Nutrient availability and flooding stress interact to affect growth and mercury concentration in
Taxodium distichum (L.) Rich. seedlings

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Abstract

Plant growth can be limited by nutrient availability and/or flooding stress but their relationship is understood too poorly to predict when they act independently or to predict which dominates the relationship. Nutrient availability also reduces uptake of toxic metals under some conditions but enhances uptake under others. We studied how flooding stress and nutrient availability affected growth and mercury uptake by *Taxodium distichum* (L.) Rich., which is a tree that dominates freshwater wetlands in the southeastern United States. We hypothesized that nutrients would negate flooding stress and enhance mercury uptake. We also hypothesized that leaf chemistry could serve as an indicator of factors limiting growth. We planted 432 one-year old seedlings in soil with one of four nutrient availabilities (no enhancement, or enhanced with 57, 283, or 1,132 g N m⁻² and other nutrients) and allowed the seedlings to grow for two seasons with one of six flooding regimes ranging from <1% to 96% flooding each month. The highest level of nutrient availability killed 82% of the seedlings almost immediately but after one year, nutrient availability and flooding interacted such that seedlings given 57 g N m⁻² negated effects of flooding stress on stem length. After two years, nutrient availability and flooding stress interacted such that seedlings given 283 g N m⁻² grew more than less fertilized seedlings except in the most flooded treatment. Mercury in leaves was related to flooding after the first year but to nutrient availability after the second year. The C:N and N:P ratio in leaves could not be used to indicate nutrient limitation in *T. distichum* because flooding also altered those ratios. The Ca:Mg ratio was related to nutrient availability but we found no chemical indicator of flooding stress. Research is needed to determine if flooding enhanced uptake of atmospheric mercury by leaves or soil mercury by roots.

Key Words: nutrients, flood stress, growth, mercury, wetland, baldcypress, *Taxodium*

1. Introduction

Resources, such as nutrients and sunlight, often limit plant development and productivity, influence the outcome of competition among plant species (*e.g.*, Newman et al. 1996), and influence herbivore behaviour through their effects on plant tissue chemistry (*e.g.*, Ialeggio and Nyman 2014). Likewise, stresses such as flooding and salinity often limit plant productivity and influence the outcome of competition among plant species (*e.g.*, Gough and Grace 1998). Research is more often focused at studying interactions between two limiting resources (*e.g.*, N and P limitation reviewed by Harpole et al. 2011) or between two stresses (*e.g.*, flooding and salinity reviewed by Barrett-Lennard 2003) than between a limiting resource and a stress (but see Day 1987, Merino et al. 2010). The relationship between a stress and a limiting resource can be classified according to whether the relationship is dominated by the stress or by the resource, and whether the stress and the resource act independently or interact. There are four possible outcomes (Figure 1): (a) the resource and stress act independently with the stress dominating, (b) the resource and stress act independently with the resource dominating, (c) the resource and the stress interact with the interaction dominated by the stress, and (d) the resource and the stress interact with the interaction dominated by the resource. This classification scheme was developed as a consequence of an experiment focused on *Spartina patens* (Ait.) Muhl. (Merino et al. 2010) that demonstrated that nutrient limitation and salinity stress interacted such that salinity stress negated effects of nutrient availability (Figure 1c).

Wetland plants provide an interesting model in which to study interactions between a limiting resource and a stress because wetland plants dominate a portion of the landscape that experiences a wide range in nutrient availability, flooding stress, salinity stress, and sulphide stress. In freshwater wetlands, nutrients often are a limiting resource, flooding is a common

stress, and nutrient acquisition and flooding stress are related. For example, flooding stress slows photosynthesis and N uptake in two wetland *Quercus* species (DeLaune et al. 1998) and also slows P uptake in *Typha domingensis* (DeLaune et al. 1999). Despite flooding stress, plant productivity increases with increasing nutrient availability in natural wetlands (e.g., Brantley et al. 2008) and agricultural wetlands where, for example, recommended N fertilization rates for rice range from 6.2 to 14.2 g m⁻² (Saichuck et al. 2011). Although not designed with the stress/resource classification scheme (Figure 1), some previous studies of nutrient availability and flooding stress can be viewed in this context. Day (1987) concluded that nutrient additions had the greatest effect on *Acer rubrum* L. that were most flood stressed, which would be most likely where an interaction between a limiting resource and a stress was dominated by the resource (Figure 1d); whereas Mayence and Hester (2010) concluded that flooding stress and nutrient additions acted independently in *Panicum hemitomon* Schultes with aboveground biomass responding more to nutrient availability and belowground biomass responding more to flooding, which would most likely be classified as independent, resource dominated (Figure 1a) and independent, stress dominated (Figure 1b), respectively.

Nutrient availability also reduces uptake of toxic metals under some conditions but enhances uptake under others (see Gothberg et al. 2004 and literature cited therein). Mercury (Hg) is a common metal pollutant. It is widely believed that plant uptake of Hg from soil is low and that there is a barrier to mercury translocation from roots to leaves (Patra and Sharma 2000). Mercury generally is more concentrated in roots than in leaves (Patra and Sharma 2000, Leonard et al. 1988a) with leaves serving as sites of net Hg loss where soil Hg concentrations are high (Leonard et al. 1998b) but sites of net Hg gain where atmospheric concentration of Hg are high (Erikson and Gustin 2004). Mercury accumulation in plants also may increase in response to

flooding stress as indicated by observations that plants growing on wetter soils seem to have higher foliar Hg (Overesch et al. (2007) and that leaf tissue Hg can be greater in species that grow closer to the water table (Moore et al. 1995). Such increases might partly result from effects of flooding on Hg, which is more likely to convert from the less labile elemental form to the more labile methylated form in flooded soils (Selvendiran et al. 2007). Such increases might also partly result from effects of flooding stress on plants. Flooding alters stomatal conductance, leaf expansion, leaf age, and/or leaf surface chemistry (Kozlowski and Pallardy 1984), which might enhance leaf uptake of atmospheric Hg. Flooding also decreases the ability of roots to exclude undesirable minerals (Kozlowski and Pallardy 1984), which might increase root uptake of soil Hg.

We studied how flooding stress and nutrient availability affected growth and Hg uptake by baldcypress (*Taxodium distichum* (L.) Rich.), which is a tree that dominates freshwater wetlands in the southeastern United States. Baldcypress tolerates intermittent flooding well (Anderson and Pezeshki 1999, Krauss et al. 2009) but persistent flooding and soil anoxia can slow growth, photosynthesis, and stomatal conductance (Kludze et al. 1994, Krauss et al. 2009), and belowground production (Megonigal and Day 1992, Krauss et al. 2009). Root restriction, whether mechanically induced or induced by flooding stress, slows growth in baldcypress (Pezeshki and Santos 1998). Several studies demonstrated that flooded baldcypress responds to nutrient additions (Brown 1981, Hesse et al. 1998, Day et al. 2006, Effler et al. 2006, Hunter et al. 2009a); that relationship is possible in all four scenarios in Figure 1 but is more likely where the relationship is dominated by nutrient availability (Figures 1b and 1d). We're aware of two studies that showed flooded baldcypress failed to respond to nutrient additions (Day et al. 2006,

Keim et al. 2012), which implies that nutrient availability and flooding stress interact in a way that is dominated by flooding stress (Figure 1c).

We hypothesized that nutrients would offset flooding stress (Figure 1d) and enhance Hg uptake because they would enhance growth under flooded conditions. We also hypothesized that leaf chemistry could serve as an indicator of factors limiting growth because leaf tissue chemistry has a long history of being used to diagnose nutrient deficiencies in agriculture (Bates 1971, Campbell 2000) and forestry (Lopez-Serrano et al. 2005) and because Tobias et al. (2010) recently showed that leaf tissue chemistry could be used to diagnose N limitation and salinity stress in *S. patens*.

2. Materials and Methods

We grew one-year-old baldcypress seedlings for two growing seasons while we manipulated flooding stress and nutrient availability. The first year, we compared growth among the treatments non-destructively; the second year we compared growth among the treatments destructively. In both years, we measured the chemical content of baldcypress leaves. We identified chemical signatures in leaves most related to flooding stress and nutrient availability.

2.1 Data Collection

We modified a recently developed field-based technique that creates six levels of flooding stress termed “organs” (Morris 2007). Although developed for the field where water levels vary naturally, we used organs in a controlled setting. Our organs consisted of 36 15-cm diameter PVC pipes, each hosting a plant, arranged in six rows of pipes with each row having a different height; each row had six replicate pipes (Figure 2). The lengths of the pipes in our organs were 51, 58, 66, 74, 81, and 89 cm (soil volume of 36.0, 41.0, 46.6, 52.3, 57.2, and 62.9 l,

respectively). It is possible that this design confounded physical root restriction with flooding stress but we assume otherwise because our shortest pipes were larger than the 24 cm-diameter, 24-cm tall, 10-l volume containers used by Pezeshki and Santos (1999) in their study of root restriction and larger than the 20-l containers and the 22-l containers used by Effler and Goyer (2006) and Krauss et al. (2009), respectively, in their studies that lasted over two growing seasons. Most importantly, our pipes were open at the bottom but we never observed roots emerging from the bottom of our pipes as did Pezeshki and Santos (1998). The pipes were filled with locally purchased soil (73% sand, 20% silt, and 7% clay), were open at the bottom (a small sandbag was placed at the bottom of each organ to prevent soil from flowing out the pipes), and each of the 12 organs was placed in a separate 1 m³ tank in which water levels were lowered by siphoning and raised by adding tap water. Rain and evaporation also affected water levels in the tanks, which were exposed to the elements on campus. All organs were oriented such that the tallest rows were on the north and the shortest rows were on the south so as to delay shading of the plants in the shorter rows by plants in the taller rows.

We created a range of nutrient availabilities by randomly fertilizing some organs once at the beginning of the experiment. Nutrient availability was not increased in any of the 36 pipes of three organs. Nutrient availability was enhanced by one of three amounts in the remaining nine organs. All 36 pipes in three organs received one 5-gram commercially available fertilizer tablet (20-10-5 Planting Tablets purchased from Forestry Suppliers); all 36 pipes in three organs received five tablets in each pipe, and all 36 pipes in the other three organs received 20 tablets in each pipe. Nutrients could be carried by water among pipes within an organ but nutrients could not move from one nutrient availability treatment to another because each organ was in a separate water tank. Here-in-after, we refer to the treatments as 0, 57, 283, and 1,132 g N m⁻²

but availability of other elements was also increased (Table 1). Availability of N and P remained elevated throughout our experiment (Table 2). Our nutrient availability levels spanned an extremely wide range and our highest level may be the highest yet used. Loading rates in natural wetlands vary tremendously with rates approaching zero where wetlands depend upon atmospheric deposition and biological nitrogen fixation. Effluent from municipal wastewater treatments facilities result in loading ranging from $0.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ to $26.8 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Hunter et al. 2009b). Fertilization rates recommended for rice, which can be viewed as an agricultural wetland, range from 6.2 to $14.2 \text{ g m}^{-2} \text{ yr}^{-1}$ in Louisiana (Saichuck et al. 2011). Even higher loading rates appear to occur in artificial wetlands designed to treat wastewater such as reported by Thullen et al. (2002) ($360 \text{ g N m}^{-2} \text{ yr}^{-1}$) and in scientific experiments such as in the one reported by Darby and Turner (2008) (372 g N m^{-2} in a five-month period) and in our experiment ($1,132 \text{ g N m}^{-2}$).

Over a 5-day period in February, 2010, each pipe was planted with a one-year-old baldcypress seedling purchased from the Louisiana Office of Forestry, Louisiana Department of Agriculture who grew seedlings for one season and delivered seedlings to us senescent. Seedlings averaged 76.3 cm tall (s.d. = 13.6) and 0.9 cm in diameter (s.d. = 0.3). All nutrient availability and soil were added to organs when seedlings were planted. After planting, all pipes were watered and approximately 40 cm of water was added to the tanks, which did not flood any pipes but allowed water to be wicked up into all pipes. We did not begin flooding regimes until the seedlings began to leaf out, which began in the final week of March, 2010. For the subsequent 19 months, water levels were raised or lowered systematically such that the top row was never intentionally flooded and the bottom row was never intentionally drained. Rain occasionally flooded the top rows and evapotranspiration occasionally drained the bottom rows.

187 Generally, water levels were dropped every 3 to 5 days to expose another row until only the 6th
188 row was flooded. After several days, water levels would be raised in one day to flood all but the
189 first row and the cycle was repeated. On any given day, water levels were changed in four of the
190 12 organs such that organs having the same treatment were manipulated on different days.
191 During the second half of December and the first half of January, water levels were not
192 manipulated and only the highest row was drained. The experiment was ended in October.
193 Water levels were monitored at least 5 days each week except during the end of December and
194 beginning of January. These data allowed us to estimate flooding individually for each of the
195 three replicate rows within each flooding regime. Over the entire experiment, flooding in the six
196 regimes averaged <1%, 24%, 43%, 62%, 81%, and 96%; excluding December and January,
197 flooding in the six regimes averaged <1%, 22%, 40%, 60%, 80%, and 95% (Figure 3).

198 After the first growing season, we measured stem height and diameter so that we could
199 compare seedling growth among the treatments non-destructively. After the second growing
200 season, we harvested all seedlings in October 2011 so that aboveground and belowground
201 biomass could be measured. We intended to collect all leaf biomass as well but leaf senescence
202 began earlier and more rapidly than we anticipated. Some seedlings had lost few leaves but
203 others had lost almost a quarter; we therefore collected 20-30 grams of leaves from each seedling
204 for chemical analyses but did not estimate leaf biomass.

205 We collected samples of leaf tissue for chemical analyses in August 2010 and August
206 2011. For these samples, leaf material from all six seedlings in a row within an organ (having
207 the same flooding history and nutrient treatment) was combined. Soil samples also were
208 collected in October 2011; likewise, soil from all six pipes within a row combined. This resulted
209 in three replicate samples of each of the 24 combinations of flooding and nutrient availability

treatments. Leaf tissue was rinsed with tap water, oven dried, ground in a coffee grinder, and stored in screw cap jars. Leaf tissue was analysed for C, N, P and other elements at the LSU AgCenter's Soil Testing and Plant Analysis Laboratory. Total Hg analysis was performed on dried, ground plant and wet sediment samples with a direct Hg analyzer (Milestone Inc., 25 Controls Drive, Shelton, CT 06484; DMA-80) that uses thermal decomposition, amalgamation, and atomic absorption spectrophotometry. Sample collection, preservation, quality control, and instrument calibration followed procedures outlined in USEPA Method 7473 (USEPA 1998). Total Hg in leaf and soil samples was determined by thermal decomposition, amalgamation and single beam atomic absorption spectrophotometry with sequential flow through two measurement cells at 253.65 nm (USEPA 1998). The instrument detection limit is listed at 0.005 ng total Hg with a reproducibility <1.5%. A calibration curve was generated using prepared standard solutions of Hg (0.5, 1, 5, 10, 15, 20, 35, 70, 150, 300, and 450 ng Hg). When necessary, sample weights were adjusted to stay within the Hg calibration range. Reference materials were analysed with leaf and soil samples to verify that techniques were clean enough to accurately estimate Hg in vegetation and soil. Marine sediment reference material MESS-3 from the Institute for National Measurement Standards (National Research Council of Canada) has a certified value of 0.091 ± 0.009 mg of total Hg/kg of dry sediment weight (mean $\pm$ 95% confidence interval) and SRM 1515 (apple leaves) from the National Institute of Standards and Technology (United States Department of Commerce) had a certified value of 0.044 ± 0.004 mg of total Hg/kg of dry plant weight (mean $\pm$ 95% confidence interval). The means and standard deviations of the analyzed MESS-3 and SRM 1515 samples were 0.087 ± 0.005 (n=12) and 0.043 ± 0.003 (n=10), respectively.

2.3 Data Analyses

We used analyses of variance to test for effects of treatments on growth in the organs as a completely randomized design with four levels of nutrients, with replication (*i.e.*, organs) within nutrient treatments, with a split plot of six levels of flooding within each nutrient replicate (*i.e.*, organ), and with replication of seedlings within each level of flooding (*i.e.*, row). Nutrient availability and flooding levels were classified as fixed effects. Seedling height and diameter in March 2010 were used as covariates to account for differences in seedlings at the start of the experiment. Data were analysed using Proc Mixed of SAS 9.2 (Statistical Analytical Systems, Cary North Carolina, USA) with the maximum likelihood method; AIC's were used to decide which covariates to retain in the model statement. Effects were considered statistically significant when $P < 0.05$. We examined the residuals from these models with Proc Univariate of SAS to verify that the residuals were normally distributed. Least-square means and least-square standard errors were used to generate estimates for texts and graphs; the pdiff statement of Proc Mixed was used to identify means that differed from one another. These results were used to classify the response of baldcypress to nutrient availability and flooding stress according to possible relationships described in Figure 1.

We used Pearson's correlation coefficients to determine which chemical parameters in leaf tissue were most correlated with flooding or nutrient availability; we used Proc Corr of SAS 9.2 for these analyses (Statistical Analytical Systems, Cary North Carolina, USA). We then used analyses of variance to determine which of these chemical parameters varied with only flooding or only with nutrient availability because an ideal indicator of flooding stress would differ among the flooding treatments but would be unaffected by nutrient availability and because an ideal indicator of nutrient availability would differ among the nutrient treatments but would be

unaffected by flooding. For these analyses, we tested for effects of treatments on various leaf tissue chemistry parameters as a completely randomized design with four levels of nutrients, replication (organs within a nutrient treatment), and a split plot of six levels of flooding within each replicate. Seedlings within rows could not be used as replicates for these analyses because leaves were combined from all living seedlings across a row prior to chemical analyses. Nutrient availability and flooding levels were classified as fixed effects. Data were analysed using Proc Mixed of SAS 9.2 (Statistical Analytical Systems, Cary North Carolina, USA) with the maximum likelihood method. Effects were considered statistically significant when $P < 0.05$. Least-square means and least-square standard errors were used to generate estimates for texts and graphs; the pdiff statement of Proc Mixed was used to identify means that differed from one another.

Although flooding was analysed as a fixed effect, the amount of flooding was used to identify the flooding treatments. Flooding was defined as percentage of days in a month that the soil surface of a row was under water. Different flooding regimes probably also experienced different water table depths when drained but we did not measure water table depth in the organs.

3. Results and Discussion

3.1 Survival and growth

By August of the first growing season, 82% of the 108 seedlings in the $1,132 \text{ g N m}^{-2}$ treatment were dead whereas only 16%, 20%, and 17% seedlings had died in the 0, 57, and 283 g N m^{-2} treatments, respectively. However, vigour appeared to increase with nutrient availability

within the 0, 57, and 283 g N m⁻² treatments. This pattern has been observed in agricultural conditions (Carrow et al. 2001) because nutrients limit growth at low levels, enhance growth at higher levels, and become toxic at even higher levels with toxicity attributed primarily to osmotic stress but also pH (Carrow et al. 2001). This pattern also has been observed in wetland plants with negative effects sometimes observed when nutrient addition rates are high. Darby and Turner (2008) concluded that Ca(H₂PO₄)₂ sufficient to add 6.6 g m⁻² of P reduced belowground biomass in *Spartina alterniflora* Loisel. Ket et al. (2011) showed that 50 g N m⁻² yr⁻¹ added for five years reduced belowground production in *Zizaniopsis miliacea* (Michx.). The difference in survival among the nutrient treatments was statistically significant (P < 0.0001). We excluded seedlings in the 1,132 g N m⁻² treatment from all subsequent statistical analyses because there were too few survivors in that treatment.

After two growing seasons, flooding stress and nutrient availability interacted to affect aboveground biomass (P = 0.0054) and belowground biomass (P = 0.0180). Diameter and height at time of planting were retained in the models for aboveground biomass and for belowground biomass. Seedlings in the 283 g N m⁻² treatment had more aboveground biomass than seedlings with less nutrient availability except that no differences among the nutrient treatments were apparent where flooding was most extreme and (Figure 4). Belowground biomass was more variable but exhibited a similar pattern except that less flooding stress was required to negate the effects of nutrient availability on belowground biomass than to negate the effects of flooding on aboveground biomass. The 283 g N m⁻² treatment produced more belowground biomass than the other treatments but only in the two least drained treatments (Figure 4). Our observations thus agree with previous results in that nutrients enhance growth of flooded baldcypress (Brown 1981, Hesse et al. 1997, Day et al. 2006, Effler et al. 2006, Hunter et al. 2009a) except when

flooding is most severe (Keim et al. 2012). Our belowground biomass data contradicted the idea that plants produce fewer roots to forage for nutrients when nutrients are more available and instead support findings that root production increases as nutrients become more available (e.g., Drew 1975). We concluded that above and belowground growth of baldcypress responds to nutrient availability and flooding stress in a way that would be classified as nutrient availability and flooding stress interacting with the interaction dominated by flooding stress (Figure 1c).

3.2 Leaf tissue chemistry as indicators of growth

Leaf tissue N and C:N ratio were correlated with nutrient availability (Table 3) in both years but we concluded that neither were suitable indicators for nutrient availability because ANOVA indicated that both also were related to the interaction between nutrient availability and flooding ($P < 0.0001$). Those relationships preclude accurately inferring nutrient availability to baldcypress from the N content or C:N ratio of baldcypress leaves (Figure 5). For example, flooding caused a bigger difference in C:N ratios than nutrient availability (Figure 5). This interaction agrees with previous research by Day (1987) who reported that flooding appeared to reduce the C:N ratio of *Acer rubrum* leaves. One explanation for a greater concentration of N in flood-stressed seedlings is that the flooded seedlings were able to uptake more N when N was more available but flooding stress prevented the seedlings from growing and thus diluting N as it was in more productive, less flooded seedlings (Figures 5). Despite our inability to use C:N ratios to infer nitrogen status, Tobias et al. (2010) developed a method to use C:N ratio of a wetland grass (*S. patens*) to infer N limitation even though the C:N ratio varied with N availability as well as with salinity. However, it is important to note that all of the data used by Tobias et al. (2010) was collected within one level of flooding. The N:P ratio often is assumed

to reflect nutrient availability but like the C:N ratio, it too was affected more by flooding than by nutrient availability (Figure 5). The molar ratio of Ca:Mg ratio also was correlated with nutrient availability in both years (Table 3). However, ANOVA indicated that leaf tissue Ca:Mg content was related to the interaction between flooding and nutrient uptake ($P = 0.0255$). Graphical examination of the data indicate that despite that significant interaction (Figure 5), seedlings exposed to the most nutrients generally had lower Ca:Mg ratios (mean = 1.50, s.e. = 0.06) than seedlings exposed to the least nutrients (mean = 2.25, s.e. = 0.06). During the first year (data not shown), the Ca:Mg ratio of the most fertilized seedlings was even lower (mean = 1.35, s.e. = 0.05) whereas the Ca:Mg ratio of the unfertilized seedlings (mean = 2.22, s.e. 0.05) was similar to that in the second year.

Leaf tissue %C and the N:P ratio were correlated with flooding (Table 3) in both years but we concluded that neither were suitable indicators of flooding. Percent C was significantly related to flooding ($P = 0.0165$) and to nutrient availability ($P = 0.0054$) whereas the interaction was insignificant ($P = 0.5076$) but flooding and nutrient availability caused similar changes in %C. Flooding caused %C to increase from 47.6% to 48.3% but nutrient availability also caused %C to increase from 47.7 to 48.1%. Thus, the least flooded, most fertilized seedlings had a higher %C than the most flooded, least fertilized seedlings (Figure 5). The N:P ratio also was related to the interaction between nutrient availability and flooding ($P < 0.0001$) but we concluded that it was not a suitable indicator of flood stress because it was no better than C content at discriminating among the less flooded treatments (Figure 5). For similar reasons, we concluded that the other chemical parameters correlated with flooding (Table 3) in one year or another were not suitable indicators of flooding stress.

3.3 Effects of flooding and nutrient availability on mercury.

The Hg concentrations that we observed in leaves were similar to those observed by Grigal (2003) in his review of Hg in forests. Eriksen et al. (2003) used soil that had 230 times more soil Hg than our soil and observed 6 times more leaf Hg than our leaves. In our study, leaf Hg increased from an overall mean of 0.0155 ppm (s.e. = 0.0026) the first year to 0.0197 ppm (s.e. = 0.0032) the second year. Possible mechanisms for this difference include differences in leaf age between years because senescence had begun the second year but not the first.

At the end of the first year, the leaf Hg was 44% greater in flooded seedlings than in drained seedlings and was 9% lower in seedlings that received the 283 g N m⁻² treatment than in unfertilized seedlings (Figure 6). Both terms were significantly related to Hg content, $P < 0.0001$ and $P = 0.0197$ for flooding stress and nutrient availability respectively, with the interaction between those factors also significant ($P = 0.0125$) yet difficult to interpret (Figure 6). By the end of the second year, leaf Hg was no longer related to flooding or the interaction between flooding and nutrient availability. Leaf Hg was related only to nutrient availability ($P = 0.0321$) such that leaf Hg increased as nutrient availability increased (Figure 6).

We speculate that during the first year, flooding affected Hg accumulation because roots were concentrated in the surface of the pipes where our intended flooding treatments prevailed. We further speculate that by the end of the second year, roots in pipes with low flooding stress had penetrated through all the aerobic soil and ceased growing upon reaching anaerobic soil, which caused seedlings in all flooding treatments to be exposed to different volumes of aerobic soil but to a similar area of interface between aerobic and anaerobic soil. Such interfaces are hotspots of chemical transformation in general and for Hg (Ullrich et al. 2001). Our first year findings agree with previous research showing that anoxia promotes the conversion of inorganic

Hg to the more biologically available methylmercury (National Science and Technology Council 2004, Driscoll et al. 2007) and with previous research indicating that plants growing on wetter soils have higher leaf Hg (Overesch et al. 2007) and that leaf Hg tends to be greater in species that grow closer to the water table (Moore et al. 1995). The intermingling of branches of seedlings from different flooding treatments virtually precludes the possibility that seedlings in different flood levels were exposed to different levels of atmospheric Hg. Either flooding enhanced uptake and retention of atmospheric Hg by leaves, or flooding increased root uptake and translocation of Hg from soil through roots and then to stems and leaves. In either case, soil conditions associated with flooding controlled leaf Hg concentrations during the first year of our experiment.

By the end of the second year however, seedlings with greater nutrient availability had higher concentrations of Hg in their leaves, agreeing with reports that nutrient availability decreases toxic metal under some circumstances but increases uptake of toxic metal under other circumstances (see Gothberg et al. 2004 and literature cited therein). Possible mechanisms include larger differences in root biomass among the nutrient treatments the second year that increased uptake of soil Hg.

We measured soil Hg only in surface soils and only after the second year. Flooding increased soil Hg in the two most flooded treatments 56% relative to the other treatments (Figure 6). Flooding must have altered soil Hg by depleting Hg from drained soil and/or from accumulating Hg in flooded soils. Less flooded treatments probably lost more Hg via photooxidation, which controls Hg emissions from wetland sediments (Smith and Reinfelder 2011). Less flooded treatments also probably had more flushing of porewater as water levels were raised and lowered every two to three weeks. More flooded treatments thus had greater

opportunity to be flooded with that porewater as well as with leachate from senesced leaves.

Baldcypress bioaccumulated Hg as indicated by the greater concentration of Hg in leaves (mean = 0.0154, s.d. = 0.0026) than in soil (mean = 0.0095 ppm, s.d. = 0.0035).

4. Conclusions

Below toxic levels of nutrients, nutrient availability increased growth of baldcypress across a wide range of flooding, even exceeding 80% flooding, but not when flooding was virtually continuous. We classified this response as nutrient availability and flooding stress interacting with the interaction dominated by flooding stress (Figure 1c). This classification allows one to understand why different studies of baldcypress reached different conclusions. For example, Brown (1981), Hesse et al. (1998), Day et al. (2006), Effler et al. (2006), Hunter et al. (2009a), and Shaffer et al. (2015) concluded that nutrient additions increase baldcypress growth but Keim et al. (2012) concluded that baldcypress failed to respond to nutrient additions. Significantly, Keim et al. (2012) studied baldcypress that had been flooded continuously for at least 13 years. Predictability of management and restoration may increase with such understanding. The classification of stress and resource effects on plant growth also can be extended to other stressors, resources, and species. Nutrient ratios of leaf tissue that are commonly used to indicate nutrient status of vegetation should not be used to indicate the nutrient status of this species because flooding stress also affected those ratios. The Ca:Mg ratio was related to nutrient availability across a wide range of flooding.

Baldcypress leaves accumulated higher concentrations of Hg than in soil in all treatments, but differences in Hg concentrations appeared to vary with root and soil conditions. During the first year, Hg in baldcypress leaves was increased by flooding stress and decreased by

nutrient availability, presumably when roots were smaller, but Hg uptake was increased by nutrient availability the second year when nutrient availability also increased root biomass and allowed roots of even drained treatments to penetrate down to reduced soil where methylation of Hg is more likely. Such complexity complicates predictions regarding landscape hotspots of Hg methylation.

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Table 1. Nutrient availability rates (g m^{-2}) used in experiment designed to study effects of nutrient availability and flooding on growth of *Taxodium distichum* (L.) Rich. In addition to controls (treatment 1) that received no nutrient enhancement, nutrient availability was enhanced by one of the following three amounts. Nutrients were applied once; seedlings were allowed to grow two seasons before they were harvested.

Element	treatment 2	treatment 3	treatment 4
N	56.6	282.9	1,131.8
P	28.3	141.5	565.9
K	14.1	70.7	282.9
S	5.6	28.3	113.2
Fe	7.1	35.4	141.5
Mn	5.6	28.3	113.2
Mg	6.4	31.8	127.3
Zn	3.3	16.7	66.8

Table 2. Characteristics of surface soil after burying nutrients and imposing different amounts of flooding for two growing seasons. The initial concentration of N and P was 0.031% and 21.4 ppm, respectively. Soil deeper in the profile likely differed from these surface soils. No estimate of standard deviation is available for some nitrogen estimates because we inadvertently analysed soil from only one organ for some treatments.

flooding	-----nutrient treatment-----				
	0	1	5	20	mean
mean Nitrogen (%) and standard deviation					
<1%	0.049 (.)	0.062 (.)	0.048 (0.011)	0.072 (0.002)	0.058 (0.013)
24%	0.033 (.)	0.051 (.)	0.055 (0.011)	0.067 (0.001)	0.055 (0.013)
44%	0.044 (.)	0.047 (.)	0.055 (0.003)	0.069 (.)	0.056 (0.011)
62%	0.039 (.)	0.043 (.)	0.047 (0.004)	0.066 (0.008)	0.051 (0.012)
81%	0.047 (.)	0.041 (.)	0.045 (.)	0.072 (0.011)	0.055 (0.016)
96%	0.039 (.)	0.041 (.)	0.060 (.)	0.062 (0.009)	0.053 (0.012)
Mean	0.042 (0.006)	0.0048 (0.008)	0.052 (0.007)	0.068 (0.006)	
mean Phosphorus (ppm) and standard deviation					
<1%	22.8 (5.0)	23.0 (0.6)	20.9 (2.5)	103.1 (76.9)	42.4 (49.2)
24%	28.4 (4.3)	30.3 (1.0)	26.5 (7.1)	66.7 (60.2)	38.0 (31.2)
44%	31.7 (6.8)	29.5 (1.6)	24.3 (2.7)	65.9 (45.4)	37.8 (26.0)
62%	28.0 (4.6)	27.1 (2.3)	26.3 (3.5)	71.1 (45.8)	38.6 (28.6)
81%	31.1 (2.3)	28.0 (2.2)	33.1 (12.0)	45.5 (14.9)	34.4 (11.0)
96%	27.9 (10.0)	25.3 (2.7)	45.1 (28.6)	57.0 (56.1)	38.8 (30.4)
Mean	28.3(6.1)	27.5 (3.1)	29.4 (13.7)	68.2 (48.7)	

Table 3. Chemical parameters in leaf tissue that were significantly related in an ANOVA with nutrient treatment (0, 57, or 283 g N m⁻²) or flooding treatment (1 through 6).

parameter	year	mean (std)	nutrient	flooding	interaction
C (%)	1	48.7 (0.98)	*	*	*
“	2	48.0 (0.61)	*	*	ns
N (%)	1	1.67 (0.57)	*	*	*
“	2	1.28 (2.26)	*	*	*
P (%)	1	0.09 (0.02)	*	ns	*
“	2	0.10 (0.02)	*	*	*
Ca (%)	1	0.77 (0.27)	*	*	ns
“	2	0.72 (0.16)	*	*	ns
Fe (ppm)	1	60 (17)	*	*	ns
“	2	73 (16)	ns	ns	*
Mg (%)	1	0.26 (0.04)	ns	*	*
“	2	0.22 (0.03)	*	ns	ns
K (%)	1	0.50 (0.10)	*	*	ns
“	2	0.49 (0.11)	ns	ns	*
Mn (ppm)	1	63 (16)	*	*	*
“	2	73 (23)	*	*	*
Na (ppm)	1	2,382 (1,895)	*	ns	*
“	2	9,236 (3,746)	*	*	*
S (%)	1	0.15 (0.03)	*	*	*
“	2	0.15 (0.02)	*	*	*
Hg (ppm)	1	0.0155 (0.002)	*	*	*
“	2	0.0197 (0.003)	*	ns	ns
C:N (molar)	1	28.0 (9.5)	*	*	*
“	2	33.3 (5.8)	*	*	*
N:P (molar)	1	8.4 (3.0)	*	*	ns
“	2	5.6 (1.3)	*	*	*
Na:K (molar)	1	0.3 (0.3)	ns	*	ns
“	2	1.2 (0.5)	*	ns	*
Ca:Mg (molar)	1	1.8 (0.5)	*	ns	ns
“	2	2.0 (0.5)	*	*	*

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664 Figure 1. Theoretical relationships among plant growth, a limiting resource, and a limiting
 665 stress. In all scenarios, plant growth is scaled such that 100% is reached when there is no stress
 666 and when the availability of the limiting resource is midway between minimal and optimal. In
 667 scenarios A and B, the resource and stress act independently. In scenario A, the stress is more
 668 important than the resource because growth varies more as a function of stress than as a function
 669 of resource availability. In scenario B, the resource is more important than the stress because
 670 growth varies more as a function of resource availability than as a function of stress. In
 671 scenarios C and D, resource availability and stress interact to affect growth. In scenario C,
 672 resource availability decreases in importance as stress increases such that the stress negates
 673 effects of resource availability. If there was any range in plant growth at the highest stress in C,
 674 then the stress would offset, rather than negate, the effects of resource availability. In scenario
 675 D, resource availability increases in importance as stress increases such that high resource
 676 availability offsets the stress when stress is present. If the upper line labelled “optimal
 677 resources” in D was horizontal or had positive slope, then resource availability would negate the
 678 stress.

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