

Nutrient Use Efficiency of Three Fast Growing Hardwood Species across a Resource Gradient

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Attitudes regarding traditional energy sources have shifted toward renewable resources. Specifically, short-rotation woody crop supply systems have become more prevalent for biomass and biofuel production. However, a number of factors such as environmental and inherent resource availability can limit tree production. Given the intensified demand for wood biomass production, forest and plantation management practices are focusing on increasing productivity. Fertilizer application, while generally one of the least expensive silvicultural tools, can become costly if application rates exceed nutrient uptake or demand of the trees especially if it does not result in additional biomass production. We investigated the effect of water and varying levels of nitrogen application (56, 112, and 224 kg·N·ha⁻¹·yr⁻¹) on nutrient content, resorption efficiency and proficiency, N:P and the relationship with ANPP, as well as leaf- and canopy-level nutrient use efficiency of nitrogen, phosphorus, and potassium for *Populus deltoides*, *Quercus pagoda*, and *Platanus occidentalis*. *P. deltoides* and *P. occidentalis* reached their maximum nitrogen budget with the application of water suggesting old agricultural fields may have sufficient nutrient levels to sustain short-rotation woody crops negating the application of additional nitrogen for these two species. Additionally, for *P. deltoides* and *Q. pagoda* application of nitrogen appeared to increase the uptake of phosphorus however, resorption efficiency for these two species were more similar to studies conducted on nutrient poor sites. Nutrient resorption proficiency for all three nutrients and all three species were at levels below the highest rates of nitrogen application. These findings suggest maximum biomass production may not necessarily be tied to maximum nutrient application.

Keywords: Nutrient Use Efficiency; Resorption; N:P; Biomass Production

Introduction

Changes in attitudes about energy production have 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 & Melichar, 1986; Coyle & Coleman, 2005; 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 for production purposes is limited at best.

Tree production can be limited by a number of factors such as light (Wang et al., 1991; Ellsworth & Reich, 1992; Jose & Gillespie, 1997; Jokela & Martin, 2000; Henderson & Jose, 2005), water (Lockaby et al., 1997; Albaugh et al., 1998; King et al., 1999; Allen et al., 2002; Albaugh et al., 2004), and

growing space (Cochran et al., 1991; Schubert et al., 2004; Lockhart et al., 2006; Clark et al., 2008; Curtis, 2008) or enhanced by practices such as fertilization (Singh, 1998; Will et al., 2002; Bekele et al., 2003; Allen et al., 2004; Samuelson et al., 2004a), or irrigation (Allen et al., 2005; Stape et al., 2008; Zalesny et al., 2007; 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 & Gower, 1998; Blanco et al., 2006; Schilling & Lockaby, 2006; 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 & Aerts, 1987; Aerts & Berendse, 1988; Aerts, 1996; Aerts, 1997; Wright & 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; Killingbeck, 1996). Other studies suggest higher leaf level nutrient status (Lathja, 1987) or re-

source availability (Xu & Timmer, 1999) is linked to higher or lower (Aerts & de Caluwe, 1994; Vitousek, 1998) resorption ratios or may have no effect on the ratios (Chapin & Kedrowski, 1983; Birk & Vitousek, 1986; Aerts, 1996; Wright & Westoby, 2003; Yuan & 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 & Westoby, 2003), water availability (Boerner, 1985; del Arco et al., 1991; Escudero et al., 1992; Wright & Westoby, 2003), soil chemistry (del Arco et al., 1991; Bridgham et al., 1995; Choi et al., 2005; Campo et al., 2007) as well as between members of the same species (Birk & Vitousek, 1986; Aerts & de Caluwe, 1994; Bungart & Hüttl 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 levels).

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 & Hüttl, 2004; Coyle & 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 & Hüttl, 2004; Lee & Jose, 2005; 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, or does not result in additional biomass production. 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 & Axelsson, 1986; Lockaby et al., 1997; King et al., 1999; Bekele et al., 2003; Coyle & 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 & Stock, 1995; Jokela et al., 2004; Prietzel et al., 2004; Sword Sayer et al., 2004; Ladanai et al., 2006; Saarsalmi et al., 2006; 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 excessive or limit growth.

In the present study, we investigated the effect of water and nutrient availability, on nutrient content ($\text{kg}\cdot\text{ha}^{-1}$), resorption efficiency (%), resorption proficiency (g nutrient/kg leaf 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* 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 for each 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; specifically does an increase in foliar nutrient content result in increased biomass production? 3) determine the nutrient use efficiency on a leaf- and canopy-level basis for the three nutrients and species. In particular, 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.

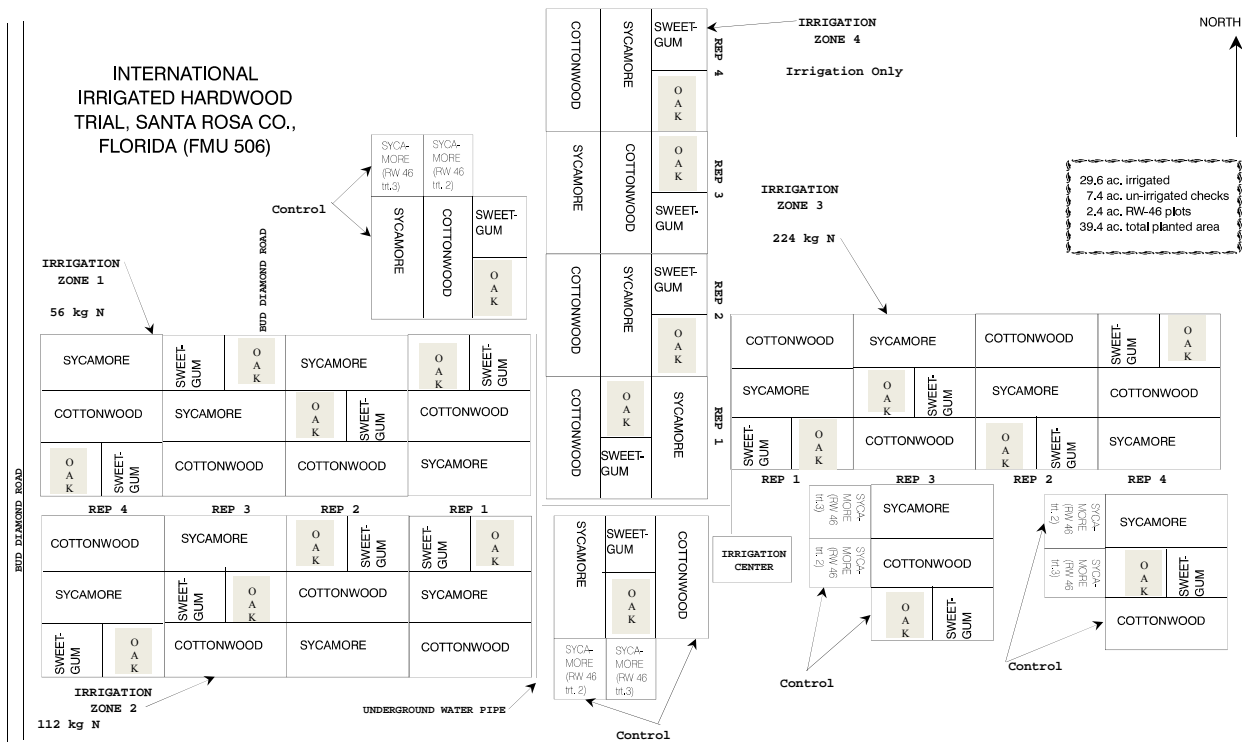
Methods

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 1700 mm, 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, RhodicPaleudult) formed in thick beds of loamy marine deposits with an average water table depth of 1.8 m (Lee & 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) ($\text{kg}\cdot\text{ha}^{-1}$). 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 $\text{kg}\cdot\text{ha}^{-1}$ (Lee & Jose 2006).

Treatment plots of *P. deltoides* and *P. occidentalis* consisted of 40 trees plot^{-1} and *Q. pagoda* contained 16 trees plot^{-1} ; (although the *Q. pagoda* plots were the smallest of the three species, and need to be treated with caution, the results reflect data collected within the study) **Figure 1**. All treatment plots were planted at 2.13 m \times 3.35 m 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 $\text{kg}\cdot\text{ha}^{-1}$ respectively, Greg Leach, personal communication). Soil pH was adjusted to 6.0, with 3363 $\text{kg}\cdot\text{ha}^{-1}$ 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; Samuelson et al., 2004b).

Herbaceous weed control consisted of combinations of

**Figure 1.**

Study layout showing planting schematic and treatment applications. For this study, only *P. deltoides* (cottonwood), *Q. pagoda* (cherrybark oak referred to in graphic as oak), and *P. occidentalis* were studied. Image reproduced from first year growth of Hardwoods under fertigation in western Florida. Unpublished international paper internal report 1996. Gregory N. Leach and Homer H. Gresham, southern forest resources technical services, western Florida region, Cantonment, Florida.

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 390 mm 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 & 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).

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, 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 0.01 g. 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 superficially 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 ~1.5 m 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 (Mg·ha⁻¹·yr⁻¹, excluding herbivory or litter of branches, bark, or fruits), 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), for year eight. 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. 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 & Kennedy, (1986) were used to calculate volume and aboveground woody biomass for both *Q. pagoda* and *P. occidentalis*. The original Schlaegel & 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 similarly as above 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.

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 & 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) Nutrient content (kg·ha⁻¹) = kg·ha⁻¹(biomass) × kg·kg⁻¹(nutrient)
- 2) Resorption (%) = (foliar_(live) - foliar_(litter)/foliar_(live)) × 100
- 3) Leaf nutrient use efficiency (g·g⁻¹) = 1 / ((g·g⁻¹) × (1 - resorption))
- 4) Canopy nutrient use efficiency (Mg·kg⁻¹) = Mg/(kg_{foliage} × kg·kg⁻¹(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 & 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. deltooides* 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). IRR and 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 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 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 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 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 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 between 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

Table 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>				
N	Bole kg·ha ⁻¹	Branch kg·ha ⁻¹	Bark kg·ha ⁻¹	Foliar kg·ha ⁻¹	Total	
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	
P						
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	
K						
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>				
N	Bole kg·ha ⁻¹	Branch kg·ha ⁻¹	Bark kg·ha ⁻¹	Foliar kg·ha ⁻¹	Total	
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	
P						
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	
K						
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)ab	104.5 (19.8)ab	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>				
N	Bole kg·ha ⁻¹	Branch kg·ha ⁻¹	Bark kg·ha ⁻¹	Foliar kg·ha ⁻¹	Total	
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	
P						
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	
K						
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	

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 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 3) followed irregular patterns. Only N and K for *P. deltooides*, exhibited significant differences between 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 (Figure 2).

N:P and ANPP

No significant relationship was found for N:P and above-ground net primary productivity (ANPP) for *P. deltooides* (Figure 3). The trend for *Q. pagoda* and *P. occidentalis* for N:P and ANPP (Figure 4) 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 1). Despite these differences, N content in *Q. pagoda* were greater at higher N application rates. Rowe et al., (2002) found a similar relationship for loblolly pine but found

Table 2.

Average % nutrient resorption efficiency (RE%) and leaf level nutrient use efficiency (LNUE g·g⁻¹) for nitrogen (N), phosphorus (P), and potassium (K) with standard deviation for *P. deltooides*, *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. deltooides</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

Table 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 ⁻¹)	P (Mg·kg ⁻¹)	K (Mg·kg ⁻¹)
<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

that genetic differences among families resulted in greater number of shoots in stem cuttings. 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 1). Water availability necessary for nutrient uptake (Lambers et al., 1998) regulates foliar production (Jose & Gillespie, 1996, 1997) and therefore the amount of woody biomass that can be produced (Henderson & 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 & 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 & Jose, 2010) but also the N treatments may have increased water requirements, which may not have been met by the fertigation treatments. Wilson et al. (2012) suggested that microbial and soil chemical processes influence plant N uptake such that colloidal soil particles or

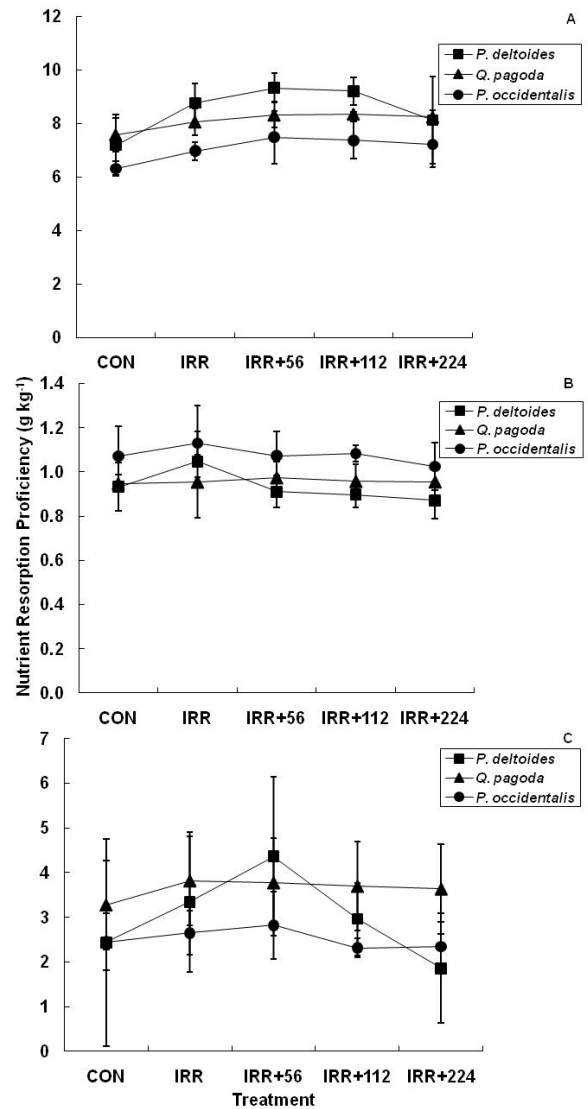


Figure 2.

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. deltooides* (square), *Q. pagoda* (triangle), and *P. occidentalis* (circle).

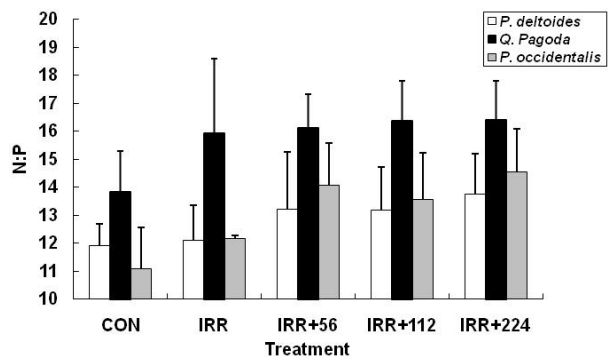


Figure 3.

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.

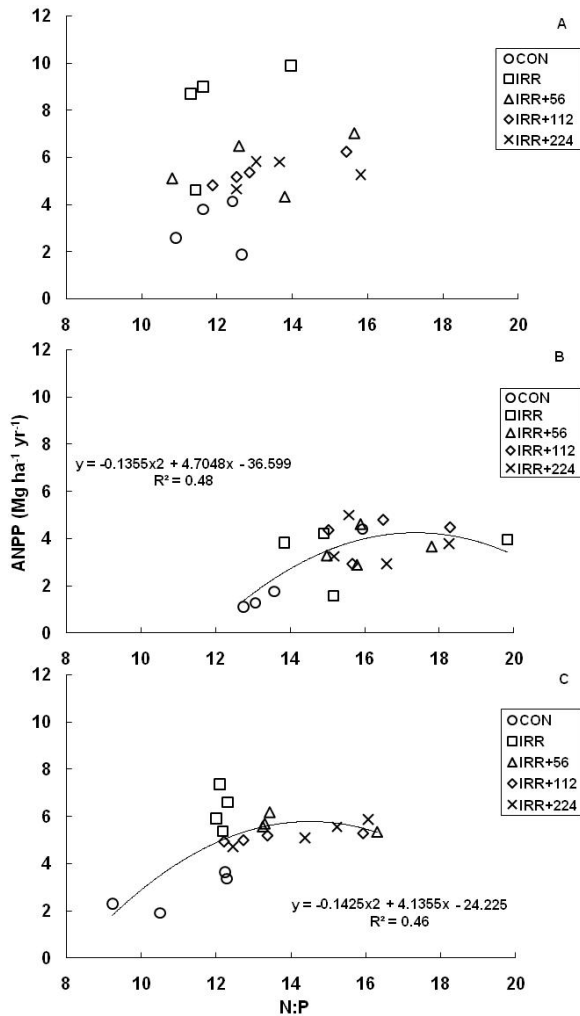


Figure 4. Biomass production ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and foliar N:P for year eight (2003) of the study for *P. deltooides* (A), *Q. pagoda* (B), and *P. occidentalis* (C) for all treatments (circle = CON, square = IRR, triangle = IRR + 56 $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$,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

microbes competed for N if additional amino acids were not supplied in addition to fertilization. Our findings were substantiated by the lack of significant differences between the treatments.

In a companion study, Lee & Jose, (2005) found that after seven years of fertigation treatments, between 46 - 60 $\text{kg}\cdot\text{N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ 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 & Jose, 2005). These findings suggest that nutrient availability in old agricultural fields may be sufficient for maximum production, and 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 & Jose, 2010). It

could also be suggested that thinning should occur to relieve below ground competition, release the most desirable trees within the stands, and that then additional N application might be utilized for additional biomass production.

The distributions and amount of N, P, and K (Table 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, site conditions, and treatments were dissimilar. For instance, Lugo et al., (2011) found similar N, P, and K ($\text{kg}\cdot\text{ha}^{-1}$) for *Spathodea campanulata* in north central Puerto Rico that were harvested from karst and volcanic sites which were comparable to the whole tree values found in this study.

A few studies have investigated the effects of thinning (Blanco et al., 2006), mixed species stands (Vogel & Gower 1998; Wang et al., 2000), or multiple aged trees (Miller et al., 1993), chronosequence studies of single species (Wang et al., 1995, 1996), or the effect of elevated CO_2 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 $\text{kg}\cdot\text{ha}^{-1}$ versus our 240 - 502 $\text{kg}\cdot\text{ha}^{-1}$ 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* were similar to the values found in the IRR + 224 treatment in this study (431 $\text{kg}\cdot\text{ha}^{-1}$ versus 439 $\text{kg}\cdot\text{ha}^{-1}$ 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 $\text{kg}\cdot\text{ha}^{-1}$ versus 22.6 - 50.6 and 168.1 - 353 $\text{kg}\cdot\text{ha}^{-1}$ of P and K, respectively). However, the findings from the Wang et al., (1996) study were based on soils without any amendments. Vogel & 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. deltooides* in our study but were similar to those found for *Q. pagoda* in the CON treatment (170 versus 168 $\text{kg}\cdot\text{ha}^{-1}$ 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 plantations 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. Further, Van Den Driessche, (2000) suggested that increased P could result in copper or zinc deficiencies after 14 weeks resulting in decreased leaf and root biomass. 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 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. deltooides* 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 1**). For K, when comparing the CON to all other treatments, all three species had increased K content with increased N application (**Table 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 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 2**) while *P. deltooides* (57% to 65%) and *Q. pagoda* (60% to 62%) RE were similar to the lower ranges Pugnaire & Chapin (1993) found for several chaparral species grown in nutrient poor soils. Other authors (Eckstein et al., 1999; Drenovsky & Richards, 2006; May et al., 2000; Cai & Bongers, 2007; Calfapietra et al., 2007) have 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. deltooides* (53 to 58%) and *P. occidentalis* (51% to 57%). These values agree with Aerts & 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 & 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 & 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; Drenovsky & Richards, 2006). The values we found for N in the leaf litter, for all three species, agree with the findings of other authors (Yuan & 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 or N application, we did find that the highest N, P, and K NRP were at levels below the highest rate of N application (**Figure 2**). 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 2**) values agree with the findings of other studies (Tateno & Kawaguchi, 2002 (70 to 130 g·N·g⁻¹ leaf litter)). However, LNUE does not necessarily correspond to patterns found for CNUE (**Table 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 (**Figure 3**) suggests 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 (<8.3 to 10.9 Millner & Kemp, 2012), (11 - 18 Graciano et al., 2006), ≤14 were likely to be N limited and ≥16 were likely P limited (Koerselman & Meuleman, 1996; Aerts & 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 & 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*. On an unfertilized site in New Zealand, Millner & Kemp, (2012) found N:P ratios were species specific and indicated some *Eucalyptus* had intrinsic abilities to accumulate macronutrients such that some could more readily accumulate P than N. 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. deltooides*, *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 (Figure 4) particular trends become apparent. At the lower bounds of the N:P for *P. deltooides* (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 N:P reached the range of balance, maximum production was observed for these species. ANPP then declined when N:P was higher (≥ 16) suggesting P was becoming more limiting for growth or that the higher rates of N application were growth limiting. At this point in the correlation, N application for both species was at IRR + 112 or 224 $N \cdot ha^{-1} \cdot yr^{-1}$, further supporting the hypothesis of a plateauing response to N application.

Bungart & Hüttel, (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 & 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 & Conner, 1999; Aerts & Chapin, 2000; Drenovsky & Richards, 2006; Specht & Turner, 2006; Millner & Kemp, 2012) 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.

Conclusion

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.

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