# Relaxation of microhabitat restriction through ontogeny of *Itea virginica* in cypress-tupelo swamps.

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**--ABSTRACT--**

Nearly all understory plant species in semi-permanently flooded cypress-tupelo swamp forests grow on microsites located above the water level, as opposed to growing on the flooded forest floor. Our field study indicates that one such species, *Itea virginica* (Saxifragaceae), has a strong association with elevated microsites that changes with life stage: adults are found significantly more often on the forest floor than seedlings, although not as frequently as expected for the amount of forest floor vs. elevated microsites present. High water level may inhibit seedling establishment, but not adult growth, thus suggesting a potential ontogenetic expansion of flooding tolerance. We conducted greenhouse flooding experiments on seedlings and adults of various sizes with three treatments: high flood (a percentage of aboveground biomass submerged), waterlogged (only root systems submerged), and control (no flooding). The effect of initial height above water and treatment on relative growth rate was significant for the seedlings: RGR decreased with increasing flood level; however, there was no significant effect for adults. Seedlings were more negatively affected by flooding than adults due primarily to their small size rather than any differences in ability to produce flood responses (i.e., enlarged lenticels or adventitious roots). Additionally, we conducted seed experiments investigating the effects of different substrates and durations of flooding on germination success; there were no significant effects of either factor on seed germination. This study increases our understanding of regeneration biology and can be valuable in planning restoration activities in cypress-tupelo swamps.

## --INTRODUCTION--

Ontogenetic niche shifts are common in nature; such shifts occur when the survival requirements or habitat associations of an individual change throughout its life cycle. Shifts in feeding behavior, diet, parasite habitats, predator-prey relationships, and morphology of animals are well detailed (e.g., Persson and Bronmark, 2002; Aznar et al., 1997; Claessen and Dieckmann, 2002; Sillett and Foster, 2000). However, research on ontogenetic niche shifts in plant species is markedly less common (Eriksson, 2002), probably because plants are only mobile in the seed stage (Schneider and Sharitz, 1988) and produce their own food, eliminating two of the main foci of heterotroph niche shift studies. However, environmental factors that specifically affect the regeneration stage of a plant could lead to an uncoupling of juvenile and adult traits and microhabitat requirements, resulting in an ontogenetic niche shift (Grubb, 1977; Parish and Bazzaz, 1985). These shifts in optimal niche conditions limit where the plant can grow at each life stage, acting as selective bottlenecks that result in the final adult distribution patterns. Knowledge of ontogenetic niche shifts would facilitate the interpretation and prediction of distribution patterns of plant species. Grubb's (1977) seminal paper on the regeneration niche in plants (i.e. the environmental conditions necessary for seed germination and seedling establishment) has been incredibly influential in plant ecology, but there have been few empirical studies explicitly designed to investigate the effects of changing niche requirements between life stages on microhabitat associations of plants.

Nonetheless, it is clear that ontogenetic niche shifts occur in plant species. Parish and Bazzaz (1985) highlighted a reduction in niche breadth in mature plants of six different annual species compared with their seed germination and seedling establishment

requirements. Eriksson (2002) detailed ontogenetic niche shifts in three different *Vaccinium* species where seed germination and seedling survival occurred at different sites than the growth of conspecific adults. Schupp (1995) discussed situations in which environmental conditions optimal for germination may actually be detrimental for seedling survivorship, leading to conflicts in optimal environmental conditions for seeds and seedlings. Such conflicts clearly apply to the transition between the juvenile and adult stages as well.

One of the major environmental conditions affecting seedling establishment and regeneration is microtopography (Jones et. al, 1994). Several studies have addressed the relationship between topographically different microsites and the regeneration niche of plants in various ecosystems. Barrett and Silander (1992) reported seedling recruitment limitation of white clover in a lawn due to differences in disturbed soil microsites. Another study transplanted fynbos species on edaphically different microhabitats and observed differences in seedling survival (Mustart and Cowling, 1993). Collins (1990) investigated shifts in microhabitat associations of tree seedling establishment in a hemlock-hardwood forest where litter depth defined the different microsites. These studies all focused specifically on the relationship of small topographic differences between microsites to ontogenetic niche shifts. The highly heterogeneous landscape of floodplain forests of the Southeastern United States may be perfect for further assessing the relationship between ontogenetic niche shifts and regeneration because of their easily distinguishable and more complex microtopography.

In the semi-permanently flooded bald cypress-water tupelo swamp forests of the Southeastern United States, there are as many as sixteen distinguishable microhabitats

(Huenneke and Sharitz, 1986; 1990). The flooding regime in these swamps is both temporally and spatially variable. Previous work has shown that the seeds of the dominant tree species were distributed nonrandomly upon certain microsites (Schneider and Sharitz, 1988). Lowest seed densities were found in open forest floor microsites, while the highest were found in the soil near emergent substrates such as trees, cypress knees, and logs. In addition, elevated microhabitats support almost all of the understory plant diversity in cypress-tupelo swamps (Schlesinger, 1978; *personal observation*); virtually no plants grow on the flooded forest floor. These patterns suggest the importance of elevated microsite availability, affected by the swamp's flooding regime, on the growth of all understory plant species in cypress-tupelo swamps.

Four Holes Swamp is a brown-water creek swamp with no major discernable channel that runs for sixty miles through the coastal plain of South Carolina to the Edisto River. Francis Beidler Forest in Four Holes Swamp is the largest stand of original-growth cypress-tupelo swamp forest in the U.S. It is a National Audubon Sanctuary consisting of 5260 hectares of bottomland hardwood and semi-permanently flooded swamp forest (Porcher, 1981). Standing water covers much of the floor of the swamp forests in all but the driest years.

The dominant tree species in the swamp forest are bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*). These species provide the structural framework underlying the distribution and abundance of other plant species in the community (Huenneke and Sharitz, 1990). Their trunks, roots, knees and buttresses create the various elevated conditions present in the system, in which numerous understory shrub and herbaceous species thrive.

*Itea virginica* (Saxifragaceae) is a perennial understory shrub distributed throughout the Southeastern United States. It thrives in wet habitats such as swamps and the banks of streams and lakes. It flowers in June-July and is semi-evergreen. It has low drought tolerance, high anaerobic (and thus flooding) tolerance, and prefers acidic, fine-grained soils. When cultivated, it is known to grow well on a variety of soil types under a variety of moisture conditions (USDA, 2005). This apparent flexibility in preferred conditions raises questions about the distribution of *Itea* in nature. Mature individuals only grow on elevated microsites: cypress knees, fallen logs, and the buttresses or sides of standing trees (Schlesinger, 1978) and often with their roots extending down into the flooded substrate. The soil of the flooded forest floor is more nutrient-rich than the woody material of the elevated microsites and could potentially provide a more suitable microhabitat for *Itea*.

In this study, we investigated causes for the adult distribution pattern of *Itea.* Its close association with elevated microsites suggests two things: 1) *Itea* seeds may be nonrandomly dispersed to these elevated microsites and/or 2) an environmental pressure may prevent *Itea* from establishing on the more abundant and potentially more suitable forest floor microsite. The most plausible environmental pressure causing this pattern is the persistent high water level in the swamp. High water level may inhibit seedling establishment, but not adult growth, thus representing a shift in flooding tolerance between life stages. In this case, we would expect seedlings to exhibit low survivorship and productivity under flooded conditions, whereas flooding would not negatively affect adult survivorship or growth. If flooding does prevent seedlings from establishing on the forest floor, this may be due either to substantial submersion of the small-sized seedlings

or to inherent differences between adult and juvenile plant traits that make juveniles less adept at handling flooding stress.

Two examples of such traits are the development of enlarged lenticels and of adventitious roots. The formation of enlarged lenticels (i.e., hypotrophy) on the stems of waterlogged plants is thought to be caused by the accumulation of ethylene in oxygen-stressed tissues (Coutts, 1982) and presumably aids in increasing gas exchange to the anoxic roots. The growth of adventitious roots is a common phenomenon but its cause and purpose is not entirely understood (Etherington, 1984). However, in one study, Jackson (1955) found that the recovery (i.e., resumption of shoot growth) of flooded sunflower and tomato plants depended on the presence of adventitious roots; plants with their adventitious roots removed did not resume growth. If adults and juveniles do not differ in their abilities to produce these flood responses, then any seedling establishment limitation occurring would be primarily due to the small size (i.e., greater amount of stem submerged) of seedlings. The main objective of our experimental manipulations is to determine if the distribution of *Itea* to elevated microsites is caused by ontogenetic differences in abiotic preferences.

## --METHODS--

♦ Field Study:

We conducted a field study with two goals in mind: 1) to estimate the amount of ground area of the swamp composed of each type of microsite present and 2) to quantitatively define the abundance of *Itea* individuals across microsites. In May 2006 we ran a total of fifteen 100x10 meter transects at five different sites. Each of the sites

consisted of old-growth cypress-tupelo swamp forest; two of the sites showed signs of logging at some point in the past. At every meter along each transect we determined the kind of microsite present by blindly dropping a pin and classifying where the pin landed. We identified seven different microsites that we placed in two different categories:

| Category | Microsite |
|---|---|
| Forest Floor | flooded forest floor |
|  | forest floor near tree (often dry) |
|  | root |
| Elevated Microsite | tree stump |
|  | cypress knee |
|  | fallen log / branch |
|  | side of living tree |

We also noted the presence of every *Itea* individual, its life stage, and what kind of microsite it grew on located within each 1,000 $m^2$ transect. The life stages were defined as follows:

| Life Stage | Definition | # Found |
|---|---|---|
| Seedling | has cotyledons, up to 5 cm tall | 6912 |
| Sapling | greater than 5 cm, less than 1 m tall | 348 |
| Adult | greater than 1 m tall, extensive branching | 119 |

We performed a chi-squared goodness-of-fit test to determine if *Itea* plants were distributed randomly in the field with respect to the prevalence of the different microsites available. The null hypotheses were that 1) the frequency of *Itea* individuals corresponded with the frequency of elevated and forest floor microsites (expected values) and 2) the distribution pattern of *Itea* did not vary through ontogeny.

♦ Seed Experiment 1—Substrate Germination:

The first seed experiment investigated the effects of type of substrate on germination rate. There were three treatments: moist paper towel (control), soil from the

swamp (forest floor microsite), and cypress wood chips from the swamp (elevated microsites). Before beginning, we incubated the field substrates in high light and moisture conditions for three weeks to germinate any *Itea* seeds that they may have already contained so as not to confound our results. We spread each substrate in ten Petri dishes for a total of thirty replicates. Next, twenty *Itea* seeds collected from the field were scattered in each Petri dish (n=600). The substrates were kept moist and monitored for 65 days beginning August 2006. The number of seeds germinated was recorded five times throughout this period.

♦ Seed Experiment 2—Flood Duration:

The second seed experiment investigated the effects of flood duration on germination. There were three flooding treatments: seven weeks, four weeks, and zero weeks. For each treatment, twenty *Itea* seeds were wrapped in a paper towel and sunk under water in a vial for the specified amount of time. For the control (zero weeks) seeds were not flooded. Then the paper towels with seeds were spread out in Petri dishes. There were ten replicates for each treatment for a total of thirty replicates. The seeds (n=600) were kept moist and monitored for 69 days beginning September 2006. The number of seeds germinated was recorded four times throughout this period.

For both seed experiments, we used a survivorship analysis to test if germination rate was a function of treatment.

♦ Seeding/Adult Flooding Experiments:

We grew seedlings and adults under different flooding conditions and investigated their responses through differences in relative growth rate based on dry biomass. We collected cuttings from reproductive adults in the field during October 2005. The cuttings

grew under a misting system until their roots established. Seeds were collected in the field and seedlings were germinated and grown for 3-4 months beginning April 2006. We sorted the plants by their initial heights which ranged from 3 cm to 58 cm for cuttings and from 1 cm to 8 cm for seedlings. Despite the fact that some were shorter than seedlings, cuttings were considered adults for the purposes of this experiment because their tissues were derived from reproductive adults in the field. Representative plants were measured and sacrificed to obtain dry biomass data. For adults, we measured the height of the plant from soil to tip of highest leaf, the diameter(s) of the stem(s) at soil level, and the lengths of the three longest branches. For the seedlings, we measured the height of the plant from soil to apical meristem, the diameter of the stem at soil level, and the number of leaves. These data were used to estimate the initial biomass of the non-sacrificed, experimental plants. We then sorted the experimental plants randomly into three treatments: 1) a well-watered and drained control, a waterlogged treatment (water to 1 cm above soil level), and a high flood treatment (water to 9 cm above soil for adults, 6 cm above soil for seedlings). We planted seedlings and cuttings in conetainers (long, thin, cone-shaped pots) and placed them in trays within Rubbermaid storage bins. We drilled drainage holes in the bottom of the control treatment bins. The seedlings and cuttings were placed in separate trays/ bins because seedlings were planted in smaller conetainers than cuttings and needed trays of a different size. Additionally, the adult experiment began a month earlier than the seedling experiment because at the time we did not know how long it would take for seedlings to grow large enough to be successfully transplanted from germination flats to conetainers. Adult flooding began in July 2006 and seedling flooding began in August 2006.  For both adults and seedlings, we replicated each treatment twice

(total adult n=126, seedling n=198). We raised the water level in the flooded treatments by 7 cm every two days so that the treatments reached their final flood level within a week. The final flood levels were maintained throughout the course of the experiment. The control plants were watered daily and all bins were regularly rotated to different locations in the greenhouse. We fertilized all of the treatments and dumped and refilled the water in the flooded treatments every two weeks. This dumping was necessary due to the buildup of algae in waterlogged and high flood treatments. At the end of the experiment (144 days adults, 94 days seedlings) we recorded the same measurements that were taken before the beginning of the experiment. Additionally, we measured two flood-induced morphological characteristics that appeared: the proportion of stem length covered by enlarged lenticels (**Fig. 1**) and the amount of adventitious roots grown (**Fig. 2**). Finally, we harvested both adults and seedlings and weighed their dried biomasses in early December 2006.

For data analysis, we first ran logistic regressions between the probability of survivorship and relative initial height above water to investigate the effects of flooding on mortality. Next, we did a multivariate analysis of variance (MANOVA) for seedlings and for adults to test the effects of treatment and initial height above water on: 1) relative growth rate, 2) enlarged lenticel proportion, 3) the ratio of adventitious root biomass to total root biomass, and 4) the root to shoot biomass ratio. Finally, we ran a series of univariate ANOVAs to explore each of the four response variables in greater depth.

## --RESULTS--

♦ Field Study:

Although elevated microsites composed only 26.7% of those available in the cypress-tupelo swamp ecosystem, 99.6% of all *Itea* individuals grew on them (**Fig.3**). The forest floor (both dry and flooded), composing the majority (73.3%) of the microsite types available, contained only 0.4% of the *Itea* individuals. The chi-squared test rejected both null hypotheses and found that: 1) *Itea* plants at all life stages were clumped on relatively scarce elevated microsites ($p<0.0001$) and 2) *Itea* seedlings were less likely to occur on the forest floor than were *Itea* adults ($p<0.0001$). Seedling and adult plants showed significantly different responses. Of the 6912 seedlings found, only 0.2% occurred on the forest floor; whereas 5.0% of 119 adults occurred on the forest floor. This is possible because the flooding regime in the swamps is very variable: forest floor microsites flooded at one point may have been previously dry long enough to allow seedlings to establish. There was no significant difference in data between logged and unlogged sites. These data suggest a relaxation of microhabitat restriction for *Itea* through ontogeny. In spite of the relatively few plants on the forest floor (n=33; total n=7379), the association of *Itea* to elevated microsites was very strong and these data support our initial observation that virtually no understory plants in this system grow on the forest floor.

♦ Seed Experiment 1—Substrate Germination:

There was no significant difference in germination success across the three types of substrate; seeds germinated equally well on soil, wood, or the control. ($p=0.93$; **Fig. 4**)

This supports the hypothesis that *Itea* seeds can germinate equally well on either the forest floor or elevated microsites.

♦ Seed Experiment 2—Flood Duration:

There was no significant difference in final germination rate across flooding treatments (p=0.45; **Fig. 5**). However, seeds that were submerged for either 4 or 7 weeks germinated significantly faster than those that were not flooded (p=0.0015). In fact, a few flooded seeds even germinated while submerged, which is generally rare since germination requires oxygen. This supports the hypothesis that *Itea* seed germination is not limited by flooding.

♦ Seedling/Adult Flooding Experiments:

**--**Mortality Analysis:  A logistic regression between mortality and treatment was not significant; however, the relative height of the plant above the flood level was. For seedlings, the mortality data indicate that the probability of survivorship increased with an increasing initial amount of stem above the water level (p=0.0552). Of the 198 seedlings, 11 died during the course of the experiment. Of these, 6 were completely submerged in the high flood treatment, 2 were submerged in the waterlogged treatment, and the remaining 3 were only 1.5-3.5 cm taller than the water level in the waterlogged treatment. Although many seedlings that were initially submerged did survive, none of the seedlings in the control treatment died.

For the adults, only 4 of the initial 126 plants died during the course of the experiment. There was no significant effect of initial height of stem above water level on mortality (p=0.34), probably because there was not enough total mortality to establish a pattern.

MANOVAs:  We ran separate MANOVA models for adults and for seedlings because the experiments were conducted at different times and in separate bins. Both of the overall MANOVA models included treatment (drained control, waterlogged, high flood) and initial height above water as explanatory variables with relative growth rate, proportion of stem with enlarged lenticels, adventitious root mass ratio, and root:shoot ratio as response variables. For seedlings, the MANOVA was significant for both treatment (p<0.0001) and initial height above water (p<0.0001). Similarly for adults, the MANOVA was significant for both treatment (p<0.0001) and initial height above water (p=0.0002). Thus, we explored univariate analyses for each response variable.

--Relative Growth Rate:  The effect of flooding treatment and initial height above water together on RGR was highly significant for both seedlings (p<0.0001; $r^2$=0.81) and adults (p=0.0014, $r^2$=0.12). However, much more of the variation in RGR is explained by treatment and initial height above water in seedlings (81%) than in adults (12%). For seedlings, as flood level increased across treatments, the average RGR decreased (p<0.0001; **Fig. 6a**). Conversely, there was no significant depression of RGR under flooded treatments for adults (p=0.142; $r^2$= 0.12; **Fig. 6b**).

The effect of initial height above water on RGR for seedlings was significant (p=0.0188); RGR decreased with higher initial height for control plants, but the opposite response occurred for plants in both flooded treatments (**Fig. 7a**) indicating a clear response to flooding (i.e., RGR increased for taller seedlings when flooded). The effect of initial height above water on RGR for adults was significant as well (p<0.0001, **Fig. 7b**). As with seedlings, RGR decreased with increasing initial height for control adults. However, this pattern also occurred for waterlogged plants and RGR barely increased for

taller high flood adults. These data suggest that flooding had a greater negative effect on seedlings than adults; being taller under flooded conditions resulted in greater positive slopes in RGR for seedlings than for adults.

--Enlarged Lenticels:  The proportion of final stem height covered with enlarged lenticels was significantly correlated with treatment and initial height above water together for seedlings (p=0.0003; $r^2 = 0.099$) and for adults (p<0.0001; $r^2 = 0.43$).

For seedlings, both treatment (p=0.0037) and initial height above water (p=0.002) were significant on their own as well. Plants in the waterlogged treatment showed the highest proportion of stem covered with enlarged lenticels (**Fig. 8a**). Additionally, enlarged lenticel proportion increased with increasing initial height above water.

For adults, enlarged lenticel proportion was a function of treatment (p<0.0001) and showed a trend to increase with increasing initial height above water (p=0.065). This indicates that small adults were not much worse at producing enlarged lenticels than large adults. In contrast with the seedlings, adults with the highest proportion of stem covered by enlarged lenticels were in the high flood treatment, followed by those in the waterlogged treatment (**Fig. 8b**). This difference is due to the fact that even in the high flood treatment, adults had much more stem above the water level than seedlings.

--Adventitious Roots:  The proportion of adventitious root mass to total root mass produced was significantly correlated with treatment and initial height above water together for seedlings (p<0.0001; $r^2 = 0.27$) and for adults (p=0.0008; $r^2 = 0.13$).

For seedlings, treatment had a highly significant effect on adventitious root mass growth (p=<0.0001); plants in the waterlogged treatment had the highest average adventitious root mass ratio, followed by plants in the high flood treatment (**Fig. 9a**).

Control plants did not produce adventitious roots. Initial height above water had little effect on adventitious root mass growth (p=0.0959).

For the adults, adventitious root biomass was highly dependent on treatment (p<0.0001). Plants in both flooded treatments had significantly more adventitious root biomass than control plants; however, unlike the seedlings, there was no difference in adventitious root biomass between the waterlogged and high flood treatments (**Fig. 9b**). Initial height above water had no significant effect on adventitious root growth for adults (p=0.14).

--<u>Root:Shoot Ratio</u>: The proportion of root to shoot biomass was significantly correlated with treatment and initial height above water together for both seedlings (p<0.0001; $r^2$=0.155) and adults (p=0.00114; $r^2$=0.086).

For seedlings, control plants had significantly higher (p<0.0001) root:shoot ratios than both flooded treatments (i.e., flooding lead to proportionally lower root mass) but there was no significant difference between the waterlogged and high flood treatments (**Fig. 10a**). Initial height above water also significantly affected root:shoot biomass (p<0.0001). As initial height above water increased, root:shoot ratios decreased.

For adults, initial height above water alone does not significantly influence root:shoot biomass as in seedlings (p=0.70), but treatment does (p=0.0041). Similar to seedlings, adult plants in both flooded treatments had proportionally lower root biomass (**Fig. 10b**).

## --DISCUSSION--

In cypress-tupelo swamps, *Itea* plants are located almost exclusively on elevated microsites and are rarely found on the forest floor. When they are, the individual is likely to be a full-grown adult with substantial photosynthetic material located above the flood level. Since adults do grow large and their roots usually extend down through elevated microsites into the flooded soil anyway, we believe that adults can thrive on the flooded forest floor. Thus, the adult distribution of *Itea* exclusively to elevated microsites is a mystery until considered along with the niche requirements of its other life stages.

Our seed experiments indicated that germination rate was affected by neither substrate type nor length of flooding. *Itea* seeds germinated equally well on both soil and cypress wood, suggesting that successful seed germination on either the forest floor or elevated microsites would be the same. Contrary to typical seed behavior, *Itea* seed germination was not depressed by flooding; in fact, in our experiment, flooding actually resulted in faster germination. It is known that seeds of some wetland species actually benefit from temporary oxygen deprivation because it breaks their dormancy (Côme et al. 1991); this could explain the faster germination of flooded seeds in our study. According to niche requirements of the seed stage, there should be just as many *Itea* adults found on the forest floor as there are on elevated microsites.

An alternate hypothesis to explain adult distribution is that seeds are preferentially dispersed to elevated microsites. It was impractical to explore this hypothesis for *Itea* because *Itea* seeds are <1 mm in size and tracking their trajectories in the field would have been impossible. They are also black in color and blend in completely with the dark water, wood, and soil substrates of the swamp. Schneider and Sharitz (1998) have shown

that the dominant tree species in the swamp disperse their seeds nonrandomly via water to emergent substrates. The hydrochory patterns of these considerably larger fruits would indeed lead to a nonrandom adult distribution to elevated microsites if they were the same for *Itea*. However, it is likely that *Itea* seed dispersal is much more highly affected by wind. In one study, *Itea* seeds were found in soil cores of both swamp and nearby bottomland hardwood communities (Schneider and Sharitz, 1986) even though *Itea* individuals are rarely found in the hardwood forests and the sampling techniques used were size-biased against finding *Itea* seeds. Because the seeds are so small, they potentially could travel and settle almost anywhere within the swamp, relaxing any patterns caused by hydrochory.

Placing seed dispersal aside and knowing that seed germination cannot account for adult distribution, we are left with the hypothesis that the location of adults in the field is a result of seedling establishment limitation. A shift in flooding tolerance likely occurs between the seedling and adult life stages. This hypothesis is strongly supported by our experimental differences in RGR between life stages: seedlings showed significantly less productivity under flooded conditions than adults. Additionally, there was some mortality for seedlings and negligible mortality for adults. Seedlings also visibly suffered more than adults: all plants in the high flood treatment became frail and limp, and plants in the waterlogged treatment withdrew their chlorophyll (i.e., turned reddish-purple in color) and dropped many of their leaves. The effects of flooding were not nearly as visibly dramatic for the adults.

Finally, it is worth considering whether seedlings performed worse under flooded conditions than adults due to their small size alone or due to some other intrinsic

characteristic. Interestingly, seedlings proved able to produce both enlarged lenticels and adventitious roots in response to flooding. Seedlings produced proportionally fewer enlarged lenticels than adults, which is expected since the amount of enlarged lenticels formed was a function of initial height above water for both life stages. Seedlings had much less stem available above water than adults and enlarged lenticels would serve no gas exchange purposes if submerged. However, seedlings produced proportionally more adventitious roots than adults, the growth of which was not correlated with height. Additionally, both adults and seedlings showed the same pattern for root:shoot ratio and treatment. These data suggest that there is nothing intrinsically different between juvenile and adult tissue that would prevent seedlings from growing on the flooded floor; seedling establishment limitation is most likely due to their small size.

## --CONCLUSIONS—

Although rarely documented in plants, it appears that a niche expansion in flooding tolerance does occur between the juvenile and adult life stages of *Itea*. Despite their ability to produce both enlarged lenticels and adventitious roots, seedlings were simply too small to withstand flooding; too much of their shoot material was submerged. Adults, however, were relatively unaffected by flooding. Flooding also had no effect on *Itea* seed germination. Thus, it is the needs of the seedling stage that restrict adult distribution in the field to sites elevated above the flood level. This information enhances our understanding of the regeneration niche of *Itea* and possibly of several other understory species that grow only on elevated microsites. Knowledge of how the flooding

regime of cypress-tupelo swamps affects understory plant communities is essential for

conservation and restoration of this important wetland system.

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