation treatments for leaf level A_{max} and LAI corroborate these findings while revealing the restrictions placed on aboveground production when one or more resources are limiting.

While the IRR treatment alone had a significant impact on *Q. pagoda* and *P. occidentalis* A_{max} over the CON treatments, the addition of N through the irrigation system further increased A_{max} for all species. Several studies have shown similar photosynthetic responses to increased resource availability, such as N, (Ellsworth and Reich 1992, Sullivan et al. 1996, Gardiner et al. 2001, Binkley et al. 2009 and Liberloo et al. 2009) as well as to the simultaneous applications of water and N (Samuelson et al. 1998, Samuelson 2000, Samuelson et al. 2001, Jose et al. 2003, Binkley et al. 2009, and van Kuijk and Anten 2009). All species in our study showed significant gains in A_{max} with the addition of N for both sun and shade leaves through the IRR+112 treatment. However, the sharp increase observed in A_{max} declined significantly with the highest rate (IRR+224) of fertilization (Fig. 3-1). This decline was associated with a corresponding decline in SLN for all three species. Significant positive correlations

were also observed between SLN and leaf A_{\max} for both sun and shade leaves in all the species (Fig. 3-3). This is not surprising considering the widely recognized correlations between foliar nitrogen and RuBP carboxylase activity (Evans 1986) and foliar nitrogen and chlorophyll content (Evans 1987). The biochemical basis for these correlations are explained in a review by Evans (1989) and hence not described here.

The factors contributing to reduced SLN and subsequent reduction in A_{\max} in the highest N treatment are not obvious. As explained earlier, A_{\max} will be limited by N when available N for enzyme and protein (mainly for RuBP carboxylase) synthesis is limited (Evans, 1989; Reich et al., 1991; Coleman et al. 1998 and Warren and Adams 2001). SLN for the IRR+224 treatment was, in fact, similar to the SLN of the CON treatment for both sun and shade leaves (Fig. 3-2). A dilution effect might be considered the cause for reduced N content on a leaf area basis in the IRR+224 treatment, if SLA and LAI were greatest in these treatments. SLA, in general, was similar or lower in the IRR+224 treatment compared to the IRR or IRR+56 and IRR+112 treatments. Peak LAI for *P. deltooides* and *P. occidentalis* reached in the IRR only treatment and was not significantly different from the LAI found in the N treatments. Peak LAI for *Q. pagoda* reached in the IRR+56 treatment with no differences among the N treatments. These findings suggest that a dilution effect was minimal for *Q. pagoda* and *P. occidentalis* and did not exist for *P. deltooides*.

Knecht and Goransson (2004) suggested that the rate of uptake and use of any nutrient might be down-regulated if other essential nutrients were not available in sufficient supply to meet the demand. That is, a specific ratio is necessary to sustain a given growth rate regardless of any excessive amount of any nutrient. All nutrients

must be maintained in a specific ratio. It is possible that repeated fertilization for six years at the rate of 224 kg N ha⁻¹ has changed the soil chemistry and created nutrient imbalance in the soil and foliage. Some changes in soil properties have already been reported from the study site. For instance, in a companion study, Lee and Jose (2003) observed a reduction in soil CO₂ efflux and microbial carbon along the same increasing resource gradient. In another study, these authors reported that estimated NO₃-N leaching at a depth of 0.9 m was 97% of the applied N in the IRR+224 treatment whereas it was only 70 and 72% in the IRR+56 and IRR+112 treatments, respectively (Lee and Jose, 2005). This, perhaps, is an indication of N saturation in the soil, which could result in nutrient imbalance.

ANPP reached a plateau in the IRR only treatments for *P. deltooides* and *P. occidentalis* and additional N did not result in any appreciable increase in production. *Q. pagoda* ANPP was significantly higher in the IRR only treatment compared to the CON, but fertilization at IRR+112 and IRR+224 further increased production. Allen et al. (2004) observed a similar response for four-year old sweetgum (*Liquidambar styraciflua* L.) and *P. occidentalis* plantations in Georgia, USA. They observed that irrigation alone was sufficient for increasing volume production in *P. occidentalis*, whereas 85 rather than 114 kg N ha⁻¹ yielded the best volume production in sweetgum. Although the physiological basis for this phenomenon was not explored in detail, they observed strong correlations between light interception and volume growth. Light interception (which is a function of canopy LAI) is an indicator of the carbon fixation potential; however, canopy A_{\max} may better explain the interactive effects of LAI and foliar A_{\max} . For example, the relationship between canopy A_{\max} and ANPP showed that

productivity, for all species, reached a plateau well below the maximum estimated canopy A_{\max} . The optimum level of canopy A_{\max} that yielded the maximum ANPP was in the IRR only treatment for *P. deltooides* and *P. occidentalis* and in the IRR+112 treatment for *Q. pagoda*. This clearly indicates that an increase in LAI alone with no additional increase in foliar A_{\max} was sufficient for *P. deltooides* and *P. occidentalis* to result in optimum canopy A_{\max} and provide the maximum production potential. However, the combined effect of LAI and foliar A_{\max} in controlling ANPP was evident for *Q. pagoda*. Despite having higher LAI in all the N treatments (Fig. 3-4), increased LAI alone was not sufficient, but an increase in foliar A_{\max} was also necessary to yield optimum canopy A_{\max} and maximum ANPP in this species.

The positive impact of irrigation and fertilization on productivity has been well documented. However, as suggested by Allen et al. (2004), the reasons for increased growth response are less evident. Several factors related to canopy dynamics have been identified by others (Albaugh et al. 1998, Samuelson 1998, 2000) and were explored in detail in our study. As expected, SLA, SLN, LAI, A_{\max} and ANPP varied across the supplied soil resource gradient for all three species. Irrigation alone was sufficient in *P. deltooides* and *P. occidentalis* to increase SLA whereas SLA responded to both IRR and fertilization in *Q. pagoda*. A corresponding increase in LAI, similar to that of SLA, was also observed for all three species. A_{\max} reached peak rates for all species in the IRR+112 treatment for both sun and shade leaves and showed strong positive correlations with SLN across the gradient. ANPP exhibited a curvilinear relationship with canopy A_{\max} with peak production occurring well below the maximum estimated canopy A_{\max} . An increase in LAI alone was sufficient to achieve maximum ANPP in

both *P. deltoides* and *P. occidentalis*. However, an increase in both LAI and foliar A_{\max} resulted in the maximum ANPP in *Q. pagoda*. Although we hypothesized that increased foliar A_{\max} in combination with an increase in LAI would be necessary to increase ANPP along the increasing resource gradient, our results indicate that an increase in LAI alone can increase canopy A_{\max} and lead to increased productivity. An increase in foliar A_{\max} may or may not be necessary to yield the highest ANPP depending on the species. Further research is needed to determine the relationship between N and other potentially limiting nutrients so that the role of nutrient imbalance can be better understood. Given the appeal for managing short-rotation plantations with fertigation, this study should give land managers a solid scientific basis for developing efficient fertigation strategies.

Table 3-1. Year six specific leaf area (SLA) for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* sun and shade leaves along a soil resource gradient. Capital letters indicate significant differences between sun and shade leaves and lower case letters indicate significant differences among treatments.

Treatment	Sun SLA (m ² kg ⁻¹)			Shade SLA (m ² kg ⁻¹)		
	<i>P. deltooides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>	<i>P. deltooides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>
CON	11.96 Aa	12.98 Aa	12.68 Aa	19.26 Ba	18.81 Ba	21.65 Ba
IRR	19.08 Ac	13.30 Aa	16.90 Ac	24.74 Bb	21.99 Bb	28.87 Bb
IRR+56	15.70 Ab	17.63 Ab	15.34 Abc	20.25 Ba	25.89 Bc	27.93 Bb
IRR+112	14.48 Ab	14.23 Aa	14.06 Aab	19.47 Ba	23.52 Bc	22.63 Ba
IRR+224	14.61 Ab	15.72 Aab	16.91 Ac	24.39 Bb	24.77 Bc	26.94 Bb

Table 3-2. Year six ANPP of *P. deltoides*, *Q. pagoda* and *P. occidentalis* along a soil resource gradient. Lower case letters indicate significant differences among treatments.

Treatment	ANPP (Mg ha ⁻¹ yr ⁻¹)		
	<i>P. deltoides</i>	<i>Q. pagoda</i>	<i>P. occidentalis</i>
CON	2.25 b	1.47 c	3.39 b
IRR	4.48 a	2.44 b	4.73 a
IRR+56	5.37 a	2.54 b	4.48 a
IRR+112	4.34 a	2.97 ab	4.39 a
IRR+224	4.46 a	3.75 a	5.11 a

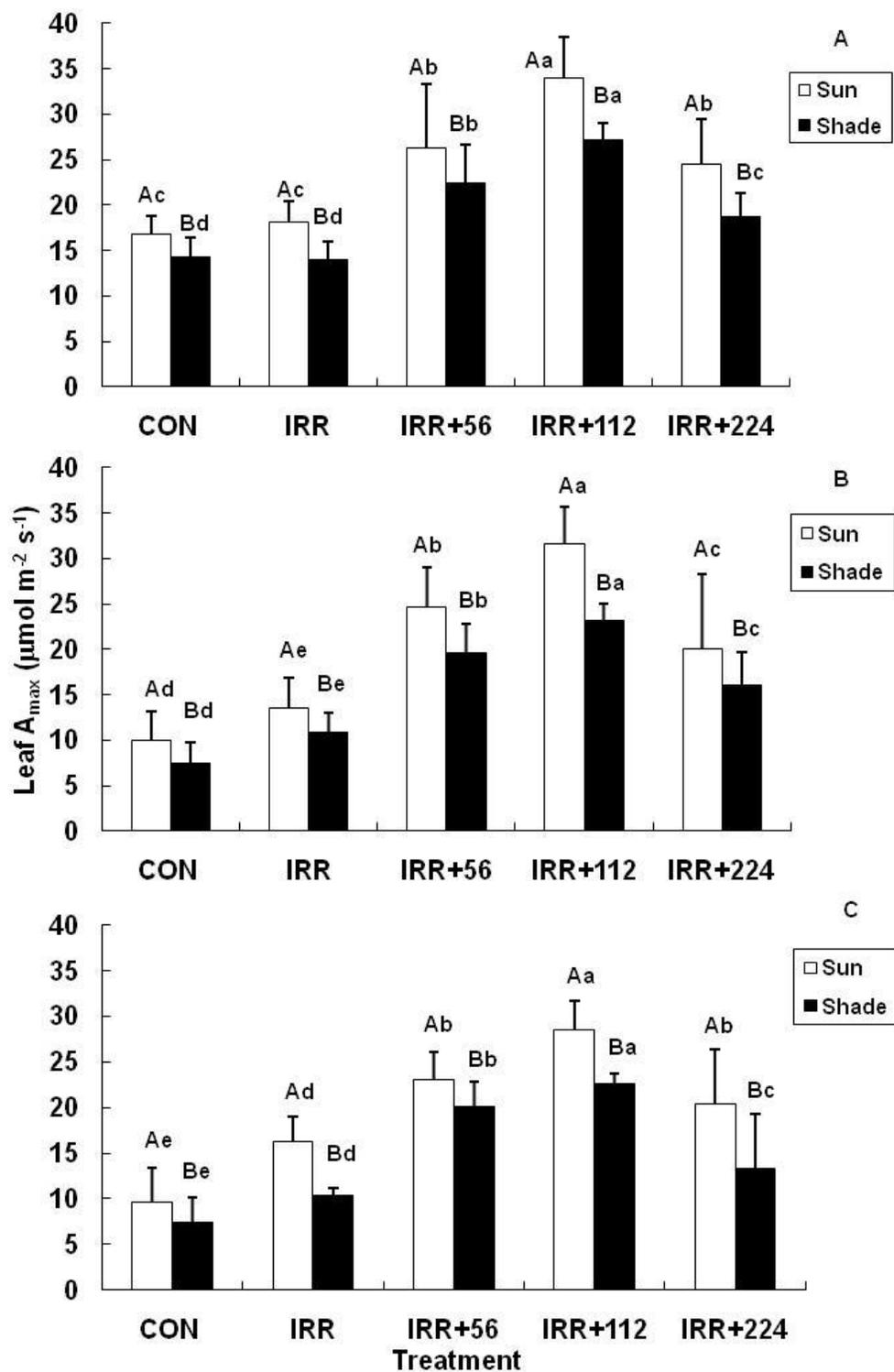


Figure 3-1. Average light saturated photosynthesis for 6-year-old *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) leaves. Capital letters indicate significant differences between sun and shade leaves ($p \leq 0.05$). Lower case letters indicate significant differences among treatments ($p \leq 0.05$).

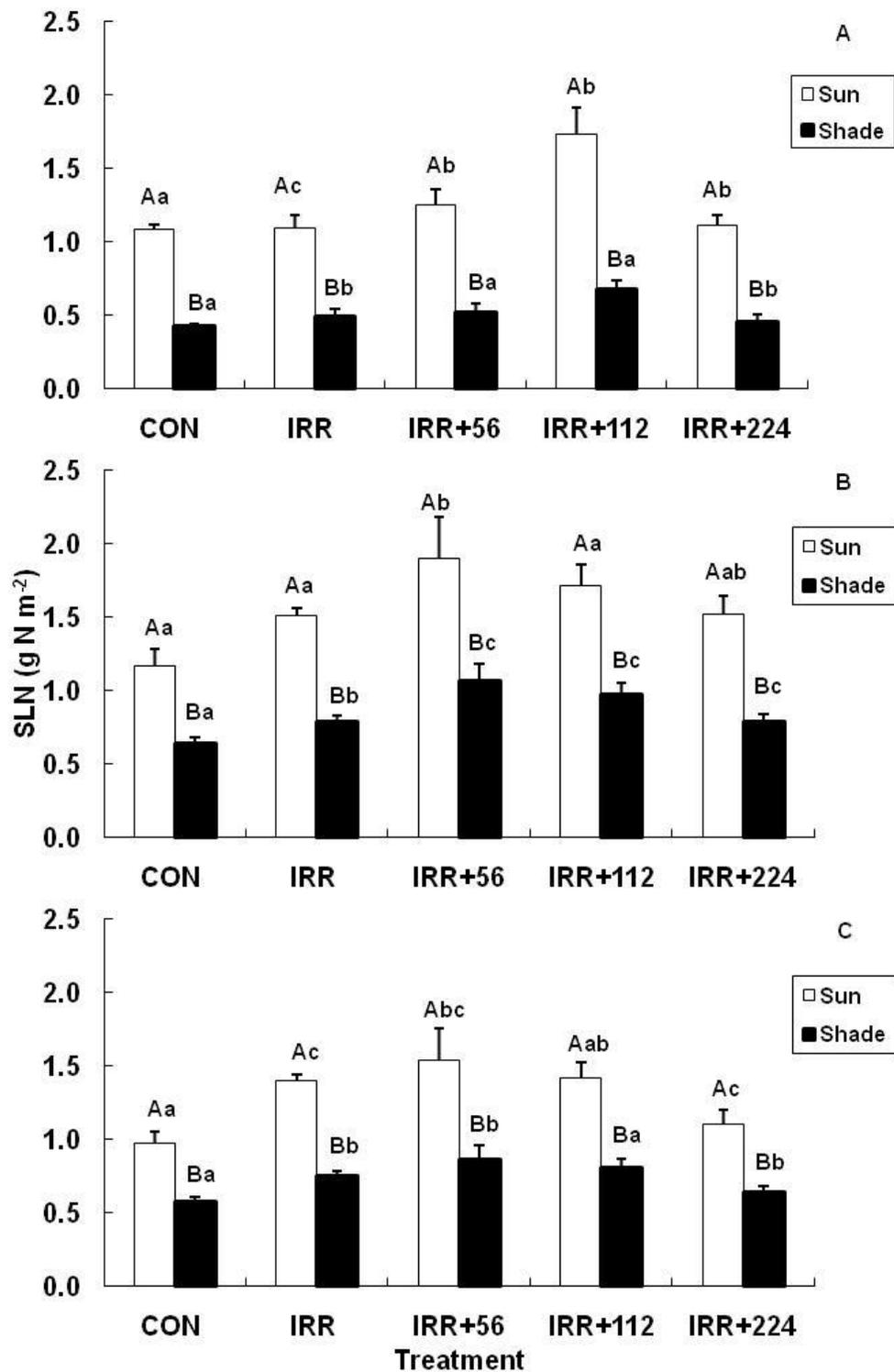


Figure 3-2. Average specific leaf nitrogen for 6-year-old *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) leaves. Capital letters indicate significant differences among sun and shade leaves ($p \leq 0.05$). Lower case letters indicate significant differences among treatments ($p \leq 0.05$).

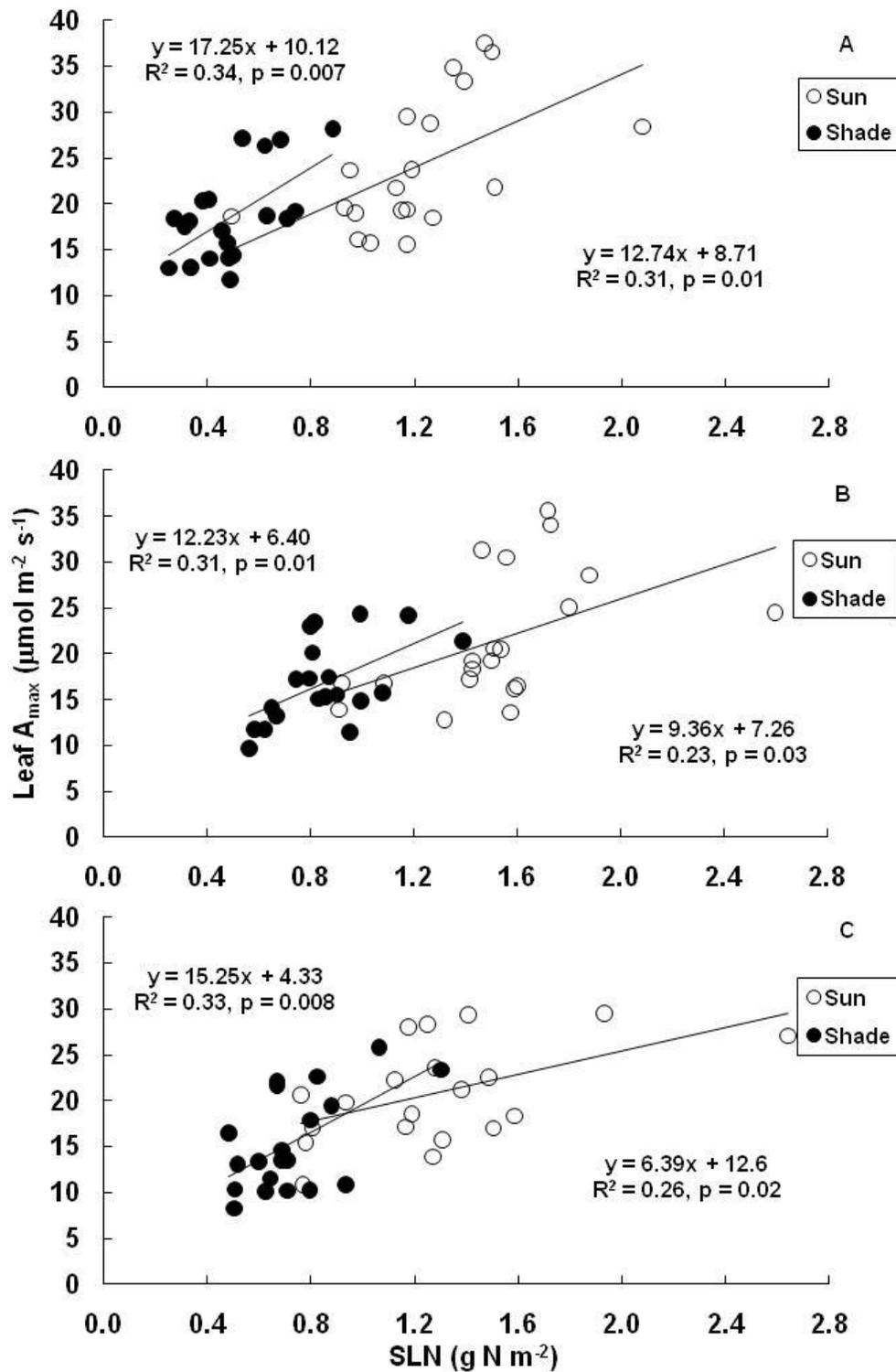


Figure 3-3. The relationship between specific leaf nitrogen and light saturated photosynthesis for 6-year-old *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) sun and shade leaves.

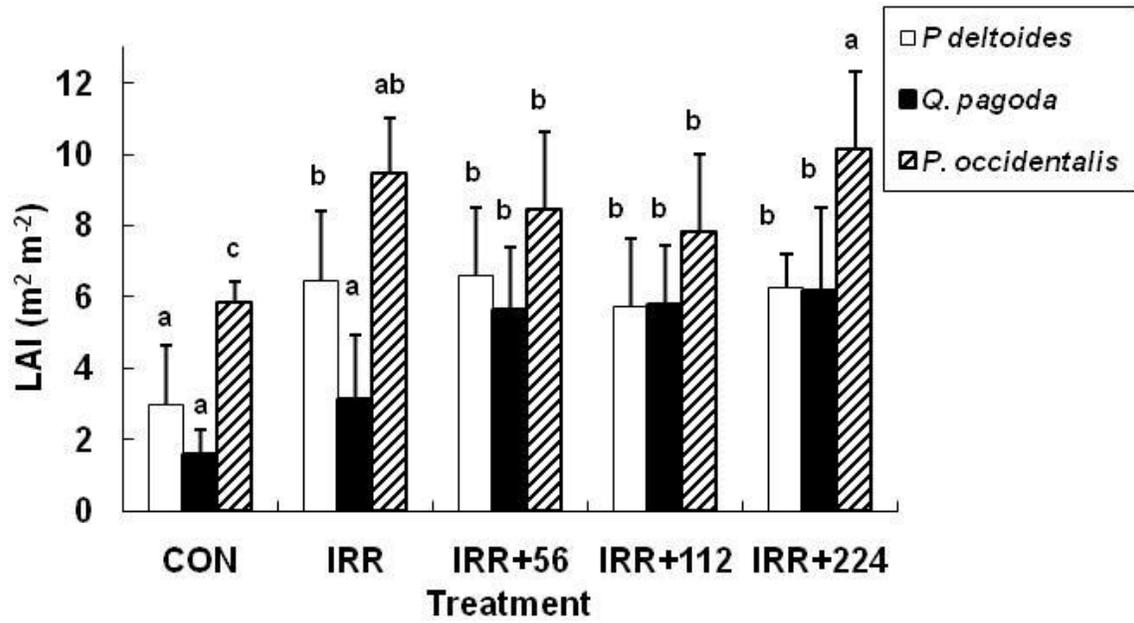


Figure 3-4. Average leaf area index for 6-year-old *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) leaves. Lower case letters indicate significant differences among treatments ($p \leq 0.05$).

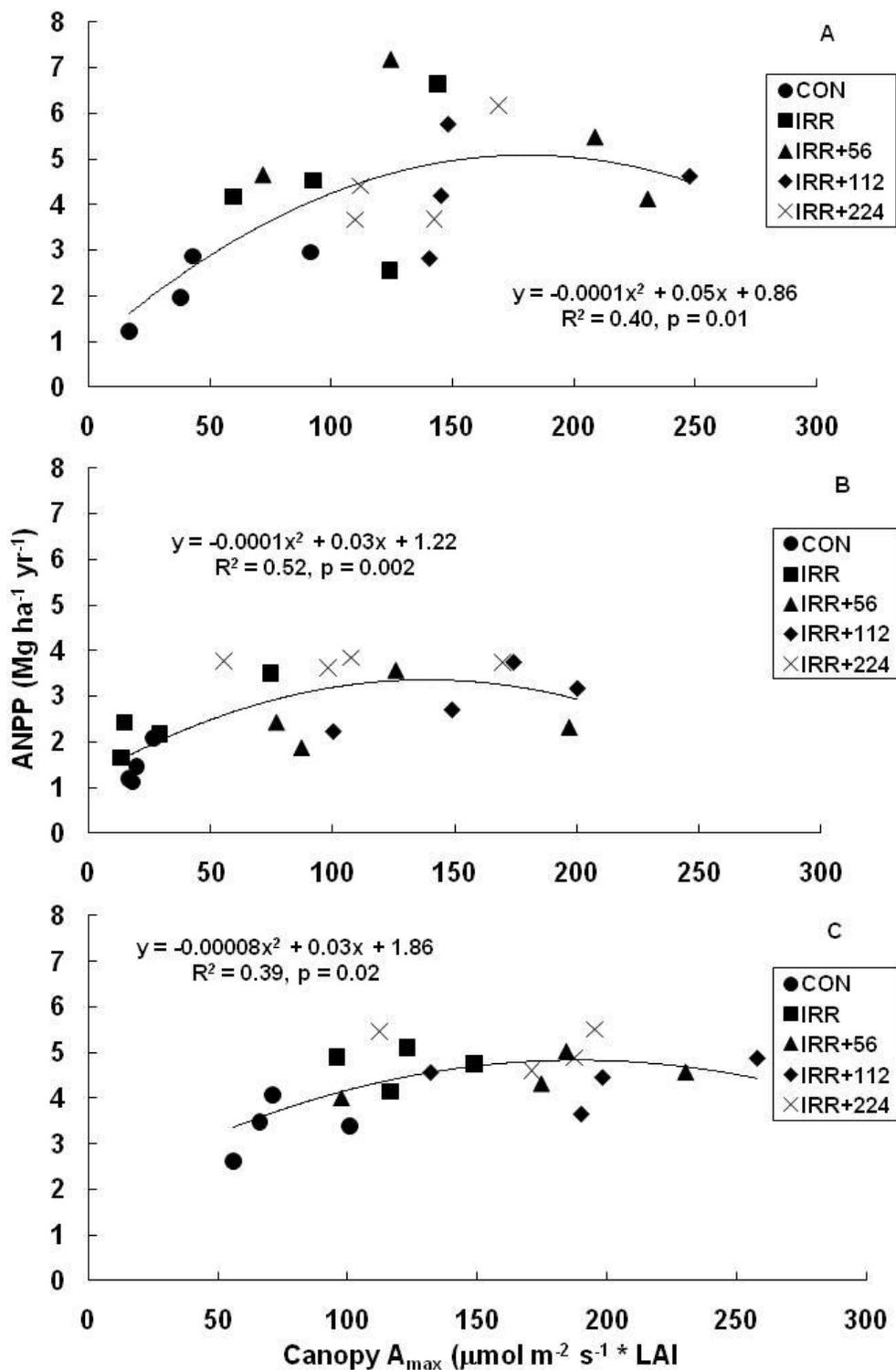


Figure 3-5. The relationship between canopy photosynthesis and aboveground net primary productivity (ANPP), for 6-year-old *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C).

CHAPTER 4 NUTRIENT USE EFFICIENCY OF THREE FAST GROWING HARDWOOD SPECIES ACROSS A RESOURCE GRADIENT

Changes in attitudes about energy production shifted interest from traditional energy sources and techniques toward renewable resources in recent years (Dickmann 2006). One target of the focus on renewable energy is fast growing hardwood species with the concentration placed on species that could be harvested on rotations ranging from as little as six (Tuskan 1998) or up to 15 years (Dickmann 2006). The concept of short-rotation woody crop (SRWC) supply systems were first formalized nearly 50 years ago (Tuskan 1998). In some areas of the United States, forest management practices that had previously focused on extensive management for fiber production have shifted to intensive management for biomass and biofuel production using SRWC systems (Geyer and Melichar 1986, Coyle and Coleman 2005, and Augusto et al. 2009). Techniques for increasing production potential of SRWC such as high stocking rates, hybrid selection/development, and intensive stand management have become industry standards (Dickmann 2006). However, our knowledge about fertilizer uptake patterns and use by these fast growing species is limited at best.

Tree production can be limited by a number of factors such as light (Wang et al. 1991, Ellsworth and Reich 1992, Jose and Gillespie 1997, Jokela and Martin 2000, and Henderson and Jose 2005), water (Lockaby et al. 1997, Albaugh et al. 1998, King et al. 1999, Allen et al. 2002, and Albaugh et al. 2004), and growing space (Cochran et al. 1991, Schubert et al. 2004, Lockhart et al. 2006, Clark et al. 2008, and Curtis 2008) or enhanced by practices such as fertilization (Singh 1998, Will et al. 2002, Bekele et al. 2003, Allen et al. 2004, and Samuelson et al. 2004a), or irrigation (Allen et al. 2005, Stape et al. 2008, Zalesny et al. 2007, and Zalesny et al. 2008). Most frequently,

biomass accumulation and stand development are restricted to inherent resource availability within a site or by community composition (Wang et al. 1995, Wang et al. 1996, Smith et al. 1998, Vogel and Gower 1998, Blanco et al. 2006, Schilling and Lockaby 2006, and Yan et al. 2006).

As a counter to nutrient losses, plants have mechanisms to minimize nutrient losses such as nutrient resorption or retranslocation (Vitousek 1982, Berendse and Aerts 1987, Aerts and Berendse 1988, Aerts 1996, Aerts 1997, and Wright and Westoby 2001). Although it would seem somewhat intuitive, the nature of, and driving force behind, nutrient availability, uptake, and resorption are not well understood as is indicated by inconsistent findings between studies. Some studies indicate nutrient limitation should lead to higher rates of resorption efficiency and proficiency (actual nutrient level within leaf litter; a reflection of soil resource) and that low rates of resorption could contribute to nutrient limitations, reduced biomass production, and survival (Boerner 1984, Killingbeck 1984, Killingbeck 1986, Killingbeck 1993, and Killingbeck 1996). Other studies suggest higher leaf level nutrient status (Lathja 1987) or resource availability (Xu and Timmer 1999) is linked to higher or lower (Aerts and de Caluwe 1994, Vitousek 1998) resorption ratios or may have no effect on the ratios (Chapin and Kedrowski 1983, Birk and Vitousek 1986, Aerts 1996, Wright and Westoby 2003, and Yuan and Chen 2010). However, it appears that reaction to and indications of nutrient use can vary in response to site fertility (Bloom et al. 1985, Wright and Westoby 2003), water availability (Boerner 1985, del Arco et al. 1991, Escudero et al. 1992, Wright and Westoby 2003), soil chemistry (del Arco et al. 1991, Bridgham et al. 1995, Choi et al. 2005, and Campo et al. 2007) as well as between members of the

same species (Birk and Vitousek 1986, Aerts and de Caluwe 1994, and Bungart and Hützl 2004). Nutrient resorption proficiency (NRP), has been described as a way to measure the success of nutrient conservation and to reflect environmental constraints of site conditions (Killingbeck 1996), particularly for nitrogen (N) and phosphorus (P). NRP can be described as the realized resorption or the quantity of nutrient remaining in senesced tissue after retranslocation. NRP trends between species (deciduous versus evergreens) across varying levels of environmental limitations (nutrients and water) appear to influence processes such as nutrient uptake and productivity (Killingbeck 1996). Killingbeck (1996) further pointed out that the variation found within his results could be attributed to forest stand conditions as well as the relationship between inter-nutrient dependence (i.e. N and P).

Given the intensified demand for SRWC worldwide and interest in increasing wood biomass production, determining ways to enhance yield is paramount for plantation development (Chang 2003, Bungart and Hützl 2004, Coyle and Coleman 2005, DesRochers et al. 2006). Intensive culture of hardwoods is often accompanied by site preparation, competition control, genetically improved planting stock, and selection of fast-growing species to increase the production potential (Fang et al. 1999, Chang 2001, Samuelson et al. 2001, Bungart and Hützl 2004, Lee and Jose 2005, and DesRochers et al. 2006). By far the most advantageous of the silvicultural methods used to increase production is fertilization (Allen 1987). Fertilizer application, while generally one of the least expensive silvicultural tools, can become more costly than necessary if application rates exceed nutrient uptake or demand of the trees. When coupled with irrigation, fertilization has the capability to increase production on infertile

sites, in areas where rainfall is limited, or on soils that lack necessary water holding capacity (Axelsson and Axelsson 1986., Lockaby et al. 1997, King et al. 1999, Bekele et al. 2003, and Coyle and Coleman 2005). Many studies have indicated that growth response to differing fertilization rates for economically important tree species are species specific and/or vary with site resource levels (Wienand and Stock 1995, Jokela et al. 2004, Prietzel et al. 2004, Sword Sayer et al. 2004, Ladanai et al. 2006, Saarsalmi et al. 2006, and Moscatelli et al. 2008). However, questions remain regarding the extent that production could be enhanced by increasing resource availability, and at what levels additional resources become luxury?

In the present study, we investigated the effect of water and nutrient availability, on nutrient content (kg ha^{-1}), resorption efficiency (%), resorption proficiency ($\text{g nutrient kg litter/senesced tissue}$), and leaf- and canopy-level nutrient use efficiency of nitrogen (N), phosphorus (P), and potassium (K) for *Populus deltoides* Bartr. (cottonwood), *Quercus pagoda* Raf. (cherrybark oak, previously *Quercus falcata* var. *pagodafolia* Ell.) and *Platanus occidentalis* L. (sycamore), (nomenclature follows USDA, NRCS Plants Database 2009). Our objectives were to: 1) determine the aboveground nutrient content for each nutrient and species across a nitrogen/water gradient; specifically, what rates of fertilization are actually captured and utilized by the canopy to influence production?, 2) quantify the nutrient resorption efficiency and proficiency of N, P, and K for all three species; does an increase in foliar nutrient content result in increased biomass production? and 3) determine the nutrient use efficiency on a leaf- and canopy-level basis for the three nutrients and species. Is nutrient use efficiency decreased in similar magnitudes as the application of fertilization? Are the amounts of fertilizer that

are taken up reflected in the magnitude of resorption? We hypothesized that nutrient levels, budget, efficiencies, and ratios would peak well below the maximum level of nitrogen supplied.

Methods

Study Site

Our study was conducted in a fertigation trial established on an abandoned agricultural field (30.50'N, 87.11'W) in Santa Rosa County, Florida, USA. The climate is temperate with mild winters and hot, humid summers. Average rainfall is 1700mm, with average minimum and maximum temperatures of 10 and 27 °C, respectively (NOAA, 2003). The soil is characterized as a well-drained, Redbay sandy loam (a fine-loamy, siliceous, thermic, Rhodic Paleudult) formed in thick beds of loamy marine deposits with an average water table depth of 1.8m (Lee and Jose 2003). Soil variables calculated after this study ended include pH (5.8, down from the original pH of 6.0), cation exchange capacity (4 CEC meq/100 g), and soil nutrient levels of phosphorus (34 and 55), potassium (92 and 122), calcium (599), and magnesium (179 and 146) (kg ha⁻¹). To our knowledge, nitrogen levels were not measured prior to the study, but were expected to be relatively high given the site was an abandoned agricultural field. Nitrogen levels measured within the control plots during a companion study indicated total inorganic nitrogen ranged from near 2.5 to 4.5 kg ha⁻¹ (Lee and Jose 2006).

Treatment plots of *P. deltooides* and *P. occidentalis* consisted of 40 trees plot⁻¹ and *Q. pagoda* *Q. pagoda* contained 16 trees plot⁻¹; (although the *Q. pagoda* plots were the smallest of the three species, and found for this study should be treated with caution, the results reflect data collected within the study). All treatment plots were planted at 2.13m X 3.35m spacing (1400 trees ha⁻¹). The study design was a

randomized complete block (RCB) with four replications of each treatment. Site preparation included disking and subsoiling to facilitate planting. Fertilization at the time of planting included broadcast application of diammonium phosphate, dolomitic lime, potash, and a micronutrient mixture. These treatments added elemental calcium, nitrogen, phosphorus, magnesium, zinc, copper, and manganese (1009, 50, 56, 126, 3, 3, and 2 kg ha⁻¹ respectively, Greg Leach, personal communication). Soil pH was adjusted to 6.0, with 3363 kg ha⁻¹ of dolomitic lime, based on recommendations from a similar trial at North Carolina State University Research Cooperative (Coleman et al. 2004, Samuelson et al. 2004a, and Samuelson et al. 2004b).

Herbaceous weed control was attained with combinations of chemical (sulfometuron methyl and glyphosate) and mechanical (mowing and manual pulling) treatments during the first and second growing seasons. Installation of the nutrient supply system and planting of trees occurred during spring 1995. The irrigation system operated for approximately two hours each day (on average 390mm water Greg Leach, personal communication) during the growing season (May-Sep.) with nitrogen application occurring two to eight minutes each day creating the nitrogen gradient across the treatments (Lee and Jose 2003; 2006).

Five treatments were established including control (CON), irrigation only (IRR), and three nutrient supplements supplied through irrigation including 56, 112, and 224 kg N ha⁻¹ yr⁻¹ (referred to as IRR+56, IRR+112, and IRR+224, respectively). Each treatment was applied to each plot of *P. deltoides*, *Q. pagoda* *P. occidentalis*. For each species, each plot consisted of 40 trees for *P. deltoides* and *P. deltoides*, and *Q. pagoda* contained 16 trees per plot due to space constraints; (although the *Q. pagoda*

plots were the smallest of the three species, and found for this study should be treated with caution, the results reflect data collected within the study). All treatment plots were planted at 2.13m X 3.35m spacing (1400 trees ha⁻¹). The study design was a randomized block design with four replications of each treatment for each species.

Data Collection

Leaf samples were collected from upper one-third (sun leaves) and lower one-third (shade leaves) of the canopy on a monthly basis during the eighth growing season. Samples were collected within each plot for each species, bagged, labeled for identification purposes, and placed in a cooler for transport. Leaf area (cm²) was determined by passing each leaf through a Li-Cor LI-3300 Leaf Area Meter and then weighed to the nearest 0.01g. Specific leaf weight (SLW) was determined by dividing the foliar weight by area. Samples of bark, branches, and wood were collected in mid-growing season. Ten trees per treatment, per each species were randomly selected for woody component (bark, branch, and bole) nutrient analysis and combined, to obtain a treatment level sample for nutrient content for each tissue type. Bark sample removal was completed by surficially scraping, cutting, breaking, or peeling samples from the trees of each species. Collection of branches from the same randomly selected trees, were gathered by pruning newly formed branches from the lower and upper third of the canopy for each species. Collection of bole material consisted of coring each randomly selected tree at DBH (diameter at breast height ~ 1.5m above ground level) with an increment borer. Foliar and woody samples were dried at 70 °C for 48 hours, ground to a fine powder and analyzed for total nitrogen (N) (Kjeldahl), phosphorus (P) (EPA

Method 200.7 - ICP (Inductively Coupled Plasma) Spectrophotometer), and potassium (K) at the University of Florida Analytical Research Laboratory (ARL).

For biomass calculations used with nutrient data, diameter at breast height (DBH) and height of all trees in each plot within each treatment were measured yearly. Standing biomass (Mg ha^{-1}), ANPP ($\text{Mg ha}^{-1} \text{ yr}^{-1}$, excluding herbivory or litter of branches, bark, or fruits, as defined on page 9), LAI ($\text{m}^2 \text{ m}^{-2}$, calculated by multiplying weight (g) and area (m^2) of leaf litter collected in litter trays by SLA ($\text{m}^2 \text{ g}^{-1}$) of randomly selected canopy leaves, as defined on page 9), for year eight. Whole-tree allometric equations developed by Shelton et al. (1982) were used to calculate volume and aboveground woody biomass for *P. deltooides*. Their equations for *P. deltooides* were developed from trees of comparable age range, and soil type, grown in areas with similar longitude, latitude, and climate as this study. Standing woody biomass consisted of all woody components (bark, branches, and trunk/bole). Foliage biomass was determined by summing the weight of annual litter fall collected monthly (May to January) from five litter traps (0.5 m^2) for *P. deltooides*.

Biomass equations developed by Schlaegel and Kennedy (1986) were used to calculate volume and aboveground woody biomass for both *Q. pagoda* and *P. occidentalis*. The original Schlaegel and Kennedy (1986) equations used diameter measured at approximately 15 cm above ground level. All *Q. pagoda* and *P. occidentalis* DBH data were corrected to reflect the dbh measurements of the equations at 15 cm height above ground level, by using regression equations developed from sampling 100 trees per species measured at the appropriate height (data not shown, $R^2 = 0.97$ and 0.93 respectively for *Q. pagoda* and *P. occidentalis*). Foliage biomass was

determined by summing the weight of annual litter fall collected from five and two litter traps (0.5 m²), for *P. occidentalis* and *Q. pagoda* respectively in each plot.

To determine nutrient use on a leaf and canopy level, projected LAI, was calculated from the weight (g) and area (m²) of the leaf litter trays and SLA (scaled to the canopy level – m² g⁻¹) for each species within each treatment. Care was taken to ensure only leaf litter from the species within the plot was processed. If litter from other species fell or were blown into the tray, it was removed prior to collection. Leaf litter was dried for 48 hours at 70 °C and weighed to the nearest 0.01g.

Nutrient content of each species for each aboveground component was calculated for N, P, and K using the equations used for the purpose of biomass production estimation developed by Shelton et al. (1982) and Schlaegel and Kennedy (1986) and for the calculation of the nutrient concentrations for woody and foliar components (Equation 1). The RE was calculated by determining the difference between peak nutrient concentration of green leaves and those found in fresh leaf litter (Equation 2). Leaf level nutrient use efficiency LNUE was calculated using leaf level nutrient content and leaf litter resorption rates (Equation 3). Canopy nutrient use efficiency (CNUE) was calculated using aboveground biomass produced in year eight divided by the peak production (peak foliar production was determined from monthly leaf litter collection), and nutrient content of green leaves for each species in each treatment (Equation 4). Resorption proficiency was reported as the nutrient content in senesced leaves (g N kg⁻¹ litter, i.e. realized resorption).

$$(1) \text{ Nutrient content (kg ha}^{-1}\text{)} = \text{kg ha}^{-1} \text{ (biomass)} * (\text{kg kg}^{-1} \text{ nutrient})$$

$$(2) \text{ Resorption (\%)} = (\text{foliar}_{\text{(litter)}} - \text{foliar}_{\text{(live)}}) / \text{foliar}_{\text{(live)}} * 100$$

(3) Leaf nutrient use efficiency (g g^{-1}) = $1 / ((\text{g g}^{-1}) * (1 - \text{resorption}))$

(4) Canopy nutrient use efficiency (Mg kg^{-1}) = $\text{Mg} / (\text{kg}_{\text{foliage}} * (\text{kg kg}^{-1}_{\text{nutrient}}))$

Analysis

All the measured and calculated variables were compared among treatments using analysis of variance (ANOVA) (SAS Institute Inc. 2001) with treatment assigned as a random effect in the model. If significant differences ($\alpha = 0.05$) among treatments were revealed, multiple pairwise comparisons of means were performed using Tukey's multiple mean test for mean separation and determining significance. Linear regression was used to analyze the relationships between ANPP and N:P. It has been suggested that as soil nitrogen levels increase, uptake of nitrogen can be limited by the availability of other nutrients (Aber et al. 1989). Furthermore, because of results from studies like Pastor and Bridgham (1999) and Bridgham et al. (1995) we hypothesized that the highest rate of nitrogen application would be far greater than the trees could utilize. As such, curvilinear functions were chosen *a priori* to ANOVA analysis and in accordance with our hypothesis that nutrient use variable responses were likely to plateau well below the maximum level of N supplied by the treatments.

Results

Nutrient Content

The N content of aboveground components (bole, branch, bark and foliage – 4.0, 17.1, 1.8, and 217.7 kg ha^{-1} , respectively) and the total N (240.5 kg ha^{-1}) of the combined aboveground biomass in *P. deltoides* were significantly lower in the control (CON) treatment compared to that of the IRR and IRR + Fertilizer treatments (IRR+56,

IRR+112, and IRR+224). The IRR and all the IRR + Fertilizer (IRR+56, IRR+112, and IRR+224) treatments had similar total N content (502.9, 415.8, 422.1, and 439.0 kg ha⁻¹, respectively, Table 4-1). In other words, N content for year eight reached its highest at a level below the maximum N application (502.9 kg ha⁻¹ in the IRR treatment). The overall trend for each component (branch, bark, foliage) or total tree was to reach the highest N content in the IRR treatment with significant differences found among the CON and all IRR treatments. The only exception to this trend was for the bole content, which reached its peak at the IRR+56 treatment (10.5 kg ha⁻¹, Table 4-1) which was not significantly different from the other IRR or IRR + Fertilizer treatments.

Branch, foliar, and total tree P nutrient budget for *P. deltooides* exhibited similar trends as N by reaching its peak in the IRR treatment (11.9, 37.6, and 50.6 kg ha⁻¹, respectively) with significant differences found among treatments for each component. Bole and bark P content reached their peaks in the IRR+224, which was significantly different from all other treatments, and IRR+122 treatments (1.4 and 0.3 kg ha⁻¹, respectively, Table 4-1). Significant differences were found among the Con and all other IRR treatments. *P. deltooides* branch, bark and total tree components for K reached its maximum content in the IRR treatment, (70.6, 1.2, and 353.0 kg ha⁻¹, respectively, Table 4-1), and were significantly different from the CON treatment. Maximum K content for the bole and foliar components were found in the IRR+56 and IRR+224 treatments (29.9 and 267.8 kg ha⁻¹, respectively) with significant differences found among treatments.

Maximum N content for bole, branch and bark for *Q. pagoda* (6.3, 8.9, and 4.8 kg ha⁻¹, respectively) was found in the IRR+224 treatment and significant differences were

found among treatments for these components (Table 4-1). Maximum N for the foliar and total tree occurred in the IRR+112 treatment (367.1 and 382.2 kg ha⁻¹, respectively) with significant differences found only among the control and IRR+112 treatments. For P, the bole and bark components were greatest in the IRR+224 treatment (0.3 and 0.2 kg ha⁻¹, respectively) while branch and foliar components reached the highest levels in the IRR+56 and IRR+112 treatments (0.8 and 22.7 kg ha⁻¹, respectively). Significant differences for the bole component were found among the CON and IRR+224 treatments and among treatments for the branch component. The total tree peak P was found in the IRR+122 treatment, and was likely influenced by the foliar P content level (23.7 kg ha⁻¹), although no significant differences were found among treatments. For Q. *pagoda*, the highest K for bole, branch, and bark in the IRR+224 treatment (5.9, 6.6, and 1.7 kg ha⁻¹, respectively). Foliar and total tree peak K nutrient content was found in the IRR+112 treatment with significant differences found among the CON and IRR+112 treatments (151.6 and 162.1 kg ha⁻¹, respectively).

P. occidentalis had its highest N and K contents in the IRR treatment for branch, bark, foliar, and total tree components (8.9, 4.7, 536.6, and 559.1 kg N ha⁻¹ and 6.6, 1.3, 257.5 and 275.7 kg K ha⁻¹, respectively) with significant differences found among treatments. Both N and K bole content were greatest in the IRR+112 treatment (11.9 and 12.3 kg N ha⁻¹ and kg K ha⁻¹, respectively) with significant differences found among treatments. Maximum P content for *P. occidentalis* occurred in the IRR+56, IRR, CON, and IRR treatments for bole, branch, bark, foliar and total content (2.2, 1.6, 0.4, 41.7, and 45.6 kg P ha⁻¹, respectively) with significant differences found among treatments.

Nutrient Use, Resorption Efficiency and Proficiency

No significant differences were found for RE or LNUE for any of the three species across all treatments for N, P, or K (Table 4-2, RE ranged from 65.1 CON to 57.0% IRR+112, 57.6 CON to 52.8% IRR+112 and 85.2 CON to 72.2% IRR+56, for N, P, and K, and LNUE ranged from 136.3 CON to 106.6 g g⁻¹ IRR+112, 1231.7 CON to 1103.2 g g⁻¹ IRR+56, and 732.4 CON to 331.2 g g⁻¹ IRR+224 for N, P, and K, respectively). CNUE for all three species and nutrients (Table 4-3) followed irregular patterns. Only N and K for *P. deltooides*, exhibited significant differences among treatments. N and K peaked in the IRR+56 (5.1 and 5.6 Mg kg⁻¹, respectively) and IRR treatments respectively. For both nutrients, CNUE was lowest in the IRR+112 treatment (3.3 and 3.8 g g⁻¹, respectively). For RP no significant differences were found for any of the three species across all treatments for N, P, or K (Fig. 4-1).

N:P

N:P ratios were based on foliar levels of N and P. The only significant difference found for N:P among treatments for all three species occurred for *P. occidentalis* (Fig. 4-2). N:P was lowest in the CON treatment (~11) but was not significantly different from the IRR, IRR+56, or IRR+112 treatments (~12, 14, and 14). There was a significant difference between N:P for CON and IRR+224 (~14.5).

N:P and ANPP

No significant relationship was found for N:P and aboveground net primary productivity (ANPP) for *P. deltooides* (Fig. 4-3). The trend for *Q. pagoda* and *P. occidentalis* for N:P and ANPP (Fig. 4-3) was a significant ($p > 0.05$) curvilinear relationship with the peak occurring at or near the N:P ratio of 17 and 14 respectively. For both species, when N:P increased past these points, ANPP tended to decrease.

Discussion

We wanted to determine how resources were utilized for biomass production, with respect to varying levels of irrigation, nitrogen, or the combined application of irrigation and nitrogen application (fertigation, IRR+56, IRR+112, and IRR+224). The differences between N uptake and utilization, reflected in the N content of the combined aboveground parts, for *P. deltooides* and *P. occidentalis* was likely influenced by the greater biomass production of these two species than was seen in *Q. pagoda*, and was more highly influenced by the irrigation treatment for *P. deltooides* and *P. occidentalis* than for *Q. pagoda* (Table 4-1). Despite these differences, N content in *Q. pagoda* were greater at higher N application rates. Our hypothesis of nutrient levels peaking well below the maximum rate of N application was true for two of the three species.

For the combined aboveground parts N, P, and K nutrient content were highly affected by the large foliar fraction for all three species (Table 4-1). Water availability necessary for nutrient uptake (Lambers et al. 1998) regulates foliar production (Jose and Gillespie 1996 and 1997) and therefore the amount of woody biomass that can be produced (Henderson and Jose 2010). Soils for this area are sandy and well drained; suggesting, for this combination of species and soil parameters, low water storage capacity and therefore water availability may be as limiting for growth and production as N for these early successional species. In fact, the last five years of this study (1999-2003), combined irrigation application and annual rainfall totals were either below or consistent with historic rainfall averages for this site (Henderson and Jose 2010). Lockaby et al. (1997) suggested that cultural treatments could exacerbate moisture needs of early successional species in well-drained soils. *P. deltooides* and *P. occidentalis* reached their maximum N budget in the IRR treatment. Given the inherent

fertility of an abandoned agriculture field, these species may have had their nutrient requirements met by past land management techniques. From our analysis, it appears that not only did the fertigation treatments not significantly alter nutrient uptake or biomass production in year eight, (Henderson and Jose 2010) but also the N treatments may have increased water requirements, which may not have been met by the fertigation treatments. This finding was substantiated by the lack of significant differences between the treatments.

In a companion study, Lee and Jose (2005) found that after seven years of fertigation treatments, between 46-60 kg N ha⁻¹ yr⁻¹ was lost in groundwater on an annual basis in the IRR+56 treatment. They found that between 65 and 96 % of the nitrate applied in the *P. deltooides* treatments was leached from the site and suggested that N application rates above the IRR+56 treatment could not be utilized for increased growth exceeding the biological and non-biological N retention capacity of the system (Lee and Jose 2005). These findings suggest that nutrient availability in old agricultural fields may be sufficient for maximum production, and additional N application would be underutilized and likely lost. Depending on the desired length of rotation for short-rotation woody crops (SRWC), it could be suggested from this study that by year eight, any advantage of N application would not be realized in additional uptake or biomass production (Henderson and Jose 2010). At this time, it could also be suggested that additional N application may not be necessary for additional biomass production, or that thinning should occur to relieve below ground competition and release the most desirable (dominant or co-dominant) trees within the stands.

The distributions and amount of N, P, and K (Table 4-1) within each tissue component for these three species are reflective of both the range in biomass produced between the treatments and the nutrient availability supplied by each treatment. Other studies have found similar nutrient content values, on an area basis, for the same set of tissue components to those found in the CON and IRR treatments. For these studies, direct comparisons of nutrient content values are marginal at best as species, nutrients studied, site conditions, and treatments were dissimilar. A few studies have investigated the effects of thinning (Blanco et al. 2006), mixed species stands (Vogel and Gower 1998 and Wang et al. 2000), or multiple aged trees (Miller et al. 1993), chronosequence studies of single species (Wang et al. 1995 and 1996), or the effect of elevated CO₂ on nutrient contents (Calfapietra et al. 2007) but did not entail analysis of nutrient budgets across a fertilization gradient.

In a thinning study of unfertilized 32-year old stand of *Pinus sylvestris* L., conducted by Blanco et al. 2006, they found N total content values ten times higher than were found in this study (4193-5641 kg ha⁻¹ versus our 240-502 kg ha⁻¹ for *P. deltooides*). A study conducted by Wang et al. (1996) consisting of a mixed *Betula papyrifera* Marsh and *Abies lasiocarpa* (Hook) Nutt., total tree N content for 75-year old *B. papyrifera* was similar to the values found in the IRR+224 treatment in this study (431 kg ha⁻¹ versus 439 kg ha⁻¹ found in our study). The values of P and K reported by these authors were higher and lower, respectively, than were found in our study (65 and 217 kg ha⁻¹ versus 22.6-50.6 and 168.1-353 kg ha⁻¹ of P and K. respectively). However, the findings from the Wang et al. (1996) study were based on soils without any amendments. Vogel and Gower (1998) found much lower total N values in a mixed stand of *Pinus banksiana*

Lamb. and *Alnus crispus* (Ait.) Pursh. than were found for *P. deltoides* in our study but were similar to those found for *Q. pagoda* in the CON treatment (170 versus 168 kg ha⁻¹ found in our study). The conditions for their study consisted of a much shorter growing season and degraded soils making direct links between the two studies only superficially comparable. In a study designed to determine NUE for *Eucalyptus* spp., Safou-Matondo et al. (2005) found similar total N, P, and K content for a similarly aged plantation that had been fertilized at the time of planting. Their findings suggest that species or clones selected for superior growth produce high quantities of biomass with low levels of nutrient availability. If the species selected for this study had been hybrid or clonal varieties, it is likely much greater amounts of biomass could have been produced.

Lambers et al (1998), suggests that at least on a short-term basis, the application of one nutrient can force additional uptake of other nutrients. The question could then be asked, can the application of one specific nutrient (N) not only alter the rates of uptake of other nutrients (P and K), but would these effects be long-term so that increased induced nutrient contents are reflected in the content of bole, branches, and bark components? For our study, when compared to CON, it appears that increased levels of N application increased the P content of all components of *P. deltoides* and *Q. pagoda* for all treatments. *P. occidentalis* had similar results, with the exception of P content for branches in the IRR+112 and IRR+224 treatments (Table 4-1). For K, when comparing the CON to all other treatments, all three species had increased K content with increased N application (Table 4-1). Our hypothesis of aboveground nutrient

content for N, P, and K peaking well below the maximum input of N can only be partially supported.

In general, studies have found that plants growing in nutrient poor habitats have mechanisms to conserve and recycle nutrients more efficiently than those found in nutrient rich environments (Aerts 1996, Feller et al. 1999, May et al. 2005). No significant differences were found for RE in our study (Table 4-2) and the relationships in our findings were not strong enough to support our hypothesis of RE peaking below the maximum level of N application. The RE levels we found for N, P, and K for all three species were similar to other studies for N. Pugnaire and Chapin (1993) found RE levels ranging from just over 60 % and up to slightly greater than 80 %. *P. occidentalis* had the highest rates of RE ranging from 66 % in the IRR+224 treatment to 74 % in the CON treatment (Table 4-2) while *P. deltoides* (57 to 65 %) and *Q. pagoda* (60 to 62 %) RE were similar more similar to the lower ranges Pugnaire and Chapin (1993) found for several chaparral species grown in nutrient poor soils. Eckstein et al. (1999), Drenovsky and Richards (2006), May et al. (2005), Cai and Bongers (2007), and Calfapietra et al. (2007) reported similar RE values. Feller et al. (1999) found P RE values for P fertilized *Rhizophora mangle* (red mangrove) trees (approximately 48 to 55 %) similar to *P. deltoides* (53 to 58 %) and *P. occidentalis* (51 to 57 %). These values agree with Aerts and Chapin (2000) for deciduous species and Kozovits et al. (2007) for two savanna tree species *Qualea parviflora* and *Schefflera macrocarpa* for P RE. Hagen-Thorn et al. (2006) and Chatain et al. (2009) found K RE values for *Quercus robur* L., (English oak) and *Nothofagus* species (approximately 38 % and 40 %, respectively) that were similar for *Q. pagoda* in this study (37 to 45 %). Blanco et al.

(2009) found K RE values that were more similar (upwards of 80 %) to those found for *P. deltooides* (72 to 85 %) and *P. occidentalis* (73 to 85 %). The three species in this study could be described as being moderately efficient at resorption (Killingbeck 1993). When these findings are considered singularly, a slight decrease in nutrient resorption might seem unimportant and would suggest that the nutrient levels in an abandoned agricultural field would be sufficient to allow biomass production for SRWC. However, when compared to the IRR and fertigation treatments for all three species, significant biomass production differences were found (Henderson and Jose 2010). Together these findings indicate that while RE was not significantly altered by the application of N, which would suggest ample nutrient availability, for *P. deltooides* RE for all three nutrients was very similar between the CON and IRR+224 treatments suggesting something other than N supply may have been controlling RE for this species. This relationship was not reflected in the RE patterns for the other two species, with the exception of N for *Q. pagoda*, indicating a species-specific mechanism for *P. deltooides* RE. If the sink strength (Nambiar and Fife 1991) of the woody biomass produced were the constraint for nutrient resorption, then the trends of RE should mirror the trends we found for biomass. Although the relationship appears to be minor, the additional biomass in the IRR fertigation treatments did not appear to be the cause of similar RE values across treatments.

Nutrient resorption proficiency (NRP) can be used as a measure to judge the level by which species reduce nutrients in their senescing leaves (Killingbeck 1996). To this end, NRP can be utilized as an index of soil fertility, site ability to supply adequate nutrients in proper ratios for biomass production, and determine potential and realized

resorption (Killingbeck 1996 and Drenovsky and Richards 2006). The values we found for N in the leaf litter, for all three species, agree with the findings of other authors (Yuan and Li 2007 for N 6 g kg^{-1}). Most studies report NRP either as a percentage or on an area basis. However, due to lack of leaf area data for the litter, we report NRP on the dry weight basis similar to the above studies. Although the lack of significant findings suggests our results cannot support the hypothesis of NRP peaking well below the maximum level of N application, we did find that the highest N, P, and K NRP were at levels below the highest rate of N application (Fig. 4-1). While no studies could be found that reported P and K NRP on a dry weight basis, we suggest that because the N-, P-, and K-NRP values for all three species were so similar between the species, no one species appeared to minimize nutrient loss for these specific nutrients. Percent resorption for all three nutrients and all three species exceeded the $>1.0\%$ Killingbeck (1996) used to describe incomplete resorption (data not shown). It appears that adequate balance of all three nutrients were available such that the trees were not attempting to conserve any one specific nutrient.

Our LNUE (Table 4-2) values agree with the findings of other studies (Tateno and Kawaguchi 2002 (70 to 130 g N g^{-1} leaf litter)). However, LNUE does not necessarily correspond to patterns found for CNUE (Table 4-3). LNUE appeared to be more closely related to regulating nutrient balance, as supported by the lack of significance for resorption, while CNUE appear to be more highly influenced by the amount foliar biomass needed to support the woody biomass accrued, although sink strength would not appear to be the driving factor. For this study, it could be suggested that the decomposition and nutrient release from leaf litter was N dependent, such that

because of the apparent increased rates of P and K found with increased N application (within various woody components) were needed to retain nutrient balance. Both foliar and woody components influenced and were integral in the calculation of CNUE. With these findings, we cannot fully support our hypothesis of CNUE peaking well below the maximum input of N, as *P. occidentalis* P- and K-CNUE peaked in the IRR+224 treatment, but not significantly.

Our findings for the N:P (Fig. 4-2) support that as more N was applied through the fertigation system, more P was taken up. All three species, although not significant for *P. deltooides* or *Q. pagoda*, show slightly increased N:P with increased N application (11-13, 13-16, 11-14 for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* CON vs. IRR+224). N:P ratios have been used to identify nutrient limitations that limit plant growth indicating either N or P deficient growing conditions. Several authors have suggested ranges of N:P that indicate nutrient deficiencies (11-18 Graciano et al 2006), ≤ 14 were likely to be N limited and ≥ 16 were likely P limited (Koerselman and Meuleman 1996, and Aerts and Chapin 2000, and <10 or >10 Lambers et al 1998), although a few studies have indicated ratios as high as 27 (Vogt et al 1986).

Knecht and Goransson (2004) suggest that plants require nutrients in optimal ratios, but that these ratios may not be constant across species depending on which nutrients are limiting for growth. They also suggest that nutrients may be taken up in excess of the levels required for growth. Further, Song et al. (2010) found that moderate application of N increased the P concentrations in leaves and roots of *Bauhinia faberi* seedlings with the addition of water, but also noted that high levels of N application decreased growth. In another study, Graciano et al. (2006) found that the

addition of P increased the absorption of N in young *Eucalyptus grandis*. When comparing the relationship between N and P and N and K nutrient content for the wood component in our study, regression analysis indicates strong relationships for all three species (R^2 0.51, 0.87, 0.78, 0.95, 0.45, and 0.96 for *P. deltoides*, *Q. pagoda*, and *P. occidentalis*, respectively, data not shown). Relationships for the other components would be expected to be similar as the nutrient content for N, P, and K in the wood component was the lowest for all of the components investigated. Our findings would support the need for plants to maintain nutrient balance.

In further support of these findings, when ANPP was plotted against N:P (Fig. 4-3) particular trends become apparent. At the lower bounds of the N:P for *P. deltoides* (CON and IRR), production was lowest suggesting N may be limiting biomass production. At the point where N and P would appear to be in the correct ratio, the largest ANPP gains were detected. Significant trends were apparent for *Q. pagoda* and *P. occidentalis*. For both species, the lowest rates of ANPP were in the range of N:P that would suggest N limitation. As the ratio reached the range of balanced N:P maximum production was observed. ANPP then declined when N:P was higher (≥ 16) suggesting P was becoming more limiting for growth. At this point in the correlation, N application for both species was at IRR+112 or 224 N ha⁻¹ yr⁻¹ further supporting the hypothesis of a plateauing response to N application.

Bungart and Huttli (2004) report both biomass production and N:P for *Poplar* clones. Although their data suggests greater biomass production may have been related to clonal differences, the N:P between plots of varying hybrids also indicates a compensatory mechanism of nutrient uptake and balance to biomass production for this

species. Lockaby and Conner (1999) also found that within an optimum range of N:P (approximately 12), greater leaf biomass was produced. Like our study, other authors have found that these relationships are likely species specific (Lockaby and Conner 1999, Aerts and Chapin 2000, Drenovsky and Richards 2006, and Specht and Turner 2006) and are potentially tied to genotype. It could be suggested that periodic testing of N:P in SRWC would assist fertilization management to obtain maximum biomass by circumventing nutrient imbalance.

We found that aboveground nutrient content, nutrient resorption efficiency and proficiency, and leaf- and canopy-level nutrient use efficiency are not necessarily influenced by increased nitrogen availability. Although nutrient contents and levels tracked over several growing seasons, might indicate differing levels of nutrient uptake, use, storage, and remobilization, we believe our findings are representative of this entire study length as nutrient application was consistent across years. While many plants have adaptations to conserve nutrients when nutrient levels are low, the available resources supplied by an abandoned agricultural field appear to be sufficient as to not alter the mechanism for nutrient conservation. Additionally, we found that maximum biomass production was not necessarily tied to maximum nutrient input. Production as well as nutrient requirements are species specific and may include a compensatory mechanism providing sufficient resources available from the site, to deter nutrient imbalance. These findings could suggest that if N and P are supplied simultaneously, regular inspection of the N:P should occur throughout a rotation to ensure nutrient uptake remained balanced for maximum biomass production for SRWC species.

Table 4-1. Average nutrient and standard deviation for nitrogen, phosphorus, and potassium content of bole, main branches, bark, foliage, and total tree for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* during year eight (2003) of the study. Letters indicate significant differences among treatments.

<i>P. deltooides</i>						
	Bole kg ha ⁻¹	Branch kg ha ⁻¹	Bark kg ha ⁻¹	Foliar kg ha ⁻¹	Total	
Nitrogen						
CON	4.0 (1.5) a	17.1 (6.2) a	1.8 (0.6) a	217.7 (44.1) a	240.5	(50.1) a
IRR	9.2 (2.0) b	56.1 (17.5) b	4.8 (1.4) b	432.8 (115.4) b	502.9	(135.8) b
IRR+56	10.5 (3.0) b	46.5 (13.2) b	4.4 (1.2) b	354.4 (45.6) b	415.8	(62.2) b
IRR+112	9.1 (2.2) b	42.8 (9.9) b	4.2 (0.9) b	366.0 (26.5) b	422.1	(36.1) b
IRR+224	10.0 (2.0) b	48.7 (9.5) b	3.8 (0.7) b	376.5 (34.0) b	439.0	(37.6) b
Phosphorus						
CON	0.5 (0.2) a	3.6 (13.3) a	0.1 (0.0) a	18.4 (3.7) a	22.6	(5.0) a
IRR	0.8 (0.2) a	11.9 (3.7) c	0.3 (0.1) b	37.6 (10.0) b	50.6	(13.9) b
IRR+56	0.8 (0.2) a	8.4 (2.4)bc	0.2 (0.1) b	26.8 (3.4)ab	36.2	(6.0)ab
IRR+112	0.7 (0.2) a	7.6 (1.8)ab	0.3 (0.1) b	27.9 (2.0)ab	36.6	(3.6)ab
IRR+224	1.4 (0.3) b	9.4 (1.8)bc	0.3 (0.1) b	28.2 (2.5)ab	39.3	(3.6) b
Potassium						
CON	8.3 (3.1) a	20.0 (7.3) a	0.4 (0.1) a	139.5 (28.3) a	168.1	(37.1) a
IRR	19.5 (4.2) b	70.6 (22.0) b	1.2 (0.3) b	261.9 (69.8) b	353.0	(95.5) b
IRR+56	29.9 (8.6) c	60.7 (17.3) b	1.1 (0.3) b	220.6 (28.4) b	312.2	(53.6) b
IRR+112	17.4 (4.1)ab	61.8 (14.4) b	1.0 (0.2) b	236.5 (17.1) b	316.8	(32.4) b
IRR+224	23.9 (4.7)bc	57.7 (11.2) b	1.1 (0.2) b	267.8 (24.2) b	350.6	(30.9) b
<i>Q. pagoda</i>						
Nitrogen						
CON	1.7 (0.5) a	2.9 (0.9) a	1.6 (0.5) a	153.0 (124.4) a	159.3	(126.2) a
IRR	2.9 (1.0) a	5.4 (1.5)ab	3.0 (1.0)ab	266.1 (102.8)ab	277.4	(105.6)ab
IRR+56	2.9 (0.9) a	5.0 (1.5)ab	2.9 (0.9)ab	308.8 (58.6)ab	319.7	(61.5)ab
IRR+112	4.6 (0.8) b	6.4 (1.4) b	4.1 (0.7)bc	367.1 (33.7) b	382.2	(31.8) b
IRR+224	6.3 (0.4) c	8.9 (0.6) c	4.8 (0.3) c	294.0 (68.1)ab	314.0	(69.0)ab

Table 4-1. Continued

		<i>Q. pagoda</i>						
	Phosphorus	Bole kg ha⁻¹	Branch kg ha⁻¹	Bark kg ha⁻¹	Foliar kg ha⁻¹	Total		
CON		0.2 (0.1) a	0.5 (0.1) a	0.1 (0.0) a	11.0 (9.0) a	11.7	(9.2)	a
IRR		0.3 (0.1)ab	0.7 (0.2) a	0.1 (0.0) a	16.6 (6.4) a	17.7	(6.7)	a
IRR+56		0.2 (0.1)ab	0.8 (0.2) a	0.1 (0.0)ab	19.0 (3.6) a	20.2	(3.9)	a
IRR+112		0.2 (0.0)ab	0.6 (0.1) a	0.2 (0.0)bc	22.7 (2.1) a	23.7	(2.0)	a
IRR+224		0.3 (0.0) b	0.7 (0.1) a	0.2 (0.0) c	18.1 (4.2) a	19.3	(4.3)	a
Potassium								
CON		2.3 (0.8) a	2.5 (0.7) a	0.3 (0.1) a	64.9 (52.8) a	70.0	(54.3)	a
IRR		3.1 (1.1)ab	3.6 (1.0)ab	0.5 (0.2) a	100.4 (38.8) b	107.5	(40.6)	ab
IRR+56		3.6 (1.1)ab	4.2 (1.3)ab	0.9 (0.3) b	104.5 (19.8) b	113.2	(22.2)	ab
IRR+112		4.3 (0.7)bc	4.9 (1.0)bc	1.3 (0.2)bc	151.6 (13.9) b	162.1	(12.6)	b
IRR+224		5.9 (0.4) c	6.6 (0.5) c	1.7 (0.1) c	122.0 (28.2) b	136.2	(28.9)	ab
		<i>P. occidentalis</i>						
	Nitrogen							
CON		6.2 (0.8) a	4.3 (0.6) a	2.4 (0.3) a	278.6 (41.9) a	291.4	(41.1)	a
IRR		9.0 (0.2) b	8.9 (0.8) c	4.7 (0.2) c	536.6 (73.2) b	559.1	(74.1)	b
IRR+56		9.1 (0.6) b	8.6 (0.5) c	4.6 (0.3) c	511.5 (31.8) b	534.0	(31.9)	b
IRR+112		11.9 (0.3) c	6.7 (0.2) b	3.7 (0.1) b	470.9 (14.1) b	493.1	(13.9)	b
IRR+224		9.9 (1.3) b	8.5 (1.0) c	4.2 (0.5)bc	482.0 (47.5) b	504.6	(49.1)	b
	Phosphorus							
CON		1.0 (0.1) a	0.3 (0.1) a	0.4 (0.0) a	24.8 (3.7) a	26.9	(3.6)	a
IRR		2.1 (0.1) b	1.6 (0.2) b	0.0 (0.0) c	41.7 (5.7) c	45.6	(5.8)	c
IRR+56		2.2 (0.2) b	1.5 (0.1) b	0.0 (0.0) c	39.7 (2.5)bc	43.7	(2.5)	c
IRR+112		2.2 (0.1) b	0.9 (0.0) a	0.0 (0.0) b	34.6 (1.0)bc	38.0	(1.0)	bc
IRR+224		1.3 (0.2) b	0.9 (0.1) a	0.3 (0.0) b	33.1 (3.3) c	35.5	(3.4)	b

Table 4-1. Continued

Potassium	<i>P. occidentalis</i>					Total		
	Bole kg ha⁻¹	Branch kg ha⁻¹	Bark kg ha⁻¹	Foliar kg ha⁻¹				
CON	6.7 (0.9) a	3.6 (0.5) a	0.3 (0.0) a	146.0 (22.0) a		156.7	(21.3)	a
IRR	10.3 (0.2) b	6.6 (0.6) c	1.3 (0.1) c	257.5 (35.1) b		275.7	(35.8)	b
IRR+56	10.5 (0.7) c	6.4 (0.4) c	1.3 (0.1) c	245.5 (15.1) b		263.7	(15.5)	b
IRR+112	12.3 (0.3) c	4.2 (0.2) a	1.3 (0.0) c	226.0 (6.8) b		243.7	(6.6)	b
IRR+224	10.6 (1.4) c	5.1 (0.6) b	1.0 (0.1) b	213.0 (21.0) b		229.2	(22.1)	b

Table 4-2. Average % nutrient resorption efficiency (RE%) and leaf level nutrient use efficiency (LNUE g g⁻¹) for nitrogen, phosphorus, and potassium with standard deviation for *P. deltoides*, *Q. pagoda*, and *P. occidentalis* during year eight (2003) of the study. Letters indicate significant differences among treatments.

	RE			LNUE		
	N	P	K	N	P	K
<i>P. deltoides</i>						
CON	65 (9)a	58 (11)a	85 (8)a	136 (13)a	1250 (76)a	732 (182)a
IRR	62 (4)a	56 (6)a	81 (14)a	116 (20)a	1232 (299)a	418 (345)a
IRR+56	60 (3)a	56 (7)a	72 (8)a	112 (19)a	1103 (88)a	363 (158)a
IRR+112	57 (2)a	53 (7)a	72 (9)a	107 (7)a	1118 (74)a	361 (118)a
IRR+224	63 (5)a	57 (7)a	83 (8)a	111 (15)a	1037 (182)a	331 (183)a
<i>Q. pagoda</i>						
CON	62 (4)a	40 (6)a	64 (22)a	140 (7)a	1107 (131)a	274 (80)a
IRR	60 (5)a	39 (6)a	57 (11)a	114 (12)a	1092 (84)a	265 (31)a
IRR+56	60 (7)a	37 (2)a	54 (18)a	114 (12)a	1031 (72)a	270 (125)a
IRR+112	62 (7)a	37 (5)a	51 (8)a	113 (21)a	1049 (84)a	214 (63)a
IRR+224	61 (7)a	45 (16)a	52 (18)a	111 (23)a	1035 (95)a	218 (72)a
<i>P. occidentalis</i>						
CON	74 (4)a	57 (13)a	85 (3)a	176 (37)a	944 (112)a	476 (76)a
IRR	72 (6)a	51 (3) a	83 (6)a	144 (7)a	886 (42)a	404 (79)a
IRR+56	70 (5)a	50 (4)a	83 (5)a	132 (26)a	866 (81)a	373 (92)a
IRR+112	70 (7)a	52 (10)a	82 (4)a	126 (22)a	863 (97)a	376 (107)a
IRR+224	66 (3)a	50 (4)a	73 (11)a	134 (7) a	934 (127)a	401 (100)a

Table 4-3. Canopy nutrient use efficiency (CNUE) of unit woody biomass (Mg) per unit nitrogen, phosphorus, and potassium (kg) for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* for year eight (2003) of the study for each treatment. Letters indicate significant differences among treatments.

	CNUE		
	N (Mg/kg)	P (Mg/kg)	K (Mg/kg)
<i>P. deltooides</i>			
CON	3.5 (0.3) a	40.5 (3.3)a	4.8 (1.2)ab
IRR	4.9 (0.3) b	55.6 (9.4)a	6.3 (1.0) a
IRR+56	5.1 (0.6) b	63.6 (9.9)a	5.6 (1.0)ab
IRR+112	3.3 (0.5) a	43.5 (8.9)a	3.8 (0.7) b
IRR+224	4.1 (1.2)ab	59.8 (28.4)a	4.4 (3.5)ab
<i>Q. pagoda</i>			
CON	2.1 (0.3) a	26.3 (1.9)a	4.2 (0.4) a
IRR	1.5 (0.2) a	23.3 (4.4)a	4.0 (1.3) a
IRR+56	1.3 (0.4) a	23.2 (5.1)a	3.9 (0.7) a
IRR+112	1.3 (0.4) a	20.9 (5.1)a	3.2 (0.7) a
IRR+224	1.5 (0.7) a	23.3 (3.3)a	2.9 (0.6) a
<i>P. occidentalis</i>			
CON	1.9 (0.5) a	23.1 (7.5)a	3.0 (0.7) a
IRR	1.8 (0.8) a	22.1 (7.6)a	3.1 (1.8) a
IRR+56	1.6 (0.4) a	20.4 (2.5)a	2.6 (0.6) a
IRR+112	1.3 (0.3) a	19.6 (3.9)a	2.6 (0.7) a
IRR+224	1.8 (0.1) a	23.2 (3.7)a	3.4 (1.8) a

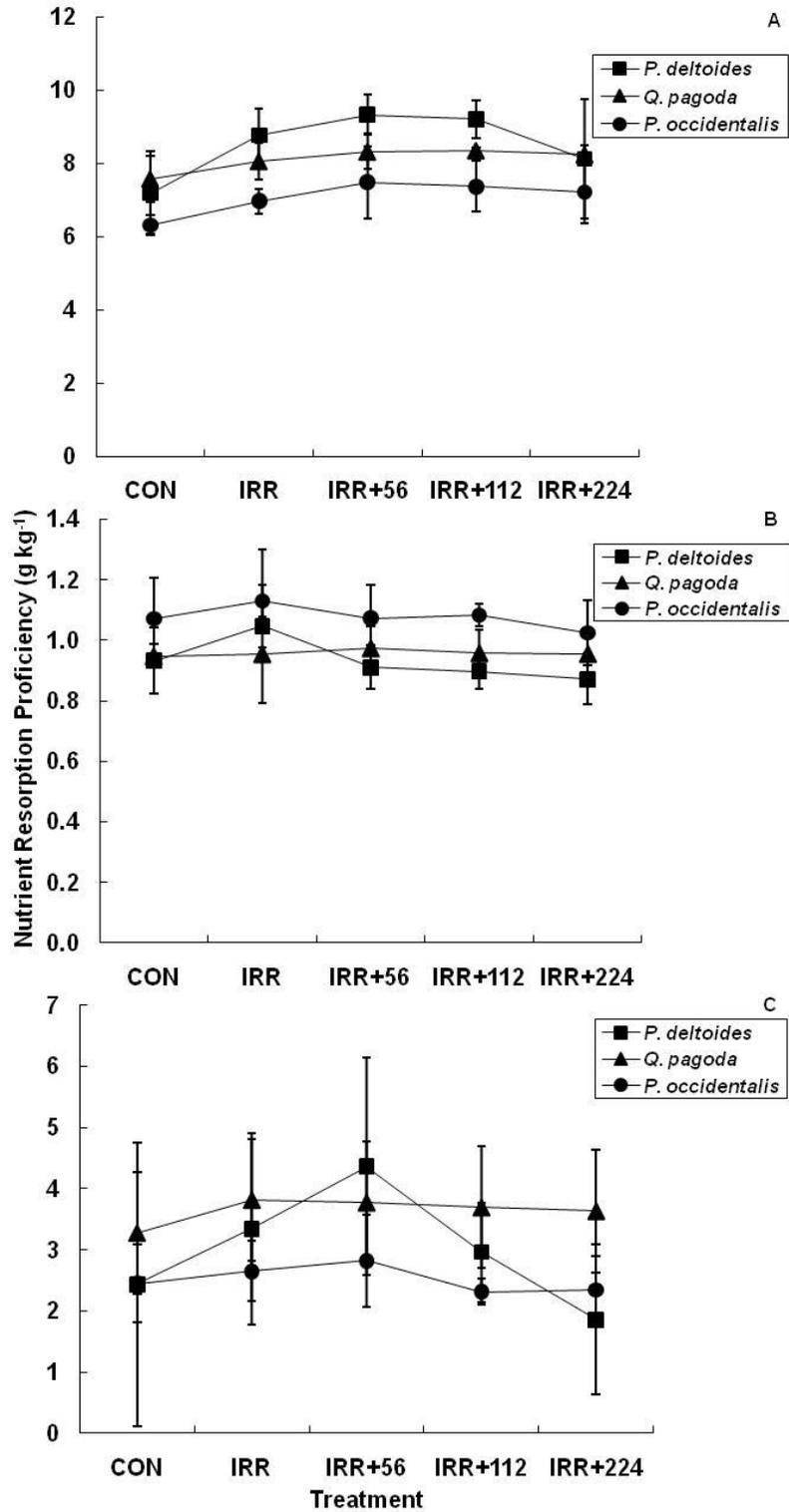


Figure 4-1. Average and standard error of nutrient resorption proficiency (g nutrient kg⁻¹ dry weight) of litterfall nitrogen (A), phosphorus (B), and potassium (C) for *P. deltoides* (square), *Q. pagoda* (triangle), and *P. occidentalis* (circle).

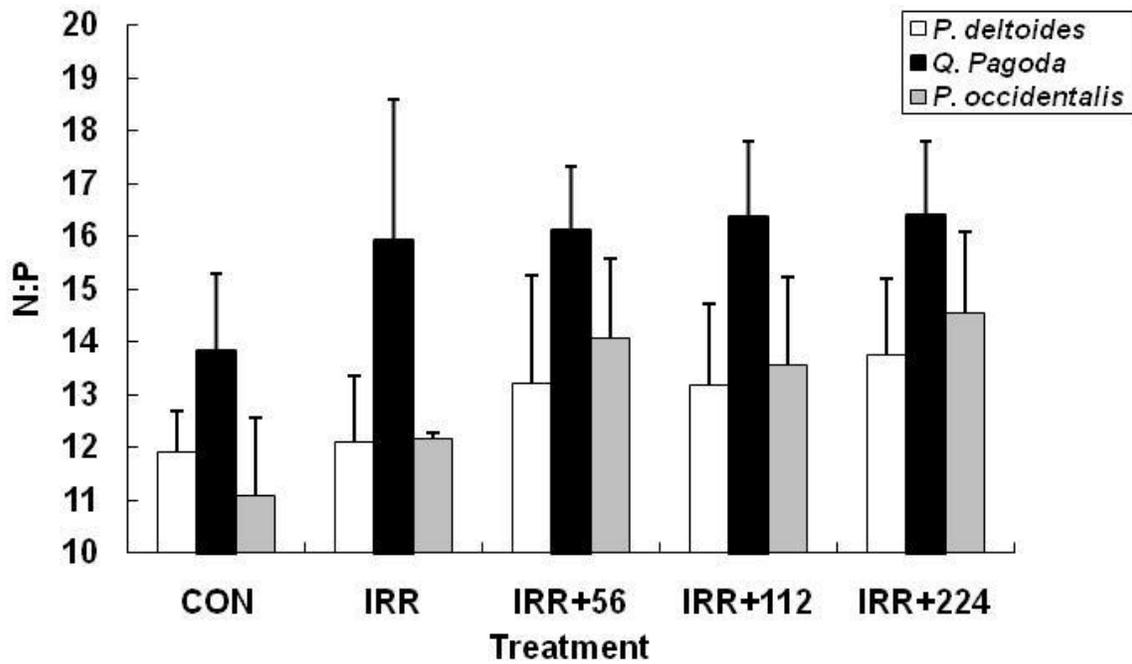


Figure 4-2. N:P foliar ratios for *P. deltooides*, *Q. pagoda*, and *P. occidentalis* for each treatment during year eight (2003) of the study. Letters above the treatments indicate significant differences.

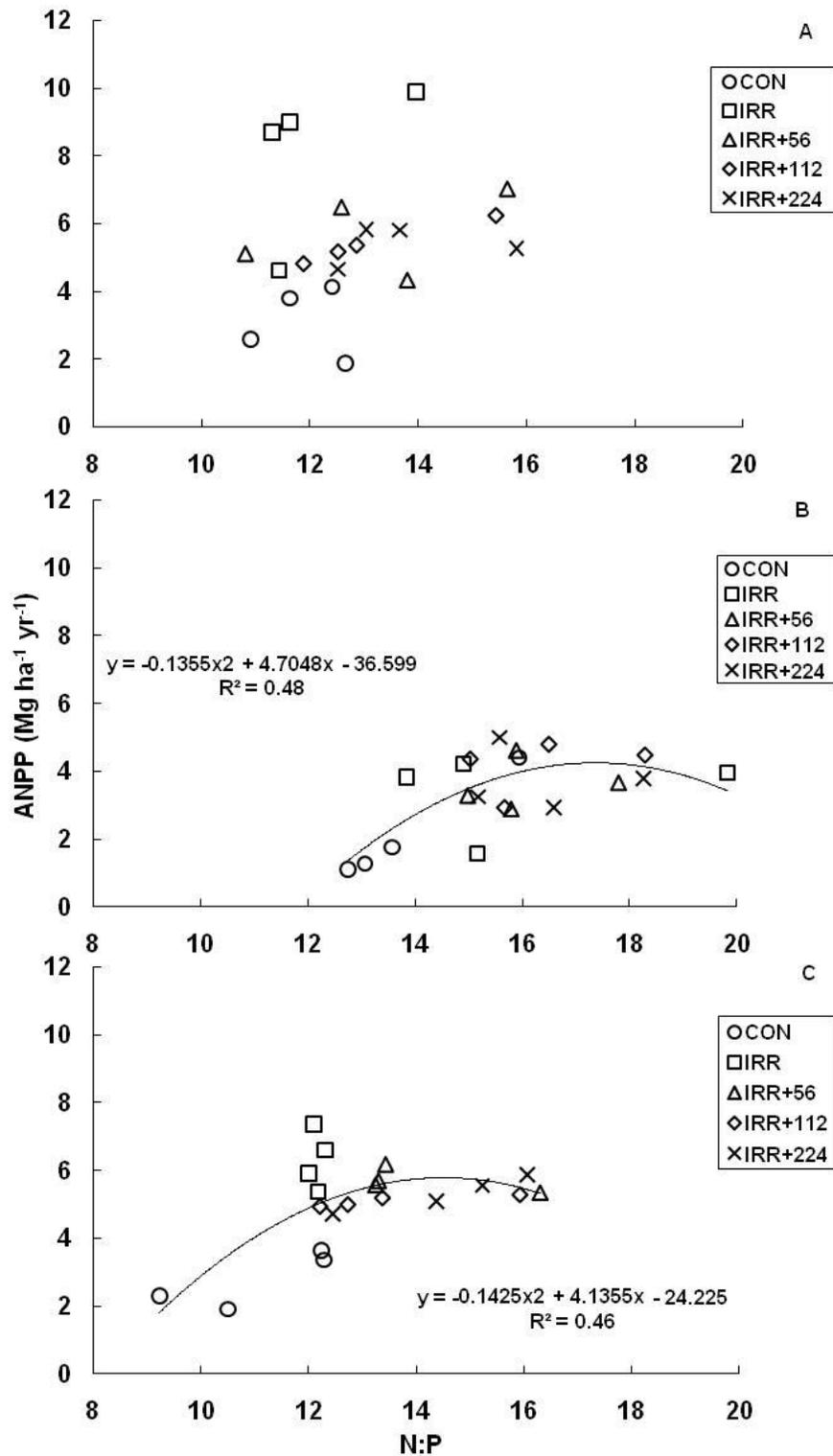


Figure 4-3. Biomass production ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) and foliar N:P for year eight (2003) of the study for *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) for all treatments (circle = CON, square = IRR, triangle = IRR + 56 $\text{kg N ha}^{-1} \text{ yr}^{-1}$, diamond = IRR + 112 $\text{kg N ha}^{-1} \text{ yr}^{-1}$, and X = IRR + 224 $\text{kg N ha}^{-1} \text{ yr}^{-1}$).

CHAPTER 5 SUMMARY OF CONCLUSIONS

The overall objective of this study was to examine the production ecology of three economically important hardwood species, *Populus deltoides*, *Quercus pagoda*, and *Platanus occidentalis*, to varying levels of resource application. Specifically, we wanted to determine how biomass production was altered, physiologically supported, and how nutrient uptake and storage within various biomass components were influenced by the resource applications of irrigation and the combined treatment of irrigation and nitrogen application (fertigation) at 56, 112, and 224 kg N ha⁻¹ yr⁻¹. The first objective was to determine the amount of woody and foliar biomass produced for the three species. Allometric equations developed by Shelton et al. 1982 were used for *P. deltoides* and equations developed by Schlaegel and Kennedy 1986 were used for *Q. pagoda* and *P. occidentalis*. These equations were used for woody biomass production and litter traps were used to determine actual foliar biomass (Chapter 2). Next, to determine how much light the canopy was capturing and the extent of which the treatments were influencing physiological mechanisms, photosynthesis data was collected from sun and shade leaves for all three species. Leaves were collected and measured, weighed, dried, and analyzed for nitrogen content (Chapter 3). Finally, we wanted to determine the aboveground N, P, and K content and use efficiencies for these three species and understand the relationship between nitrogen, phosphorus, and potassium as it pertained to the resource gradient. To determine the amount of nitrogen being utilized in various above ground tissues, versus the amount applied on an annual basis, samples were taken from the bole, branches, bark, and foliage for all three species and analyzed for nitrogen, phosphorus, and potassium (Chapter 4).

Few studies have looked at simultaneous application of irrigation with fertilizer for growing SRWC on agricultural fields. While fertigation techniques are relatively infrequent, the resource gradient allows an opportunity to study resource requirements and mechanisms necessary for maximum aboveground biomass production. Given the data collected during our study and the current literature available for these three species, several generalizations regarding the use of *P. deltooides*, *Q. pagoda*, and *P. occidentalis* in short-rotation plantations can be made. Our data indicate that plantation establishment for *P. deltooides* may not have to be restricted to bottomland sites for maximum production. The significant production response of *P. deltooides* to the IRR treatment and the lack of significant differences for the N treatments suggest that IRR alone may be sufficient to obtain maximum growth on good quality sites such as agricultural fields with similar nutrient levels as this study. *P. deltooides* may benefit from low levels of fertilization on low quality sites. *Q. pagoda*'s positive linear response to treatments applied in this study may prove beneficial for accelerating production in plantations. Its slow growth rate, compared to *P. deltooides* and *P. occidentalis*, would otherwise preclude it from short-rotation operations. Despite increased production in response to the IRR treatment, standing biomass for *P. occidentalis* was considerably lower than *P. deltooides*. Disease, crown breakage, and mortality may have confounded the production response of *P. occidentalis* to cultural treatments. Overall, our results suggest that ANPP is highly correlated with LAI; however, the relationship is species specific. Maximum ANPP was reached well below the maximum LAI for *Q. pagoda* and *P. occidentalis*. *P. deltooides* ANPP was highest at the maximum LAI, which was achieved with IRR alone.

These results suggest that species-specific cultural practices that produce the optimum LAI and maximum ANPP need to be identified before fertigation techniques can be widely adopted for increasing biomass production potential of SRWC. The high biomass production potential of SRWC such as those tested in our study will play a significant role in helping to meet renewable energy standards.

The positive impact of irrigation and fertilization on productivity has been well documented. However, as has been suggested by other researcher, the reasons for increased growth response are less evident. Several factors related to canopy dynamics have been identified by others and were explored in detail in our study. As expected, SLA, SLN, LAI, A_{\max} and ANPP varied across the supplied soil resource gradient for all three species. Irrigation alone was sufficient in *P. deltoides* and *P. occidentalis* to increase SLA whereas SLA responded to both irrigation and fertilization in *Q. pagoda*. A corresponding increase in LAI, similar to that of SLA, was also observed for all three species. A_{\max} reached peak rates for all species in the IRR+112 treatment for both sun and shade leaves and showed strong positive correlations with SLN across the gradient. ANPP exhibited a curvilinear relationship with canopy A_{\max} with peak production occurring well below the maximum estimated canopy A_{\max} . An increase in LAI alone was sufficient to achieve maximum ANPP in both *P. deltoides* and *P. occidentalis*. However, an increase in both LAI and foliar A_{\max} resulted in the maximum ANPP in *Q. pagoda*. Although we hypothesized that increased foliar A_{\max} in combination with an increase in LAI would be necessary to increase ANPP along the increasing resource gradient, our results indicate that an increase in LAI alone can increase canopy A_{\max} and lead to increased productivity. An increase in foliar A_{\max} may

or may not be necessary to yield the highest ANPP depending on the species. Further research was needed to determine the relationship between N and other potentially limiting nutrients so that the role of nutrient imbalance can be better understood. Given the appeal for managing short-rotation plantations with fertigation, this study should give land managers a solid scientific basis for developing efficient fertigation strategies.

We found that nutrient content, nutrient resorption efficiency and proficiency, and leaf- and canopy-level nutrient use efficiency are not necessarily influenced by increased resource availability. Although nutrient contents and levels tracked over several growing seasons might indicate differing levels of nutrient uptake, use, storage, and remobilization, we feel our findings are representative of this entire study length as nutrient application was consistent across years. While many plants have adaptations to conserve nutrients when nutrient levels are low, the available resources supplied by an abandoned agricultural field appear to be sufficient as to not alter the mechanism for nutrient conservatism. Additionally, we found that maximum biomass production was not necessarily tied to maximum nutrient input. Production as well as nutrient requirements are species specific and may include a compensatory mechanism providing sufficient resources are available from the site, to deter nutrient imbalance. These findings could suggest that if N and P are supplied simultaneously, regular inspection of the N:P should occur throughout a rotation to ensure nutrient uptake remained balanced for maximum biomass production for SRWC species.

The concept of SRWC supply systems are inherently tied to changes in attitudes about energy production. Fast growing hardwood species are among a suite of options considered for biopower and liquid fuels based on biomass. By studying the production

ecology of three fast growing hardwood species, we were able to make some generalizations about the applicability of using *P. deltooides*, *Q. pagoda*, and *P. occidentalis* for SRWC supply systems. Our results indicate species-specific responses to biomass production, the physiological mechanisms that control production, and the relationships between nutrient use and accumulating biomass. Understanding the interactions between the SRWC species and intensive practices such as fertilization will assist future development of biomass/biofuel practices using fast growing hardwood species for SRWC systems.

Future directions for this type of study should include hybrid or clonal varieties selected for their potential in biomass accrual, particularly if the objective is for biomass/biofuel purposes. Additionally, should co-firing of woody biomass with coal be a viable alternative for the production of electricity, tonnage of woody biomass needed for sustainable production will likely require intensive management in natural forests and dedicated energy plantations. Given the response of these three species to N application, a study with varying levels of other essential nutrients (such as P and K) should be considered to determine if biomass production could be further increased with multiple levels of nutrients.

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BIOGRAPHICAL SKETCH

Dawn Elizabeth Henderson was born in southern Illinois. It was there among the natural beauty of Illinois that an appreciation for the outdoors developed. After exploring several different vocations, she found wonder, excitement, and challenge in furthering her education. While attending St. Charles Community College she discovered her enthusiasm for science. After receiving her Associate of Arts, she began her work on a Bachelor of Science at Southern Illinois University at Edwardsville, Illinois. During the course of her bachelor's studies, she found a passion for floodplain forests and research in general. It was that drive, to more fully experience and understand her natural surroundings that compelled her to receive her Master of Science in Science at Southern Illinois University. After accepting a Research Assistantship with Shibu Jose at University of Florida her interests came to include forest ecology and physiology. She obtained her PhD in 2010. She now works for one of the nation's premier conservation agencies, Missouri Department of Conservation.