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Above- and belowground response of baldcypress and water tupelo seedlings to variable rates of nitrogen loading: Mesocosm and field studies

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ABSTRACT

A nutrient-loading mesocosm study was conducted on baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) seedlings and a field study was conducted on baldcypress seedling diameter increase at five assimilation wetlands. Nitrogen additions ranged from 0 to 400 $g\,N\,m^{-2}\,yr^{-1}$. Dependent variables included above- and belowground biomass production, root to shoot ratio, and wood density. Aboveground biomass production increased steadily to the 400 $g\,N\,m^{-2}\,yr^{-1}$ loading rate for both species, whereas belowground biomass production and root to shoot ratio increased to the 100 $g\,N\,m^{-2}\,yr^{-1}$ loading rate then decreased slightly. Wood density for *N. aquatica* was higher than *T. distichum* and wood density for both species was largely unaffected by nutrient loading rate. Diameter increase for seedlings in the five assimilation wetlands averaged from 1.1 to 2.5 $cm\,yr^{-1}$ and was about ten times higher at all sites than that of nearby natural swamps. In all, high rates of nutrient loading did not negatively affect growth of either species.

1. Introduction

Currently there is debate about the impact of nutrient additions on wetlands (Nyman, 2014) but research reflecting nutrient loading rates experienced by wetlands in natural systems is lacking, especially for freshwater forested wetlands. It has been proposed that forested wetland trees grown under nutrient enhanced conditions produce less dense wood (Baker et al., 2004; Chao et al., 2008; Muller-Landau, 2004; Slik et al., 2010) and are thus more susceptible to wind throw. Here we describe a mesocosm experiment that investigates the impact of nitrogen loading that encompasses the range experienced by coastal freshwater forested wetlands in Louisiana. N loading rate in assimilation wetlands generally ranges from 1.5 to 25 $g\,N\,m^{-2}\,yr^{-1}$ (Shaffer et al., 2015; Hunter et al., 2018). N loading for Mississippi River freshwater diversions ranges from < 5 to about 100 $g\,N\,m^{-2}\,y^{-1}$ depending on wetland size and distance from the outfall (Lane et al., 2002, 2004, 2010; Hyfield et al., 2008). We included 200 and 400 $g\,N\,m^{-2}\,yr^{-1}$ as extreme loading rates that are rarely seen in nature but have been used in experimental studies on the effects of nutrients on wetlands (e.g., Deegan et al., 2012; Darby and Turner, 2008a,b; Graham and Mendelssohn, 2016).

For this experiment, we used two major tree species in the swamp canopy, baldcypress, a gymnosperm, and water tupelo, an angiosperm, that are the most effective wetland plant species at reducing storm surge during tropical weather events (Chambers et al., 2007). It is commonly believed that trees with high growth rates typically have a lower wood density than those with slower growth rates (King et al., 2006; Muller-Landau, 2004; Roderick and Berry, 2001; ter Steege and Hammond, 2001). If wood density is inversely related to growth rate (Baker et al., 2004; King et al., 2006), then nutrient addition causing an increase in growth above ground may in turn decrease wood density, making baldcypress and water tupelo trees in nutrient-amended wetlands more susceptible to wind throw. It has been shown that mortality rates are negatively related to wood density (Chao et al., 2008; King et al., 2006). There have been varying results related to the impact of nutrients on wood density. Baker et al. (2004), Chao et al. (2008), Muller-Landau (2004), and Slik et al. (2010) reported that wood density is negatively related to nutrient availability, whereas Arnold and Mauseth (1999) and ter Steege and Hammond (2001) found that variation in wood density was not related to nutrient availability. Effects on the variation of wood density appear to vary throughout species, regions, and environmental factors (Arnold and Mauseth, 1999; Baker et al., 2004; Chao et al., 2008; Muller-Landau, 2004; Slik et al., 2010; ter Steege and Hammond, 2001).

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To test the response of nutrient loading on wood density of baldcypress and water tupelo to various loading rates, we carried out a mesocosm experiment with loading rates of 0, 10, 50, 100, 200 and 400 g N m^{-2} yr^{-1}. We controlled for natural conditions with no additional nutrients above groundwater conditions. We also carried out a growth experiment at five assimilation wetlands on baldcypress seedlings to determine if diameter increase was higher than that of nearby natural swamps.

2. Materials and methods

2.1. Experimental design

In March of 2009, 72 1-year-old baldcypress and water tupelo seedlings were planted into 144 100-liter mesocosm vessels. The vessels were arranged in rows of two, creating three blocks of trees, in a 10 × 30 m greenhouse at the Horticulture Center of Southeastern Louisiana University. To mimic conditions of the Manchac-Maurepas wetlands, seedlings were planted in an aged peat moss and Mississippi River silt mixture with a bulk density of 0.23 g cm^{-3} (Myers et al., 1995; Shaffer et al., 2009, 2015). An automated irrigation system delivered water to each mesocosm. Rubber tubes siphoned water from PVC pipes and delivered it to each mesocosm vessel in a steady drip that created a constant saturated environment. Experimental vessels received a time release fertilizer treatment (Osmocote 18-6-12). The fertilizer treatments included 0, 10, 50, 100, 200, and 400 g N m^{-2} yr^{-1}. The fertilizer was applied in March and July 2009 and again in March 2010.

2.2. Aboveground biomass

In July 2010, all leaf material was physically removed from each seedling, bagged and labeled. Simultaneously, the main stem was felled at the soil surface using a reciprocating saw, bagged and labeled. Stems and leaves were dried at 65 °C until weight stabilized (± 0.01 g).

2.3. Belowground biomass and root to shoot ratio

Belowground biomass also was sampled in July of 2010 using a 9-cm diameter, 30-cm long aluminum tube corer attached to an 18-volt cordless drill. Two root cores were sampled from each mesocosm vessel, offset from each seedling by 10 cm and parallel to each other. Root cores were carefully removed from the aluminum tube, bagged and labeled. The samples were stored at 5 °C until they could be processed. Live roots were washed and cleared of dirt using three sieves varying from 0.25 cm^2 to 0.0625 cm^2 to 0.01 cm^2 mosquito screen and dried at 65 °C until bag weight stabalized (± 0.01 g). Weight of belowground biomass was averaged and converted to g. Root to shoot ratio was determined by dividing total belowground biomass by total aboveground biomass.

2.4. Density

In August of 2010 a 5-cm section of each tree was taken from each bole 30 cm above the soil surface and the volume was determined through the water displacement method to the nearest mL (cm^3). Samples were then dried at 80 °C and weighed (± 0.01 g). Density (ρ) was calculated for each sample as mass/volume (g cm^{-3}).

2.5. Statistical analysis

This experiment was a completely randomized 2^*6 factorial (two species of seedling and six levels of fertilizer) with 12 replicates and analyzed with SYSTAT 13 (2009). The dependent variables were root to shoot ratio, belowground biomass, aboveground biomass and wood density. The residuals for all four models were tested as normal with homogeneous variance. *A priori* questions were addressed with linear contrasts.

2.6. Field plantings of baldcypress seedlings

Baldcypress seedlings were planted at five assimilation wetlands. The sites included Broussard, CHS, Hammond, Luling and Mandeville. Detailed site descriptions are given for these sites by Hunter et al. (2018) with the exception of CHS. CHS, Inc. is a large grain export terminal that handles both grain and grain by-products. It is located on the west bank of the Mississippi River about 25 km downstream of New Orleans. The facility transfers grain from barges to ocean going vessels and services about 2–3 ships per day. Because of the high volume of grain handled by the facility, grain dust and a small amount of spilled grain is deposited on the site and is washed into the stormwater system. The company has implemented aggressive stormwater management practices and regular cleaning of earthen swales and other areas at the property to lower total organic carbon (TOC) concentrations from stormwater runoff. Despite these efforts, TOC limits set by the LDEQ water discharge permit for the facility have been regularly exceeded. To address this problem, CHS, Inc. constructed two wetlands totaling 2.5 acres to reduce TOC in stormwater runoff. Baldcypress seedlings were planted at a density of 200 per acre, for a total of 500 trees. Herbaceous species were both planted and colonized the area naturally.

At each wetland site about 100 seedlings within 100 m of effluent discharge were planted and tagged in areas with no shading. Seedlings planted at each site were either 100% bare root or 100% grown in pots. Bare root seedlings were about 0.75 m in height while seedlings in pots were 1–1.5 m. All seedlings were protected with herbivore exclusion devices to protect against nutria (*Myocaster coypus*), known to be voracious consumers of unprotected seedlings (Myers et al., 1995; Shaffer et al., 2015; Sasser et al., 2018). When planted, the stem diameter was measured at the base of each tag. Seedlings were re-measured annually for three years.

3. Results

3.1. Root to shoot

Nutrient loading had a significant effect on the root to shoot ratio of the experimental seedlings ($F_{5,132}$ = 2.37, p = 0.043, Fig. 1). Across species the highest root to shoot ratio occurred for seedlings that received the 100 g N m^{-2} y^{-1} loading (mean 1.63). Seedlings with the lowest root to shoot ratios received 400 g N m^{-2} y^{-1} (mean 0.79). Root to shoot ratio increased for both species up to 100 g N m^{-2} yr^{-1}, then decreased ($F_{1,132}$ = 3.39, p = 0.068). Baldcypress seedlings had higher

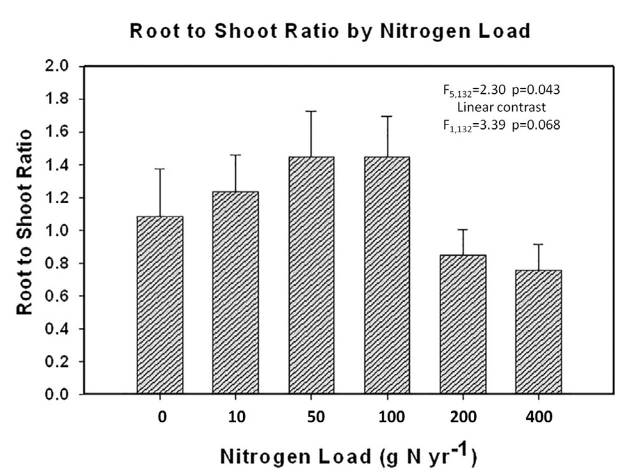

Fig. 1. Effect of nutrient loading on root to shoot ratio. Fertilizer increased baldcypress and water tupelo root to shoot ratios up to 100 g N m^{-2} y^{-1}.

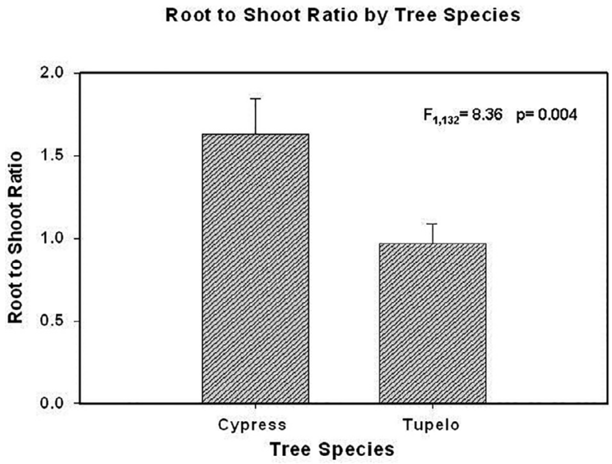

Fig. 2. Effect of species on root to shoot ratio. Baldcypress had significantly higher root to shoot ratio (1.6) than water tupelo (0.96).

root to shoot ratios (1.6, $F_{1,132}$ = 8.37, p = 0.004, Fig. 2) than water tupelo seedlings (0.96).

3.2. Belowground biomass

Fertilizer concentration affected belowground biomass production ($F_{5,130}$ = 2.30, p = 0.049, Fig. 3). The highest mean belowground biomass occurred when seedlings received 100 g N m^{-2} y^{-1} fertilizer application (mean 935.01 g m^{-2} y^{-1}). The lowest belowground biomass occurred at no (0) fertilizer (481.38 g m^{-2} yr^{-1}). Belowground biomass increased from 0 to 100 g N m^{-2} yr^{-1} ($F_{1,130}$ = 9.33, p = 0.003). Loading at 200 and 400 g N m^{-2} yr^{-1} was not significantly different from 50 g N m^{-2} yr^{-1} but higher than controls.

3.3. Aboveground biomass

Fertilizer level had a strong effect on the amount of aboveground biomass ($F_{5,132}$ = 18.77, p < 0.001, Fig. 4). Experimental seedlings produced the least (mean 444.51 g m^{-2} y^{-1}) aboveground biomass when no (0) fertilizer was added. Biomass production increased at each fertilizer level ($F_{1,132}$ = 87.43, p < 0.001). Water tupelo seedlings produced greater (mean 812.34 g m^{-2} y^{-1}) aboveground biomass than baldcypress (mean 634.22 g m^{-2} y^{-1}) seedlings ($F_{1,132}$ = 10.41, p = 0.002, Fig. 5).

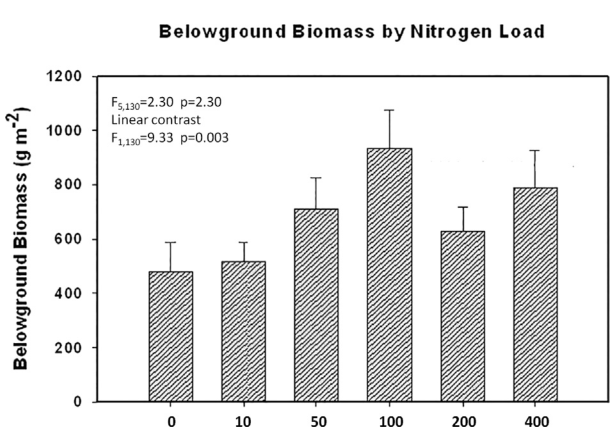

Fig. 3. Effect of nitrogen loading on belowground biomass. Belowground biomass increased from 0 to 100 g N and then decreased.

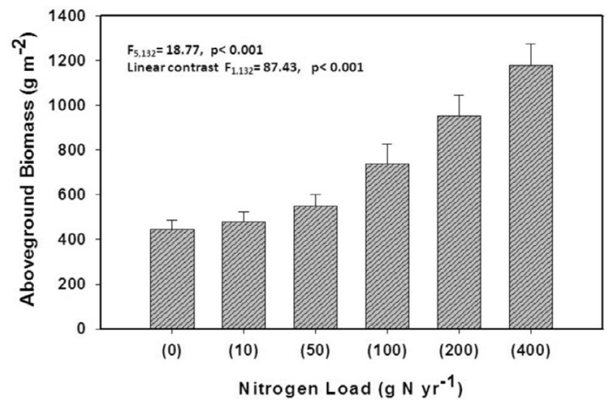

Fig. 4. Impact of nutrient loading on aboveground biomass. Aboveground biomass production increased at each successive fertilizer level.

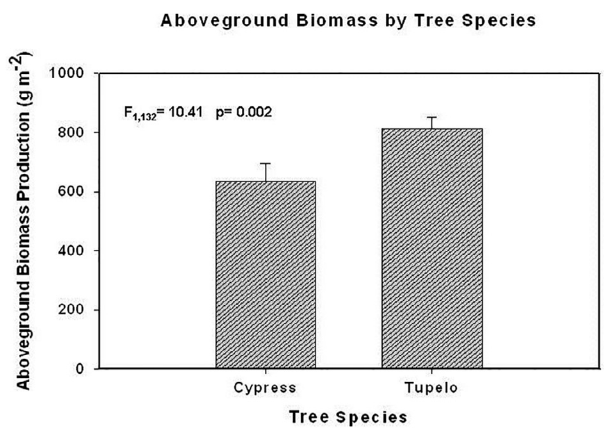

Fig. 5. Water tupelo seedlings produced greater aboveground biomass (812 g m^{-2} y^{-1}) than baldcypress (634 g m^{-2} y^{-1}).

3.4. Density

In general, there was not a large difference in seedling density between fertilizer levels when species were considered together ($F_{5,132}$ = 2.13, p = 0.066), with seedlings at 10 g N m^{-2} y^{-1} having slightly higher density (ρ = 0.411 g cm^{-3}) than seedlings grown at 400 g N m^{-2} y^{-1} (ρ = 0.382 g cm^{3}). Density differed ($F_{1,132}$ = 145.75, p < 0.001, Fig. 6) between water tupelo (ρ = 0.431 g cm^{-3}) and baldcypress (ρ = 0.360 g cm^{-3}) and there was an interaction between

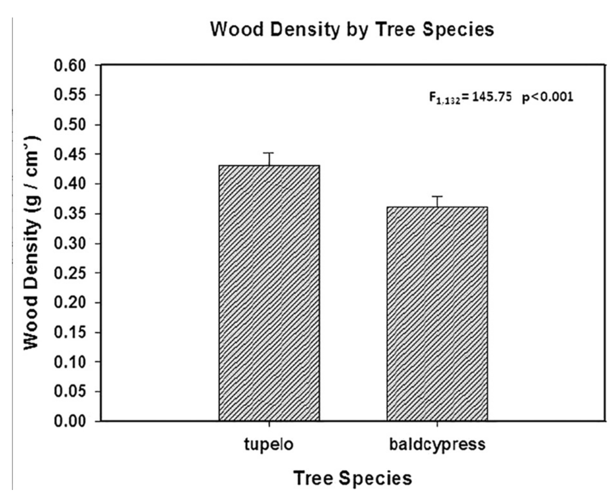

Fig. 6. Water tupelo had higher wood density than baldcypress.

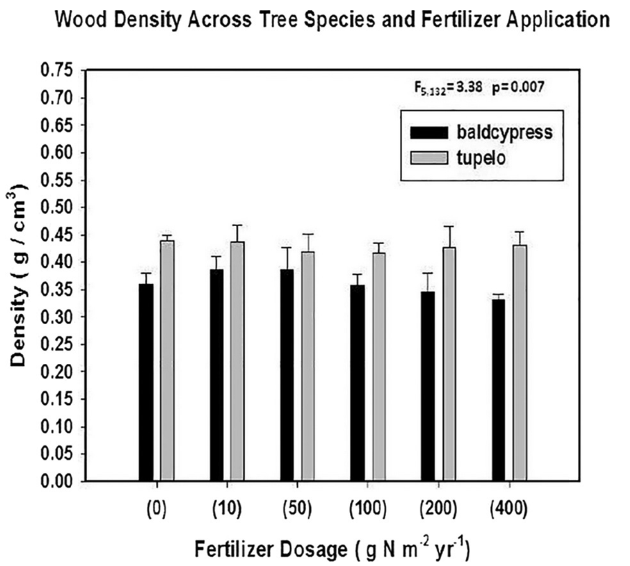

Fig. 7. An interaction occurred between species and fertilizer dosage where baldcypress slightly decreased in wood density beginning at 100 g N m^{-2} yr^{-1}.

species and fertilizer level ($F_{4,132}$ = 3.38, p = 0.007, Fig. 7). Tupelo showed no difference in density between fertilizer levels, whereas baldcypress displayed a slight but not significant decrease from 10 to 400 g N m^{-2} yr^{-1}.

3.5. Field plantings of cypress seedlings

After three years of growth, mean diameter increase exceeded 1 cm yr^{-1} at all sites and ranged from 1.1 to 2.5 cm yr^{-1}. Growth at the CHS site was significantly higher than all other sites (Fig. 8).

4. Discussion

4.1. Root to shoot

The root to shoot ratio increased for both species up to 100 g N m^{-2} yr^{-1}, then decreased (Fig. 1). Mean root to shoot ratio at 50 g N, representative of a small river diversion (Shaffer et al., 2009), was 1.47. Mean root to shoot ratio at 100 g N m^{-2} yr^{-1}, representative of a large river diversion (Lane et al., 2004), was 1.63. At these levels of nitrogen loading, the root to shoot ratios begin to approach, after two growing seasons, the root to shoot ratio (1.81) previously observed for a similar diversion scenario (90 g N m^{-2} yr^{-1}) after 5 years of growth (Hillmann et al., 2018). It seems that when limiting nutrients are present and environmental stressors are relaxed, wetland plants quickly fall into the biomass allocation patterns that allow for the most efficient use of resources to carry out plant functions.

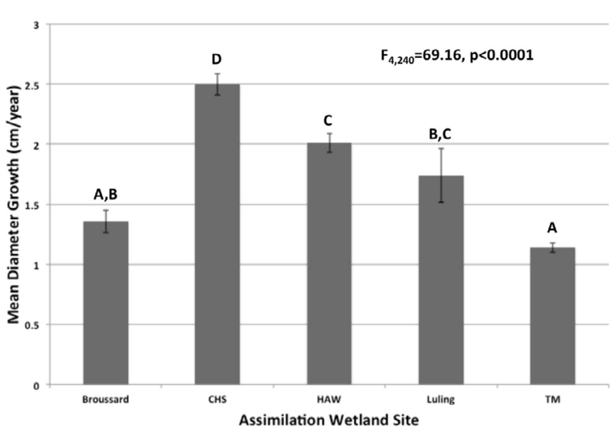

Fig. 8. Mean diameter growth per year of baldcypress seedlings planted at five assimilation wetland sites – legends under bars are site names for different assimilation wetlands: CHS is for a constructed wetland at a grain handling facility south of New Orleans on the Mississippi River, HAW is the Hammond assimilation wetland, TM is the Tchefuncte Marsh assimilation wetland. Bars with different letters are statistically different according to a Bonferroni-adjusted LSD.

Water tupelo generally allocated more biomass above ground at lower loading rates than did baldcypress, which generally invested more energy below ground. Our results generally agree with Cahill (2002), Wetzel and van der Valk (1998) and Musyimi et al. (2010).

Several studies have examined differences in root to shoot ratios between angiosperms and gymnosperms (Rodin and Bazilevich, 1967; Cannell, 1982; Cuevas et al., 1991; Kōrner, 1994; Cairns et al., 2011). Rodin and Bazilevich (1967), as well as Cuevas et. al. (1991) and Korner (1994), found that gymnosperms generally have higher root to shoot ratios, meaning they produced proportionally more belowground biomass than aboveground biomass. Cannell (1982), however, found that coniferous forests (gymnosperms) had lower root to shoot ratios than tropical forests and Cairns et al. (2011), in an analysis of worldwide forestry data, saw no differences in root to shoot ratios between angiosperms and gymnosperms. Our results agree with Rodin and Bazilevich (1967), Cuevas et al. (1991) and Kōrner (1994). In our experiment baldcypress, a gymnosperm, had significantly higher root to shoot ratios than water tupelo, an angiosperm.

4.2. Belowground biomass

Belowground biomass increased linearly up to a loading rate of 100 g N m^{-2} y^{-1} for both baldcypress and water tupelo (Fig. 3), followed by a decline at 200 and 400 g N m^{-2} y^{-1}. Loading rates between 50 and 100 g N m^{-2} y^{-1} induced approximately twice as much belowground biomass as the other treatments combined, whereas the low loading rate of 10 g N g N m^{-2} y^{-1} produced only 7.3% more root material than the control (no added fertilizer). Further, loading rates of 50 g and 100 g N g N m^{-2} y^{-1}, approximating river diversions, produced 46.8% and 94.2% more root material than the control (Fig. 3). This is opposite to the results seen by Holm (2006), Darby and Turner (2008a,b) and Langley et al. (2009) for saline marsh species. While recognizing that salt-tolerant plants may inherently respond with different belowground biomass allocation to nutrient augmentation than freshwater plants, we also noticed that hydrology type had a strong effect on shallow belowground biomass production when crossed with water quality type (Hillmann et al., 2018). The aforementioned difference in root to shoot ratios between angiosperms and gymnosperms is the result of a proportional increase in aboveground biomass by water tupelo.

4.3. Aboveground biomass

Aboveground biomass was the most dynamic variable in this experiment and was strongly affected by the nutrient gradient (F = 18.77, $p < 0.001$, Fig. 4). For both baldcypress and water tupelo there was a linear increase in aboveground biomass allocation from 0 to 400 g N. The small diversion scenario (50 g N m^{-2} yr^{-1}) produced 23% more shoot and leaf material and the large diversion scenario (100 g N m^{-2} yr^{-1}) produced 66% more shoot and leaf material than the control. Unlike belowground biomass production, aboveground production continued to increase to the highest loading rate (400 g N m^{-2} yr^{-1}). Darby and Turner (2008b) reported no statistical differences in aboveground biomass production along a similar nutrient gradient in a *Spartina alterniflora* marsh when N was added along with P and Fe in various experimental combinations. Viewed separately, water tupelo produced more aboveground biomass (812 g m^{-2}) than baldcypress (634 g m^{-2}, Fig. 5), perhaps attributable to different shoot allocation patterns between angiosperms and gymnosperms.

Taneda and Tateno (2004) explored two theories, mechanical support and hydraulic conductivity, to account for differences in shoot (differences between stem and leaf allocation) allocation between gymnosperms and angiosperms. Gymnosperms were found to be governed more by hydraulic conductivity, allocating more biomass to leaves, while angiosperms were governed more by mechanical support, allocating more biomass to stems.

4.4. Density

Increased aboveground biomass production along a nutrient gradient has elicited questions about the density of such wood. Of particular interest is wood density at 10 g N, 50 g N and 100 g N m^{-2} yr^{-1}, as these values span the range typical of both assimilation wetlands and river diversions.

The difference in density between the two species follows the general trend that angiosperms have denser wood than gymnosperms (Swenson and Enquist 2007). Average density in both baldcypress ($\rho = 0.361$ g cm^{-3}) and water tupelo ($\rho = 0.431$ g cm^{-3}) seedlings were lower than published values for adult wood densities of 0.42–0.46 g cm^{-3} and 0.46–0.5 g cm^{-3}, respectively (Gilman and Watson, 2006; Haygreen and Bowyer, 1996; Meier, 2010). This is likely due to the fact that juvenile trees put less or no energy into reproduction and more into growth, therefore growing faster and creating less dense wood, with density increasing with tree age (King et al., 2006). Our results show that nutrient loads had no effect on water tupelo wood density as in Arnold and Mauseth (1999), Roderick and Berry (2001), and Zobel and van Buijenen (1989) and only a slight negative effect on baldcypress.

The results of this study show that aboveground biomass production increased with nutrient loading up to 400 g N m^{-2} yr^{-1} for both species, whereas belowground biomass production and root to shoot ratio increased to 100 g N m^{-2} yr^{-1} then decreased. Wood density for *N. aquatica* was higher than *T. distichum* but wood density for both species was largely unaffected by nutrient loading rate. Thus, our results do not support the idea that high nutrient loading leads to lower wood density. Bodker et al. (2015) suggested that high nutrient levels caused mortality of planted seedlings at the Hammond assimilation wetland. The results of this study do not support this conclusion. Shaffer et al. (2015) concluded that the seedling mortality was caused by shading due to high growth rates of herbaceous vegetation leading to marsh plant height reaching 1.5–2.0 m. Baldcypress seedlings grown at all five assimilation wetlands had much greater growth rates than those of nearby natural swamps.

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