LATE-SEASON FLOODING REGIMES INFLUENCE THE ACCRETION AND PARTITIONING OF NITROGEN AND BIOMASS IN SILVER MAPLE SEEDLINGS

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ABSTRACT.—To better understand how late-season flooding affects survival, growth, N accretion, and N partitioning in silver maple, we subjected 1-year-old seedlings to continuous (July-November), summer (July-September), and fall (September-November) root-flooding regimes outdoors in plastic tanks. Only root growth was affected by flooding as root biomass measured in September and November was reduced in the summer and continuously flooded seedlings. Seedling N accretion was decreased only in the continuous flooding treatment. Fall flooding resulted in earlier resorption of foliar N and leaf abscission than in controls and recovering summer-flooded seedlings, thereby insuring conservation of foliar N under fall flood stress conditions. Our results indicate that silver maple seedlings can tolerate summer and fall flooding and reveal how silver maple seedlings grow, take up, and partition N as they adapt to flooding under altered hydrologic regimes.

Silver maple (*Acer saccharinum* L.) is the dominant bottomland hardwood species throughout much of the central Midwest (Bell 1974, Peterson and Bazzaz 1984, Dunn and Stearns 1987, Yin and others 1997, Nelson and Sparks 1998, Yin 1998). It commonly occurs in lowland areas in major river floodplains and at the edges of streams and lakes (Gabriel 1990). Silver maple not only is the dominant canopy tree species, but also makes up the largest proportion of the seedling and sapling classes in many areas, particularly in the upper Mississippi River floodplain north of St. Louis, Missouri (Yin and others 1997, Yin 1998).

Silver maple's ecological importance has greatly increased as natural hydrological regimes have been altered for river navigation, flood protection, and reservoir construction (Yin and others 1997, Nelson and Sparks 1998, Sparks and others 1998, Yin 1998). These alterations have resulted in flooding regimes that are irregular in seasonality, duration, and intensity. They also have led to an increase in the average annual low-water level, predisposing more bottomland areas to prolonged soil saturation at any time of the year (Yin and others 1997, Sparks and others 1998). At the same time that silver maple has increased in importance under the altered flooding regimes, woody species diversity in bottomland hardwood forests has declined in the region (Yin and others 1997, Nelson and Sparks 1998).

Silver maple's capacity to tolerate various flooding regimes probably is an important factor responsible for its increasing dominance (Bell 1974, 1980) under conditions in which it can be flooded during any month of the year. Yet no studies have examined the ability of silver maple to continue to grow and assimilate nitrogen when flooding occurs late into the growing season. Nor have the effects of late- season flooding regimes on the partitioning of biomass and nitrogen within maple seedlings been investigated. Seedling physiology is important in itself, without correlation to mature plant function, because of the need to understand the basis for seedling establishment, survival, and growth, all necessary prerequi-sites for recruitment of silver maple into larger size classes.

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A few controlled, greenhouse studies demonstrated that silver maple seedlings were able to survive either soil saturation or complete submergence for periods of 3 weeks to 2 months (Hosner 1960, Hosner and Boyce 1962, Loucks and Keen 1973). Peterson and Rolfe (1983) found that maple seedlings survived up to 40 days of complete submersion, but that biomass production, especially in the roots, was reduced more by a June flood than by an August flood. Peterson and Bazzaz (1984) reported that complete submersion was more injurious to growth than root-flooding of silver maple seedlings. Soil waterlogging for 2 months resulted in significantly reduced biomass production, particularly in the roots. Flooding of root systems for 1 month also reduced seedling photosynthetic rates, but the degree of reduction did not differ between a mid-May or a late August flood (Peterson and Bazzaz 1984).

In silver maple seedlings root-flooded for 2 months, the total shoot N content was twice that of controls (Hosner and Leaf 1962). However, root N content, initial and final seedling dry weights on a whole-plant basis, and the redox potential of the flooded system were not reported. Pezeshki and others (1999) contended that the degree of soil reduction in the flooded system must be taken into consideration in any study of flooding effects on woody plant nutrient uptake and allocation. Moreover, nitrogen is the most limiting nutrient in many wetland ecosystems (Ponnamperuma 1984). DeLaune and others (1998) stressed that information is needed on the dynamics of N uptake by wetland tree species to better predict their growth and survival under the hypoxic soil conditions imposed by flooding.

In order to better understand how growth, N accretion, and the partitioning of biomass and N in silver maple seedlings are affected by flooding when it occurs late in the growing season, we subjected 1-year-old seedlings of silver maple to summer and fall root-flooding regimes outdoors in tanks containing a nutrient solution. The summer flooding treatment began in early July and continued until early September. The fall flooding treatment was initiated in early September and ended in early November after a killing frost and when daily maximum air temperatures were less than the minima generally required for photosynthesis (Kozlowski and Pallardy 1997). A continuous flood treatment also was initiated in early July and continued through the end of the growing season in order to determine how a longer period of flood stress would impact silver maple's capacity to physiologically function. An unflooded set of maples was maintained as a control.

We hypothesized that relative to controls, flooding would affect the accretion and partitioning of biomass and nitrogen differently as the season progressed, but that silver maple would be able to survive all flooding treatments. To construct seasonal N budgets for silver maple, we assumed that all seedling N accretion was due to N uptake and that the influence of atmospheric N deposition was negligible [National Atmospheric Deposition Program (NRSP-3)/National Trends Network 2001]. The results of our study support the notion that silver maple is tolerant of flooding when it occurs late in the growing season and that the relatively minor effect that flooding had on its carbon and nitrogen economies, except when exposed to prolonged inundation, is a probable reason for its success under altered hydrologic regimes in bottomland ecosystems.

MATERIALS AND METHODS

One-year-old seedlings of silver maple from an Illinois seed source were obtained from a commercial nursery in April, 1999, and potted in 11.3-L plastic pots containing a 1:1:1 (v/v/v) mixture of vermiculite: calcined clay: sand. After a 1 month establishment period in a greenhouse, maple seedlings were transferred outdoors at the Plant Sciences Laboratory on the University of Illinois campus. Seedlings were then grown outdoors for 5 weeks before initiation of flooding treatments on July 1. Maples were arranged in a randomized block design with two blocks and were randomly assigned to one of four flooding treatments:

1) summer: maples flooded above the root collar with nutrient solution (see below) in 500-L plastic tanks from July 1 until September 5, and then allowed to recover;
2) fall: maples flooded from September 5 until November 10;
3) continuous: seedlings flooded from July 1 through November 10; and
4) unflooded control seedlings which were arranged randomly and adjacent to the flooded tanks and placed on saucers.

Within each block, maples in all treatments were randomly re-arranged every 2 weeks to minimize positional effects.

Each month the plastic tanks were drained and immediately refilled with one-quarter strength modified low-N Hoagland's solution (Hoagland and Arnon 1950) with nitrogen provided at a concentration of 14 ppm, similar to that reported previously for soil in a central Illinois silver maple stand (Peterson and Rolfe 1985). Compounds providing the macronutrients were supplied at the following concentrations (mg/L): K_2SO_4 - 109; $MgSO_4$ - 60; $Ca(H_2PO_4)_2.2H_2O$ - 63; $CaSO_4.2H_2O$ – 86; NH_4Cl - 47. N was supplied as ammonium-N only because it is the form of N that is available in flooded systems due to denitrification of nitrate (Whitlow and Harris 1979, Day 1987). Micronutrients were supplied at one-half strength (Hoagland and Arnon 1950). Unflooded control seedlings were watered daily with distilled water and leached with the same low-N Hoagland's solution every 2 weeks. There was a higher frequency of nutrient solution change for the unflooded maples. This was warranted by the lower total nutrient amount supplied to each unflooded plant in an 11.3-L pot relative to those in the 500-L flooded tanks.

Weekly measurements of solution pH were made for the tanks. At the time of each monthly nutrient solution replacement, the initial solution pH averaged 6.2 ± 0.1 and the pH stabilized at 7.1 ± 0.2 within 1 to 2 weeks after recharging. The redox potential (Eh) of soil in flooded pots was measured periodically with a platinum electrode (Orion Research Inc., Beverly, MA, USA) to verify that a hypoxic system had been established (i.e., Eh ≤ 350 mV, the redox potential at which molecular oxygen is negligible). The Eh of flooded pots averaged 288 ± 32 mV following the addition of 244 mV as an adjustment to a standard hydrogen electrode.

An initial whole-plant harvest of 15 seedlings was conducted on July 1. Subsequent harvests were made on August 4, September 5, October 7, and November 10, for four seedlings (two per block) per treatment. All harvested plants were sorted into leaves, stems, and roots, dried to constant mass at 80° C, and weighed. Tissue samples were ground to 40-mesh in a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) and approximately 50 mg of tissue from each sample was acid digested (Cataldo and others 1974). All plant nitrogen was reduced to ammonium-N and total Kjeldahl nitrogen was subsequently measured as ammonium-N colorimetrically on a spectrophotometer at 625 nm (Cataldo and others 1974).

The location of the study site on the campus of the University of Illinois at Urbana-Champaign (40° 07' N, 88° 12' W) has a temperate continental climate typified by cold, dry winters and warm, moist summers with 104 cm of precipitation and 185 frost-free days per year (Illinois State Water Survey, Champaign, Illinois). The mean summer (June - August) daily high temperature is 28° C with a mean daily low of 17° C. Mean winter (December - February) temperatures range from a daily high of 2° C to a daily low of –6° C. The total precipitation for the period of July through the end of October 1999 was 33.0 cm, slightly drier than the 30-year average of 38.3 cm for the same period. Daily maximum and minimum temperatures were used to determine monthly averages for air, the nutrient solution in a plastic tank, and for the soil in an unflooded pot at the study location (table 1).

Means and variances of dependent variables were determined for all treatments at each harvest. A common mean for each dependent variable was reported for the initial, pre-flood harvest in July. Preliminary analyses revealed no differences between blocks and this source of variation was removed from the analysis, yielding four replicates for each treatment at each harvest. All data analyses were conducted with Systat, version 9 (Systat, SPSS Science, Chicago, IL). Biomass and nitrogen content data were natural log transformed and analyzed by one-way analysis of variance separately at each harvest with flooding treatment as the independent variable. Nitrogen ratios (organ N content:seedling N content) were arcsine

Table 1.—*Mean daily maximum and minimum temperatures (°C) for each month from July through October at the study site. Nutrient solution temperatures were measured in a 500-L plastic tank and soil temperatures were taken in a pot containing an unflooded control seedling.*

	Air		Nutrient solution		Soil	
Month	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum
July	33.4	20.8	32.1	23.7	39.8	21.7
August	32.7	17.3	29.8	20.6	35.7	17.6
September	26.2	12.9	24.4	16.0	30.8	13.6
October	19.4	7.9	14.6	10.0	17.3	7.9

transformed. If the overall F test within a particular harvest was significant (P ≤ 0.05), a Fisher's protected LSD was used to compare treatment means. At a given harvest, treatment means were reported as significantly different in the results when P ≤ 0.05.

RESULTS

Survival and Flood-Induced Morphological Characteristics

Maple seedlings in every flooding treatment had 100 percent survival through the end of the growing season. All non-harvested seedlings resumed growth the following spring. Maples flooded during the summer period displayed hypertrophied lenticels on submerged portions of the stems. However, only two summer-flooded seedlings developed any noticeable adventitious roots on the stem. No fall-flooded maples developed hypertrophied lenticels. Root systems in all flooded treatments had substantial necrosis of both coarse and fine roots, but newly produced adventitious flood roots were visible on all flooded root systems. These roots were white and generally had little branching.

Leaves of summer-flooded maples turned red during the first 3 weeks of flooding, most likely due to anthocyanin production. Upon recovery in the fall, the same leaves on these seedlings became green again. The leaves of fall-flooded maples became red during the first 2 weeks of fall flooding and dropped by October 20. In the continuous flood treatment, leaves turned red during the first 3 weeks of summer flooding, began to abscise during September, and were completely abscised by October 20. Summer-flooded seedlings and unflooded controls had lost all their leaves by the end of the first week in November.

Seedling Growth and Biomass Partitioning

Flooding had little effect on seedling growth throughout most of the study. Mean whole-seedling biomass for each flooding regime did not differ significantly from unflooded controls except at the November harvest (fig. 1). In November, the mean seedling biomass of maples that had been continuously flooded since July was significantly less than the means for all other treatments. Seedling biomass of summer-flooded maples was significantly less than that of controls in November. The mean biomass of fall-flooded plants was not significantly different from the unflooded control means at any harvest.

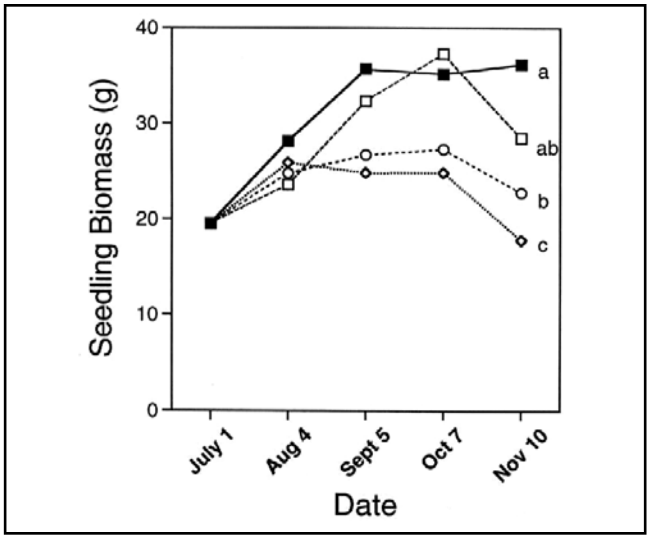

Figure 1.—*Mean whole-seedling biomass (g dry weight) for treatments at each harvest. Treatment means are denoted by black boxes for controls, diamonds for continuous flooding, circles for summer flooding, and open boxes for fall flooding (N=4 for all treatment means). An initial harvest of 15 seedlings was conducted on July 1. The starting dates for the summer and fall flood periods were July 1 and September 5, respectively. Treatment means within an individual harvest not sharing common letters were significantly different (P ≤ 0.05).*

Flooding did not affect the partitioning of biomass among leaves, stems, and roots throughout most of the study. Neither leaf nor stem biomass of any flooded treatment differed significantly from that of unflooded controls at any harvest (figs. 2a, 2b). At the September and November harvests, mean root biomass of the summer and continuously flooded maples was significantly less than that of controls. The continuously flooded seedlings did not display a net increase in root mass during the fall period (fig. 2c). Root biomass of maples in the fall flooding treatment did not differ significantly from that of controls. In unflooded controls, the biomass of woody tissues increased by 102 percent during the summer period and by 24 percent in the fall.

Nitrogen Accretion and Partitioning

A significant effect of flooding on whole-seedling N content was not evident until the November harvest. Mean seedling N content of the continuously flooded treatment was significantly less than that of controls (fig. 3). At the October harvest, mean leaf N content of both the continuous and fall flooding treatments were significantly lower than those of the controls

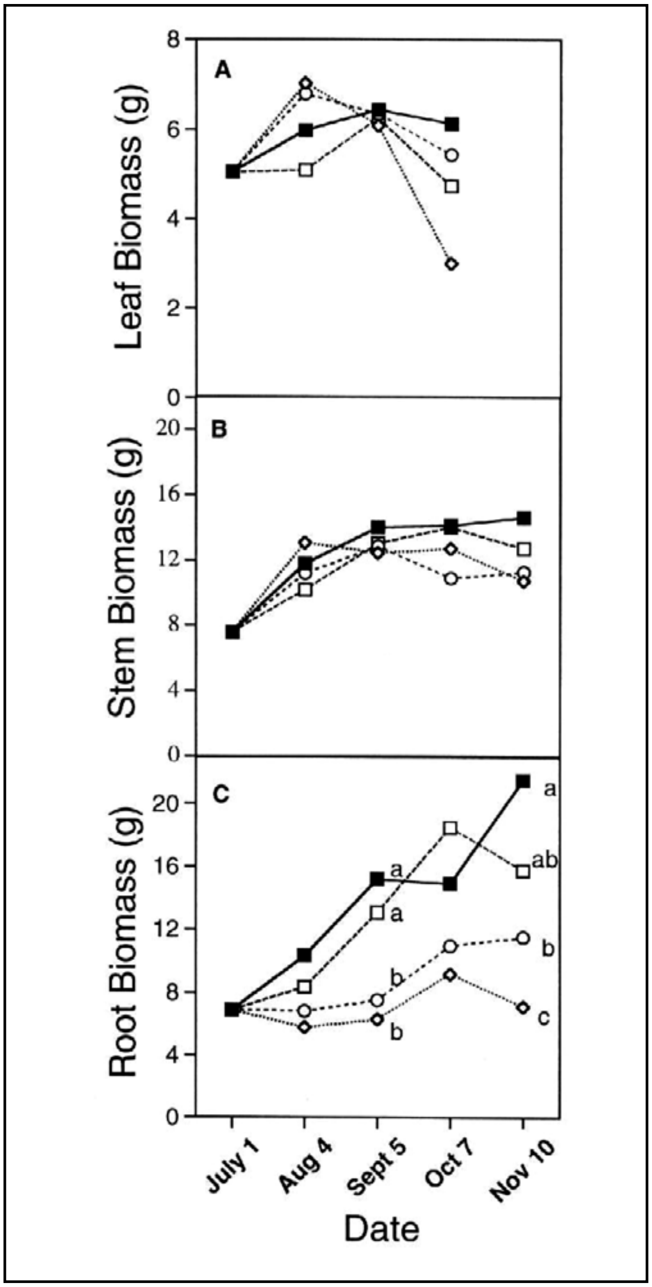

Figure 2.—*A. Mean leaf, B. stem, and C. root biomass (g dry weight) for treatments at each harvest. See figure 1 caption for explanation of symbols. Leaf masses are not included for the November harvest due to complete leaf abscission for all treatments prior to that harvest.*

and summer flooding treatment (fig. 4a). Significant differences in stem N content occurred only for the October harvest. Mean stem N content of the fall-flooded treatment was significantly greater than those of the unflooded controls and the summer flood treatment (fig. 4b). The stem N content of the fall-flooded maples also exhibited a steep upward trend during the first month of fall flooding. Mean root N content was not significantly reduced by flooding until the November harvest (fig. 4c).

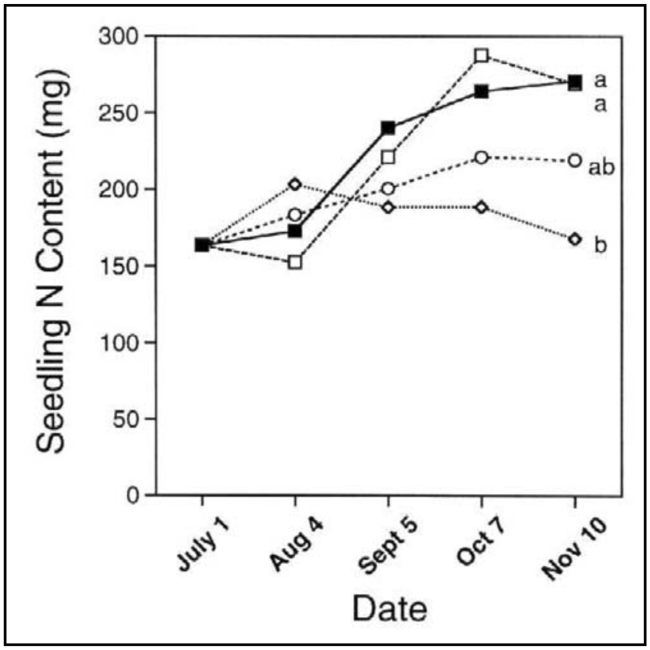

Figure 3.—*Mean whole-seedling N content (mg N) for treatments at each harvest. See figure 1 caption for explanation of symbols.*

Net fall N accretion in woody tissues was substantial among all treatments except for the continuously flooded maples. Woody tissue N content of controls increased by 87 percent in the fall. In the summer and fall-flooded seedlings, woody tissue N content increased by 60 and 95 percent, respectively, during the fall period. The ratio of N partitioned to leaves versus woody tissues was affected by flooding early in the fall flooding period. The proportion of seedling N in leaves (leaf N content:seedling N content) decreased considerably during the first month of the fall period in the continuous and fall-flooded treatments (fig. 5a). At the October harvest, the proportion of seedling N in leaves was significantly less for the continuous and fall flood treatments relative to that of the unflooded controls and summer-flooded seedlings. During the first month of the fall flood period, the proportion of seedling N in woody tissues (woody tissue N content:seedling N content) increased sharply in the continuous and fall flooded treatments (fig. 5b). In October, the proportion of seedling N in woody tissues was significantly greater for the continuous and fall flooding treatments relative to the summer-flooded maples and unflooded controls.

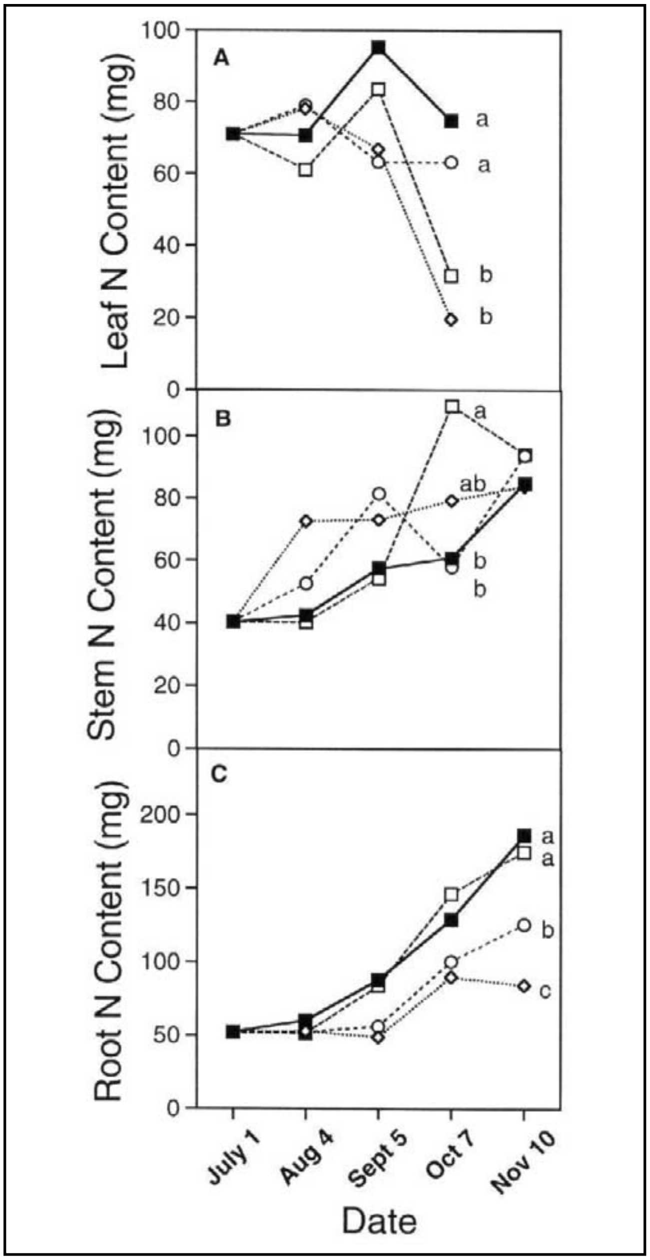

Figure 4.—*A. Mean leaf, B. stem, and C. root N contents (mg N) for treatments at each harvest. See figure 1 caption for explanation of symbols. Leaf N contents are not included for the November harvest due to complete leaf abscission for all treatments prior to that harvest.*

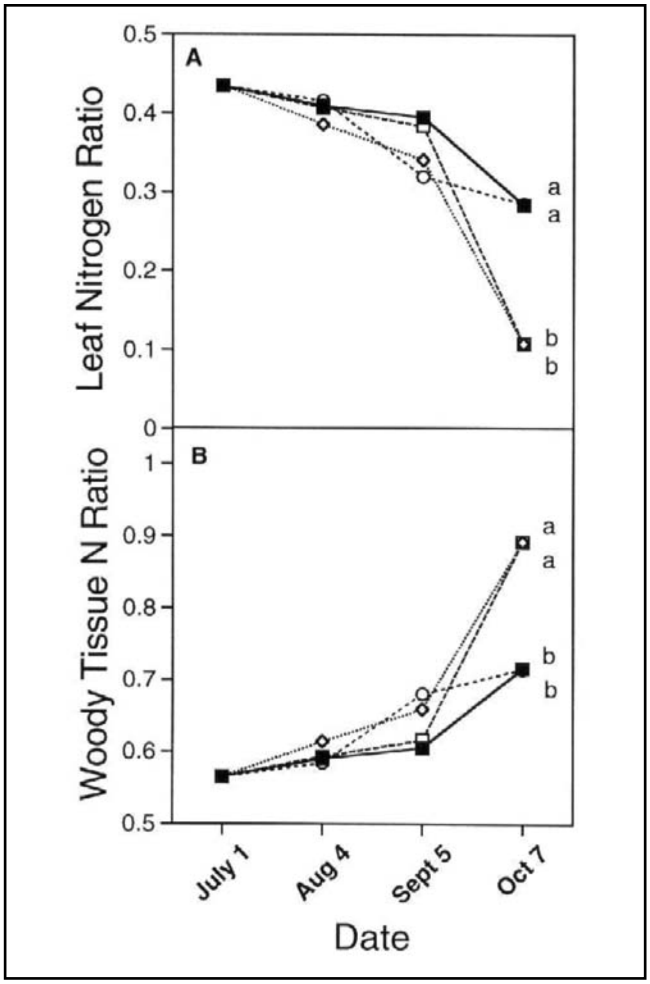

Figure 5.—*A. Mean leaf nitrogen ratio (mg leaf N content:mg seedling N content) and B. mean woody tissue nitrogen ratio (mg woody tissue N content:mg seedling N content) for treatments at each harvest. See figure 1 caption for explanation of symbols. Treatment means within an individual harvest not sharing common letters were significantly different ($P \leq 0.05$). Nitrogen ratios are not included for the November harvest due to complete leaf abscission for all treatments prior to that harvest.*

DISCUSSION

Survival and Flood-Induced Morphological Characteristics

At the outset of this study, we hypothesized that 1-year-old silver maple seedlings would be able to survive summer and fall flooding, but that accretion and partitioning of biomass and nitrogen would differ according to flooding regime. In partial support of our hypothesis, 1-year-old silver maple seedlings were able to completely survive not only summer and fall root-flooding regimes, but also continuous flooding from July through November. Our results for survival are in accordance with previous reports of no mortality for silver maple seedlings exposed to root-flooding or complete submersion for periods of 3 weeks to 2 months (Hosner 1960, Hosner and Boyce 1962, Loucks and Keen 1973, Peterson and Rolfe 1983, Peterson and Bazzaz 1984). The flood-induced hypertrophy of lenticels that we observed in the summer and continuous flooding treatments has been noted by others for silver maple (Hosner and Boyce 1962, Peterson and Rolfe 1983).

However, the lack of development of hypertrophied lenticels in our fall flooding treatment is noteworthy in that it suggests that, when flooded in early fall, silver maple may begin senescence processes prematurely and may not allocate resources to structures that would promote late-season growth. The development of hypertrophied lenticels has been documented as a mechanism by which flood-tolerant species transport atmospheric oxygen to their roots, enabling aerobic root metabolism to continue during flooding (Hook 1984, Kozlowski 1997). This internal transport of atmospheric oxygen may also lead to oxidation of the rhizosphere, thereby decreasing potentially toxic compounds that may develop under flooded conditions.

The flood-stress-induced early abscission of leaves is further evidence that fall flooding may lead to a premature initiation of normal fall senescence processes in silver maple. Leaf abscission in the continuous flooding treatment began in September while that of the fall flooding treatment started in early October. Leaves of plants in both these treatments were completely abscised approximately 3 weeks earlier than those of controls and summer-flooded maples, precluding carbon gain via photosynthesis. In addition, the leaves of the continuously, summer, and fall-flooded maples all turned red during the first 3 weeks of their respective flood treatments, most likely due to chlorophyll loss and anthocyanin production.

Rapid anthocyanin production in leaves may reflect an osmotic adjustment to avoid water stress (Chalker-Scott 1999), but most of the literature on this topic indicates that flood-tolerant woody plants generally do not develop reduced leaf water potentials when flooded (Kozlowski 1997). Anthocyanin production occurs when excess sugars accumulate due to slowing of sugar export via phloem. Flooding of roots can result in stomatal closure (Kozlowski 1997) and reduced phloem transport. However, anthocyanins produced in leaves under stress may also protect the photosynthetic apparatus against light-induced photo-oxidation (Chalker-Scott 1999). In addition to the seedlings in our study, flood-induced anthocyanin production has been noted in silver maple seedlings in floodplain ecosystems (C.M. Kaelke and J.O. Dawson, personal observations). The adaptive significance of this flood stress response in silver maple warrants further investigation.

Seedling Growth and Biomass Partitioning

We did not expect that late-season flooding would so minimally reduce biomass production. This finding may derive from the fact that much of the current year's new biomass had most likely been accreted before the outset of the study in July (Peterson and Rolfe 1983). Hosner and Leaf (1962) reported that after 62 days of soil saturation, shoot biomass of flooded silver maple seedlings was actually 32 percent greater than controls, but they did not report root biomass. In our study, seedling biomass after leaf drop was lowest in the continuous flooding treatment. This result supports the contention of Peterson and Bazzaz (1984) that flood duration is a major factor affecting physiological function in silver maple.

Yet, also in support of our hypothesis, our study suggested a seasonal factor that may influence silver maple biomass production. In November, the seedling biomass of summer-flooded plants was also significantly reduced relative to unflooded controls. Thus, flooding during the summer did result in a growth reduction that became apparent at the end of the growing season. The pattern of significance for root biomass among the treatments in November was the same as for whole-seedling biomass. Because leaves were completely abscised by the November harvest and stem biomass did not differ among the treatments, this indicates that flood-induced reductions in whole-seedling biomass by the end of the growing season were largely due to reductions in root growth. A decrease in root growth was not apparent in the fall-flooded seedlings. Both Peterson and Rolfe (1983) and Peterson and Bazzaz (1984) found the greatest biomass reduction in silver maple seedlings to be in the flooded roots. In our study, 4 months of continuous root-flooding resulted in no net increase of root biomass during the fall period, most likely due to sloughing of dead root tissues and depletion of nonstructural carbohydrate reserves.

Nitrogen Accretion and Partitioning

An effect of late-season flooding on seedling N content was not evident until November. In the continuously flooded treatment, both whole-seedling and root N content in November were reduced relative to controls. Because treatment differences did not exist for stems in November and leaves had already abscised, the flood-induced reduction in whole-seedling N content was due to reduced root N content. The significantly lower root N content was largely attributable to the lack of increase in root biomass in the continuously flooded maples during the fall. Therefore, at the end of the growing season, only seedlings that had been flooded continuously for 4 months had reduced seedling N content relative to controls, again underscoring the tolerance of silver maple seedlings to all but the most prolonged flooding regime. Hosner and Leaf (1962) found that shoot N contents of silver maple seedlings grown in saturated soil for 60 days were twice that of controls. Although they did not report root N contents or soil redox potential of their system, their results also are suggestive of silver maple's ability to continue N uptake under the reduced conditions of flooded soils.

Even though the summer and fall-flooded seedlings did not exhibit significantly lower seedling N contents than controls in November, the processes by which they arrived at similar N contents probably differed. During the first month of the fall flooding period, seedlings in both the continuous and fall-flooded treatments exhibited a precipitous decline in leaf N content. In the fall-flooded maples, this decline occurred without appreciable leaf drop whereas in the continuous flooding treatment, the decline was associated with leaf drop. Maples in the summer flooding treatment and the unflooded controls did not experience such a drop in leaf N content until the final month of the study.

At the same time that leaf N content was rapidly declining in the continuous and fall flooding treatments, stem N content increased in the fall-flooded maples. Because there was no leaf drop during the first month of fall flooding when much of the rapid decrease in leaf N occurred (fig. 4a), the foliar N decline in the fall-flooded seedlings was apparently due to flood-induced early resorption of foliar N prior to leaf abscission. The concurrent rapid decrease in leaf nitrogen ratio with a rapid increase in woody tissue N ratio during the first month of fall flooding (figs. 5a, 5b) indicates the occurrence of fall flood-induced foliar N resorption at a rate of efficiency of 62 percent [(September leaf N content - October leaf N content)/ September leaf N content]. Thus, fall flooding may induce early N resorption that could promote resumption of growth the following spring (Kozlowski and Pallardy 1997). The expedited resorption of N insures seedling N conservation with flood-induced early leaf senescence. These results support our hypothesis that N accretion and partitioning would be affected differently by flooding as the growing season progressed.

The potential N resorption pool (September foliar N) as a proportion of total net fall N accretion in woody tissue was similar among treatments (i.e., 76, 77, and 64 percent in the controls, summer-flooded, and fall-flooded maples, respectively). Although both environmental and genetic factors can determine resorption efficiencies, genetic factors seem to be more important for temperate deciduous trees (Vogel and Dawson 1993). Estimated resorption efficiencies for temperate deciduous trees range from 25 to 66 percent (Kozlowski and Pallardy 1997). Based on the high proportional value of N in the potential resorption pool to total N accretion in woody tissue in the fall and the likely range of resorption efficiencies, we conclude that N conservation is substantial in both flooded and unflooded maples.

CONCLUSION AND IMPLICATIONS

Our study demonstrated that silver maple seedlings survived, grew, accumulated N, and therefore, were tolerant of flooding in both summer and fall, but especially in the fall. Fall flooding expedited normal fall senescence processes including resorption of foliar N. Continuous flooding for the final 4 months of the growing season apparently hinders silver maple's capacity to set aside carbohydrate and mineral nutrient reserves to resume vigorous growth at the start of the following growing season. The results of our study suggest that under altered hydrologic regimes, silver maple could maintain seedling establishment, survival, growth, and N accretion better than many sympatric tree species rated as less flood-tolerant (Gill 1970, Whitlow and Harris 1979).

If the management goal is for greater woody species diversity in the bottomlands, then carefully planned measures, such as flood control and creation of floodplain mounds with dredge spoil, to promote growth of species less flood tolerant would be necessary. On the other hand, silver maple has shown promise as a rapidly growing hardwood species suitable for biomass fuel production on marginal lands (Geyer 1989, Walter and Dwyer 2003). Silver maple's versatility in surviving flooding in bottomlands may render it a desirable species for plantings intended to reduce flood damage in riparian corridors (Walter and Dwyer 2003). The capacity to continue accretion rates similar to unflooded seedlings and to favorably alter partitioning of biomass and N during various root-flooding regimes probably are important reasons for silver maple's increasing dominance in midwestern floodplain forests.

LITERATURE CITED

Bell, D.T. 1974. Tree stratum composition and distribution in the streamside forest. American Midland Naturalist. 92(1): 35-46.

Bell, D.T. 1980. Gradient trends in the streamside forest of central Illinois. Bulletin of the Torrey Botanical Club. 107(2): 172-180.

Cataldo, D.A.; Schrader, L.E.; Youngs, V.L. 1974. Analysis by digestion and colorimetric assay of total N in plant tissues high in nitrate. Crop Science. 14: 845-856.

Chalker-Scott, L. 1999. Environmental significance of anthocyanins in plant stress responses. Photochemistry and Photobiology. 70(1): 1-9.

Day, F.P. 1987. Effects of flooding and nutrient enrichment on biomass allocation in *Acer rubrum* seedlings. American Journal of Botany. 74(10): 1541-1554.

DeLaune, R.D.; Pezeshki, S.R.; Lindau, C.W. 1998. Influence of soil redox potential on nitrogen uptake and growth of wetland oak seedlings. Journal of Plant Nutrition. 21(4): 757-768.

Dunn, C.P.; Stearns, F. 1987. A comparison of vegetation and soils in floodplain and basin forested wetlands of southeastern Wisconsin. American Midland Naturalist. 118(2): 375-384.

Gabriel, W.J. 1990. *Acer saccharinum* L. Silver maple. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America, Vol. 2: Hardwoods. Agric. Handb. 654. Washington, DC: U.S. Depart-ment of Agriculture, Forest Service: 70-77.

Geyer, W.A. 1989. Biomass yield potential of short-rotation hardwoods in the Great Plains. Biomass. 20: 167-175.

Gill, C.J. 1970. The flooding tolerance of woody species—a review. Forestry Abstracts. 31: 671-688.

Hoagland, D.R.; Arnon, D.I. 1950. The water-culture method for growing plants without soil. Circ. No. 347. California Experiment Station.

Hook, D.D. 1984. Adaptations to flooding with fresh water. In: Kozlowski, T.T., ed. Flooding and plant growth. San Diego, CA: Academic Press: 265-343.

Hosner, J.F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. Forest Science. 6: 246-251.

Hosner, J.F.; Boyce, S.G. 1962. Tolerance to water saturated soil of various bottomland hardwoods. Forest Science. 8: 180-186.

Hosner, J.F.; Leaf, A.L. 1962. The effect of soil saturation upon the dry weight, ash content, and nutrient absorption of various bottomland tree seedlings. Soil Science Society of America Proceedings. 26: 401-404.

Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. Tree Physiology Monograph. 1: 1-29.

Kozlowski, T.T.; Pallardy, S.G. 1997. Growth control in woody plants. San Diego, CA: Academic Press. 411 p.

Loucks, W.L.; Keen, R.A. 1973. Submersion tolerance of selected seedling trees. Journal of Forestry. 71: 496-497.

National Atmospheric Deposition Program (NRSP-3)/National Trends Network. 2001. NADP Program Office, Illinois State Water Survey, 2204 Griffith Drive, Champaign, IL. [online]. Available: http://nadp.sws.uiuc.edu.

Nelson, J.C.; Sparks, R.E. 1998. Forest compositional change at the confluence of the Illinois and Mississippi Rivers. Transactions of the Illinois Academy of Science. 91(1-2): 33-46.

Peterson, D.L.; Bazzaz, F.A. 1984. Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) seedlings to flooding. American Midland Naturalist. 112(2): 261-272.

Peterson, D.L.; Rolfe, G.L. 1983. Effects of flooding on silver maple (*Acer saccharinum* L.) and American sycamore (*Platanus occidentalis* L.) seedlings: implications for biomass production. Transactions of the Illinois Academy of Science. 76(1-2): 91-102.

Peterson, D.L.; Rolfe, G.L. 1985. Temporal variation in nutrient status of a floodplain forest soil. Forest Ecology and Management. 12: 73-82.

Pezeshki, S.R.; DeLaune, R.D.; Anderson, P.H. 1999. Effect of flooding on elemental uptake and biomass allocation in seedlings of three bottomland tree species. Journal of Plant Nutrition. 22(9): 1481-1494.

Ponnamperuma, F.N. 1984. Effects of flooding on soils. In: Kozlowski, T.T., ed. Flooding and plant growth. San Diego, CA: Academic Press: 9-45.

Sparks, R.E.; Nelson, J.C.; Yin, Y. 1998. Naturalization of the flood regime in regulated rivers: the case of the upper Mississippi River. BioScience. 48(9): 706-720.

Vogel, C.S.; Dawson, J.O. 1993. Changes in tissue nitrogen and phosphorus and foliar free amino acids in autumn olive, black locust, American sycamore, and honey locust during autumn. Canadian Journal of Forest Research. 23: 665-672.

Walter, W.D.; Dwyer, J.P. 2003. Survival results of a biomass planting in the Missouri River floodplain. In: Van Sambeek, J.W.; Dawson, J.O.; Ponder, F., Jr.; Lowenstein, E.F.; Fralish, J.S., eds. Proceedings, 13th Central Hardwood Forest conference; 2002 April 1-3; Urbana, IL. Gen. Tech. Rep. NC-234. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station: 177-185.

Whitlow, T.H.; Harris, R.W. 1979. Flood tolerance in plants: a state of the art review. Tech. Rep. E-79-2. Vicksburg, MS: U.S. Army Corps of Engineers, Waterways Experiment Station Environmental Laboratory.

Yin, Y. 1998. Flooding and forest succession in a modified stretch along the upper Mississippi River. Regulated Rivers: Research and Management. 14: 217-225.

Yin, Y.; Nelson, J.C.; Lubinski, K.S. 1997. Bottomland hardwood forests along the upper Mississippi River. Natural Areas Journal. 17(2): 164-173.