Photosynthetic and Growth Responses of Silver Maple (Acer saccharinum L.) Seedlings to Flooding

DAVID L. PETERSON[1]

and

F. A. BAZZAZ

Departments of Plant Biology and Forestry, University of Illinois, Urbana 61801

ABSTRACT: Flooding affected several growth parameters of silver maple (*Acer saccharinum* L.) seedlings. Root biomass and leaf area were sharply reduced. Photosynthetic rates of recently germinated seedlings decreased significantly after 21 days of root-flooding and after only 3 days of submersion. In some treatments, reduced net photosynthesis/transpiration ratios after flooding indicated a decline in water use efficiency. Seedlings submersed in water containing suspended sediments had lower rates of photosynthesis than plants submersed in clear water. The timing of flooding treatments (spring vs. late summer) had no apparent effect on the pattern of decline in net photosynthesis. Two-year-old seedlings had a greater capacity for net photosynthesis after flooding than recently germinated seedlings, suggesting that recovery of normal physiological function after flooding is an important survival feature of older silver maple seedlings. Light conditions had minimal effect on seedling growth and photosynthesis. Seedlings had relatively high rates of photosynthesis over a broad range of photosynthetically active photon flux density and developed a "shade leaf" morphology when grown at low light intensity. Duration of flooding is the most important characteristic of the flood cycle affecting the survival and establishment of silver maple seedlings in floodplain habitats.

INTRODUCTION

Silver maple (*Acer saccharinum* L.) is widely distributed throughout the eastern United States. It occurs chiefly on floodplains and on the moist sites of creek bottoms, and is the dominant species in many floodplain communities in the Midwest (Bell, 1974; Franz and Bazzaz, 1977). Silver maple develops best in well-drained, moist soils (Fowells, 1965), and is extremely tolerant of flooding (Hosner, 1960; Teskey and Hinckley, 1977b). Seedlings experience periodic flooding which normally occurs during spring or summer in the Midwest. Furthermore, floodwaters vary considerably in their sediment and nutrient loads, especially in watersheds that drain agricultural fields (Peterson and Rolfe, 1982b).

It is critical that silver maple and other bottomland species have the ability to withstand periodic flooding. Excess water in flooded soils displaces air from the pore space, and the resulting poor aeration increases root resistance to water uptake (Kramer and Kozlowski, 1979). An early physiological response to flooding is stomatal closure (Regehr *et al.*, 1975; Pereira and Kozlowski, 1977), which prevents loss of leaf turgor in the absence of water uptake. Some species develop adventitious roots and hypertrophied lenticels in response to prolonged flooding (Keeley, 1979), and stomata reopen as water uptake is initiated (Kozlowski and Pallardy, 1979). Additional environmental factors, such as night temperature, have been shown to affect stomatal resistance and net photosynthesis in some bottomland tree species (Drew and Bazzaz, 1979).

The present study was initiated to determine growth and physiological responses of silver maple seedlings to flooding. Patterns of net photosynthesis and transpiration were measured for seedlings subjected to root-flooding and total submersion. Both

[1] Present address: U.S. Forest Service, Riverside Fire Laboratory, 4955 Canyon Crest Drive, Riverside, California 92507.

levels of flooding are commonly observed in floodplain environments and may have different physiological effects on tree seedlings. Periods of flooding of up to 40 days were used. Since silver maple germinates in full sunlight or shade, the effect of different light regimes on flooded plants was investigated. The capacity for photosynthetic recovery following cessation of flooding was determined, and physiological response was assessed with respect to survival and growth of silver maple seedlings in the floodplain environment.

MATERIALS AND METHODS

Growth Analysis. — Silver maple seedlings were germinated in April 1978 from seeds collected in the floodplain forest at Robert Allerton Park near Monticello, Illinois. In June 1978, 100 8-week-old seedlings were transplanted from flats to clay pots, 15 cm diam x 18 cm deep, and were placed in full sunlight for 1 week before beginning the treatments. Potting soil used for all phases of this study was composed of 3 parts silt loam field soil, 1 part sand, 1 part peat moss and 1 part "Perlite." Forty individuals served as nonflooded full sunlight controls. Ten individuals were given a nonflooded shade treatment, and 40 were given a full sunlight-flooded treatment. Flooded plants were placed in a polyethylene-lined tank with water to 4 cm above the soil level in the pots (root-flooding). Continuous water movement was maintained in the flooding treatment with a circulating pump. Nonflooded plants were watered as necessary to keep soil moist but not waterlogged. The remaining 10 plants were used for the initial harvest.

Ten individuals from the control and 10 from the flooded treatment were harvested at 2-week intervals. Nonflooded plants grown in the shade were included in the final harvest. After stem height was measured, harvested seedlings were separated into leaves, stems and roots. The number of leaves per plant was counted, and leaf area per plant was measured with a leaf area meter. Plant tissue was oven-dried at 80 C for 48 hr prior to weighing the leaves, stems and roots.

Determination of light saturation curve and leaf with maximum photosynthetic rate. — Physiological response of silver maple to various treatments was determined with a semiclosed infrared gas analysis system which measures apparent CO_2 uptake (net photosynthesis) and transpiration (Bazzaz and Boyer, 1972). All measurements were made at an air temperature of 25 C, relative humidity 50%, and CO_2 concentration of 310-330 ppm.

Photosynthesis and transpiration were measured for a range of photosynthetically active photon flux density (PPFD) levels in August 1979 for silver maple individuals which were germinated in: (1) April 1978 (1 year old) and (2) April 1979 (2 months old). PPFD levels of 0, 200, 400, 600, 900, 1600, 2200 and 2500 μmol m^{-2} sec^{-1} were used. Measurements were recorded for fully developed leaves chosen randomly from the upper three nodes of each plant, with three replications within each of the two seedling groups.

To evaluate the variation observed in photosynthetic rates of leaves at various positions along the stem, photosynthetic response was determined for leaves at several nodes. Photosynthesis and transpiration were measured at 1600 μmol m^{-2} sec^{-1} for 1-year-old plants, with three replications per node. Measurements were taken for one leaf at each node (not including the uppermost undeveloped leaves), and nodes were numbered in order from 1-7 down the stem. The node at which maximum photosynthesis was measured was used for all subsequent measurements.

Response to temporal variation in flooding. — The effect of spring and late summer flooding on photosynthesis and transpiration was investigated in 3-month-old and 1-year-old silver maple seedlings. Spring treatments were initiated in mid-May, and late summer treatments were initiated for another group of plants in late August. All plants were grown in full sunlight, and controls were maintained for each treatment. There were 10 individuals in each treatment and control group. Following initial measurements of photosynthesis and transpiration, treatment plants were placed in tanks and flooded with circulating water to 4 cm above the soil level (root-flooding). Treatment plants were flooded continuously for 4 weeks and were removed briefly at 1-week intervals to measure net photosynthesis and transpiration. Measurements were made at 1600 μmol m^{-2} sec^{-1} on four plants chosen randomly from each age class.

Response to variation in light and flooding conditions. — Because the floodplain environment may be patchy with respect to light levels, we investigated the combined effects of different light regimes and flooding conditions on net photosynthesis and transpiration in 1-month-old silver maple seedlings. Flooding treatments were initiated in late April 1979. Ten plants per treatment were completely submersed in clear water or in water containing suspended silt loam. Plants were submersed for a 40-day period in continuously circulating water. Each set of flooding conditions was maintained in full sunlight or in shade (5% full sunlight). Nonsubmersed controls were situated in full sunlight and in shade. Net photosynthesis and transpiration were measured after 10 days of submersion, with four replications per treatment and control. Submersed seedlings were returned to flooding tanks, and measurements were repeated after 20, 30 and 40 days of submersion.

Recovery of photosynthesis and transpiration after submersion. — Patterns of photosynthesis and transpiration following the cessation of flooding treatments were determined for 2-month-old and 2-year-old silver maple seedlings. In May 1980, 40 individuals which had germinated in spring 1978 were collected from the floodplain forest at Allerton Park and transplanted to clay pots. Forty new seedlings were germinated from seed collected from Allerton Park in 1980. Plants were grown in a shadehouse (80% full sunlight), and flooding treatments were initiated during the 1st week of July. Thirty individuals from each age class were placed in tanks and submersed with continuously circulating water. Ten plants from each age class were used as control groups. Ten plants of each age were removed from the tanks after 3, 11 and 21 days of submersion and were watered as necessary thereafter to keep the soil moist but not waterlogged. Net photosynthesis and transpiration were measured for treatment and control plants 1, 7 and 14 days after removal from the tanks. Five plants were randomly chosen from treatment and control groups for physiological measurements.

STATISTICAL ANALYSIS

Differences between means were tested with a t-test when two means were compared and with analysis of variance and Duncan's multiple range test when three or more means were compared. Multiple regression analysis was used to analyze data from the study on response to variation in light and flooding conditions in order to identify variables and interactions which had a significant impact on physiological response. Multiple regression models were used incorporating variables for: (1) light condition (X_1), which was sun or shade; (2) submersion condition (X_2), which was nonsubmersed, submersed with clear water, or submersed with muddy water, and (3) duration of submersion (X_3), which was 10, 20, 30 or 40 days. The models were of the form:

$Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + B_4X_1X_2 + B_5X_1X_3 + B_6X_2X_3 + B_7X_1X_2X_3$, where Y was net photosynthetic or transpiration rate.

RESULTS AND DISCUSSION

GROWTH ANALYSIS

Silver maple seedlings that were root-flooded grew significantly less than nonflooded seedlings in height, number of leaves, leaf weight, stem weight, root weight and total weight (Fig. 1). Decrease in root weight was especially large and resulted in widely disparate shoot/root ratios. Growth was minimal in flooded plants after the 2nd week of flooding, and there were significant increases in only stem weight and total weight. Reduced growth caused by root-flooding has been reported for numerous bottomland tree species. Only those species which have special morphological and physiochemical tolerance mechanisms, such as water tupelo (*Nyssa aquatica* L). and bald cypress (*Taxodium distichum* (L.) Rich.), have shown increased growth during root-flooding (Teskey and Hinckley, 1977a).

Root growth of silver maple seedlings was significantly reduced in the shade treatment. Seedlings grown in the shade had significantly larger leaf area than those grown in full sunlight, although there was no significant difference in leaf weight. This higher leaf area/leaf weight ratio is typical of "shade leaf" morphology (Björkman and Holmgren, 1963).

Light had a significant effect on the early development of silver maple seedlings,

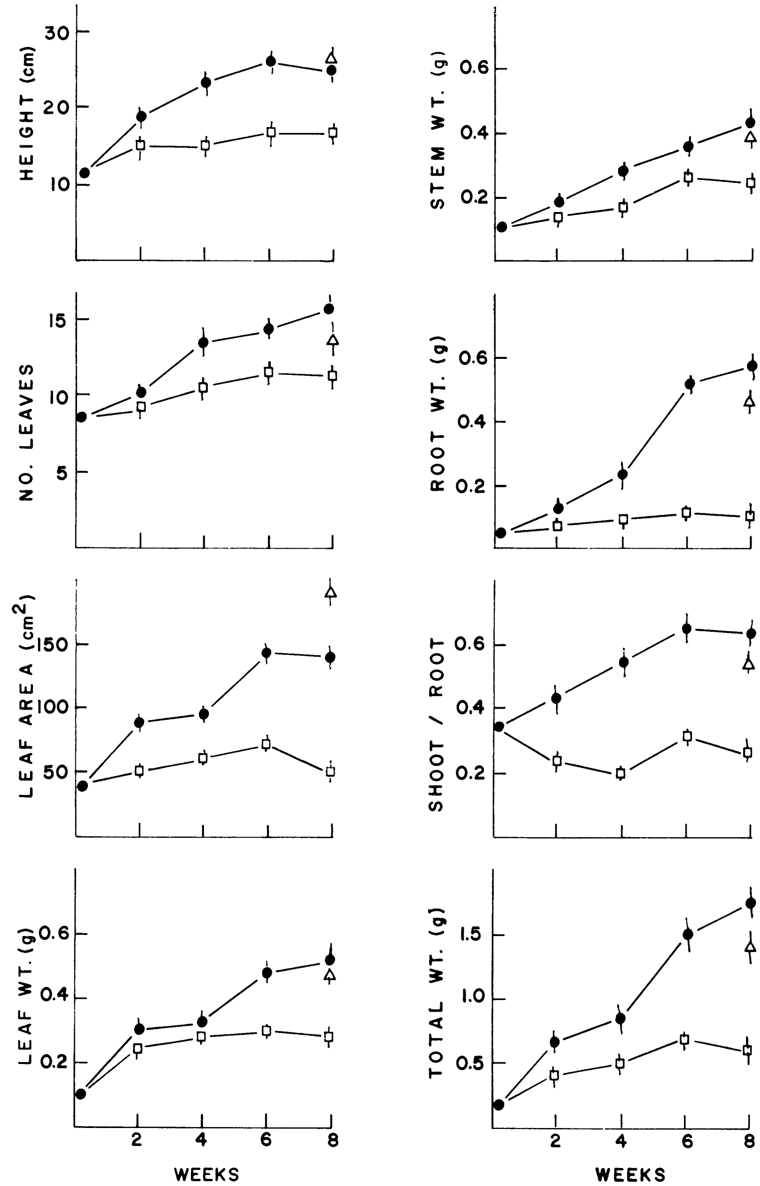

Fig. 1.—Growth characteristics of silver maple seedlings in full sunlight (•), in shade (▲) and root-flooded in full sunlight (□) for 8 weeks. Seedlings were 9 weeks old at start of treatments. Vertical bars indicate 1 SE of the mean

while flooding reduced total biomass by 70% at the end of an 8-week period. Low light conditions are apparently less critical to seedling survival than duration of flooding. Poor root production under flooded conditions may lower the competitive ability of seedlings because of a reduction in the physical stability required for establishment on floodplain sites (Lewis, 1975) and because of lower carbohydrate reserves. Although flooding during the dormant season usually has little effect on growth of bottomland species (Teskey and Hinckley, 1977a), flooding has substantial effects on the survival and growth of young silver maple seedlings.

PHYSIOLOGICAL ANALYSIS

Light saturation curve.—Maximum photosynthetic rates of 11.1 mg CO_2 dm^{-2} hr^{-1} for 2-month-old and 8.9 mg CO_2 dm^{-2} hr^{-1} for 1-year-old silver maple seedlings were measured at 1600 μmol m^{-2} sec^{-1} (Fig. 2). Photosynthesis was not significantly different within either age class at PPFD between 1200 and 2500 μmol m^{-2} sec^{-1}. Similar results were found for transpiration, although the maximum rate for 2-month-old seedlings was found at 2200 μmol m^{-2} sec^{-1}. Maximum photosynthesis in eastern cottonwood (*Populus deltoides* Marsh.) seedlings, another important floodplain species, is approximately twice as high as in silver maple, although the point of saturating PPFD is about the same (Regehr *et al.,* 1975). Cottonwood seedling transpiration is also twice as high as that of silver maple seedlings.

Net photosynthetic rate of 3-month-old seedlings was significantly higher than that of 1-year-old seedlings for PPFD$\geq$1600 μmol m^{-2} sec^{-1}, and 3-month-old seedling transpiration was higher for PPFD$\geq$200 μmol m^{-2} sec^{-1} (Fig. 2). The difference in transpiration rates at PPFD levels at which photosynthetic rates were not significantly different suggests that 1-year-old seedlings used water more efficiently at lower light levels. The higher rates of photosynthesis measured for seedlings at high PPFD demonstrate the capacity of seedlings to take advantage of high light conditions such as those found in gaps in the forest canopy. The light compensation point was low ($\leq$100 μmol m^{-2} sec^{-1}) for both seedling age classes, which indicates that silver maple can exist in the low light conditions of the understory.

Leaf with maximum photosynthetic rate.—Leaves at the second node of 1-year-old silver maple seedlings had a significantly higher rate of photosynthesis than leaves at other nodes. Leaves at node 1 (uppermost) had the lowest rate, and there was no significant difference among nodes 3 through 7. Transpiration rate was not significantly different among leaves at nodes 1 through 6, but was significantly higher at node 7, which suggests that water use efficiency was low for some of the lower (older) leaves. The difference between highest and lowest values was 4 mg CO_2 dm^{-2} hr^{-1} for net photosynthesis and 0.4 g H_2O dm^{-2} hr^{-1} for transpiration.

Temporal variation in flooding.—Net photosynthesis and transpiration decreased significantly after 28 and 21 days of root-flooding, respectively, in spring-flooded, 3-month-old seedlings, and both measurements declined significantly after 21 days for summer-flooded, 3-month-old seedlings (Figs. 3 and 4). Photosynthesis in spring-flooded, 1-year-old seedlings was not reduced significantly, although transpiration was lower after 14 days of flooding. Summer-flooded, 1-year-old plants had a lower photosynthetic rate after 28 days, but did not have a significantly lower transpiration rate.

These results suggest that 1-year-old plants may be slightly more tolerant of flooding than younger seedlings. The sharp decline in transpiration in spring-flooded, 1-year-old plants in the absence of a concurrent decrease in photosynthesis indicates an increase in water use efficiency. Tree seedlings from floodplain environments are generally more tolerant of late flooding than early flooding because of a slowdown in growth later in the growing season (Teskey and Hinckley, 1977a). There was no decrease in late summer photosynthesis in this study, however. There were lower levels of transpiration relative to photosynthesis in summer flooding treatments for both 3-month-old and 1-year-old seedlings. This suggests that older plants have increased water use efficiency. This capability to reduce water loss would enhance the survival of silver maple under both flooded and nonflooded conditions.

Light and flooding conditions.—Net photosynthetic rate of silver maple seedlings submersed in clear water was significantly less than that of nonsubmersed plants after 20 days in the shade and after 30 days in full sunlight (Table 1). Photosynthesis was significantly less in shaded seedlings submersed in muddy water than in clear water. Transpiration in submersed treatments was generally similar to that of nonsubmersed treatments, but was significantly higher after 30 days of submersion in shade (Table 2). Since photosynthesis declined with prolonged submersion, this suggests that seedlings suffered increasingly greater water loss and may have incurred greater water deficits.

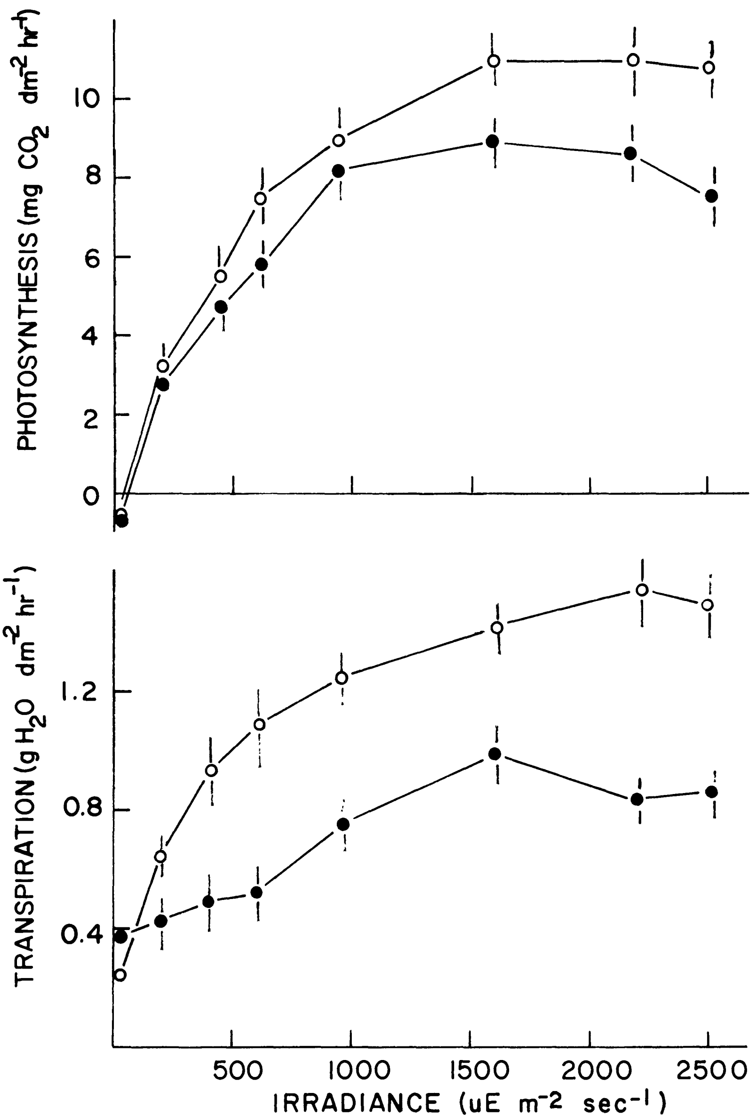

FIG. 2.—Photosynthetic and transpiration rates as a function of PPFD in 3-month-old (○) and 1-year-old (•) silver maple seedlings. Vertical bars indicate 1 SE of the mean

Regression analysis showed that the terms for submersion condition ($p<0.005$), duration of submersion ($p<0.005$), submersion condition x duration of submersion ($p<0.005$), and light condition x submersion condition x duration of submersion ($p<0.005$) all had coefficients significantly different from 0 when rate of photosynthesis was the dependent variable. The overall regression which included these terms was also significant ($p<0.005$, SE = 0.54, $r^2 = 0.71$). The effects of submersion condition (X_2) and duration of submersion (X_3) on photosynthesis are presented in Tables 1 and 2. Regression analysis showed that there was an interaction between these terms (X_2X_3), in addition to an interaction among light condition, submersion condition and duration of submersion ($X_1X_2X_3$). Although light condition (X_1) alone was not well correlated with photosynthetic rate, it apparently had some effect in conjunction with flooding parameters. The terms for duration of submersion ($p<0.005$), submersion condition x duration of submersion ($p<0.01$), and light condition x submersion condition x duration of submersion ($p<0.005$) had coefficients significantly different from 0 when rate of transpiration was the dependent variable. The overall regression which included these terms was significant ($p<0.005$, SE = 0.23, $r^2 = 0.50$). This analysis suggests that duration of submersion was related to transpiration rate. Transpiration was also correlated with the same pair of interaction terms which influenced photosynthesis.

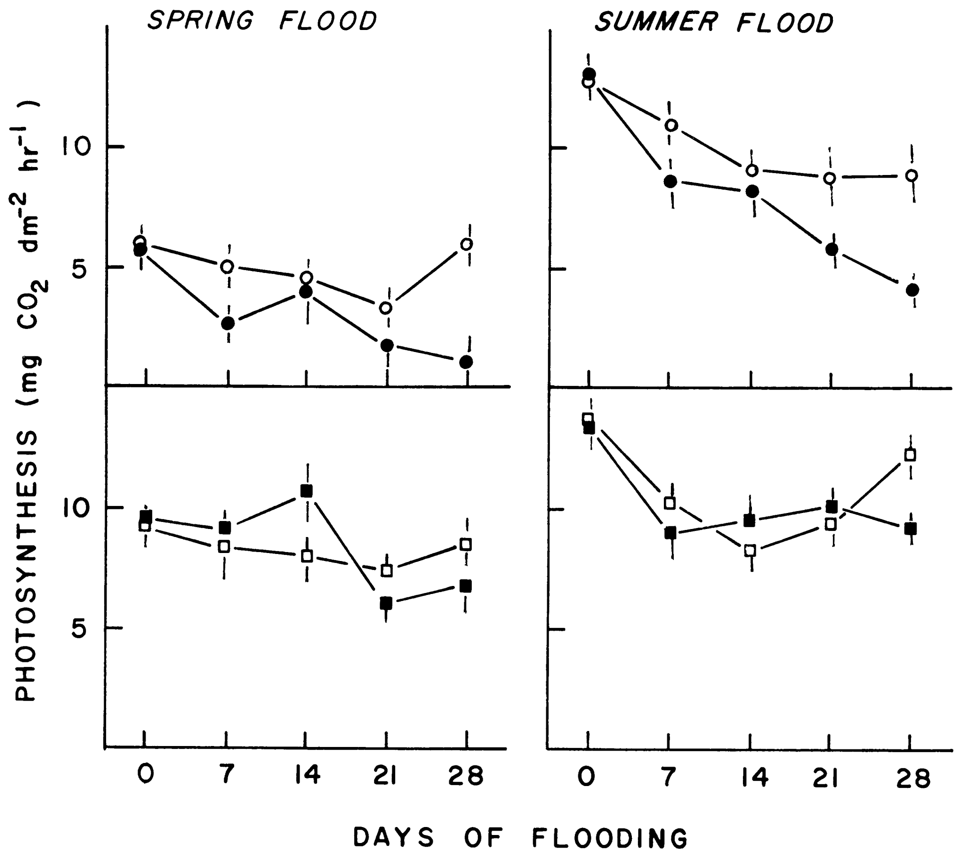

Fig. 3.—Photosynthetic rates of silver maple seedlings subjected to root-flooding in spring and late summer: flooded 3-month-old (•), nonflooded 3-month-old (control) (○), flooded 1-year-old (■), nonflooded (control) 1-year-old (□). Vertical bars indicate 1 SE of the mean

Silver maple seeds may germinate in light gaps or under a dense canopy on floodplain sites. Seedlings at lower elevations on the floodplain are flooded longer than those at higher elevations (Franz and Bazzaz, 1977). Suspended sediments in floodwater reduce light penetration during submersion and may settle out on leaf surfaces as floodwaters subside. Tang and Kozlowski (1982) suggest that recovery of stomatal function following drydown is a critical feature of flood tolerance in tree seedlings, and that green ash *(Fraxinus pennsylvanica* Marsh.) is highly tolerant because of its rapid recovery of normal stomatal function after flooding (Sena Gomes and Kozlowski, 1980). This analysis has shown that submersion affected physiological function of silver maple seedlings more than did the light condition in which they were grown. Decline in photosynthesis without a concurrent decrease in transpiration suggests that flooding may have damaged stomata, allowing considerable water loss.

Recovery of photosynthesis and transpiration.—Patterns of net photosynthesis and transpiration following the end of submersion differed considerably between 2-month-old and 2-year-old silver maple seedlings. Two-month-old seedlings which had been

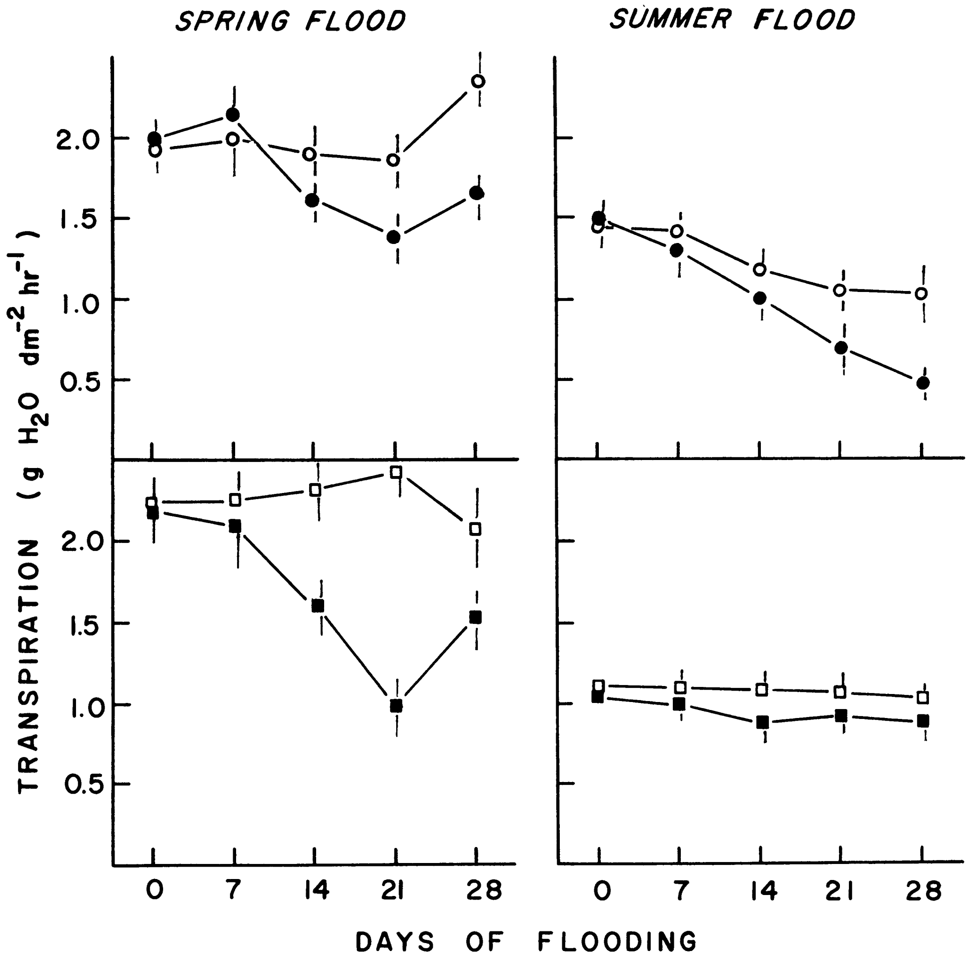

Fig. 4.—Transpiration rates of silver maple seedlings subjected to root-flooding in spring and late summer. Symbols are the same as in Figure 3. Vertical bars indicate 1 SE of the mean

submersed for 3 days and 11 days had photosynthetic rates significantly less than controls 7 days after flooding, but were fully recovered after 14 days (Table 3). The 11-day-old treatment initially had a transpiration rate lower than that of controls but had a significantly higher rate 14 days after submersion ended (Table 4), suggesting a decline in water use efficiency. Two-month-old seedlings submersed for 21 days had chlorotic leaves which showed no evidence of recovering normal physiological functions 14 days after cessation of flooding.

Two-year-old seedlings had a greater capability than 2-month-old seedlings for photosynthetic recovery after submersion. The only significant differences in photosynthetic rate between submersed treatments and controls were measured 1 day after drydown for plants which were submersed for 11 days and 21 days (Table 3). Plants from all treatments were fully recovered in 7 days after submersion ended. Transpiration in seedlings submersed for 11 days and 21 days was initially lower than that of controls, but increased at least temporarily to significantly higher levels, indicating a decline in water use efficiency. Physiological measurements for seedlings submersed for 3 days were never significantly different from those of controls.

The capability to return to normal levels of photosynthesis following a period of stress is an important factor in the fitness of a plant (Bacone *et al.*, 1976; Ormsbee *et al.*, 1976; McGee *et al.*, 1981). Tree species such as eastern cottonwood are tolerant of

TABLE 1.—Photosynthetic rates (mg $CO_2 dm^{-2} hr^{-1}$) of submersed and nonsubmersed silver maple seedlings under two light regimes. Seedlings were 1 month old at start of treatments. 1 SE of the mean is indicated in parentheses

Light regime	Days of treatment	Submersed: Clear water	Submersed: Muddy water	Nonsubmersed
Full sun	10	4.1 (0.4)	4.5 (0.3)	7.7 (0.6)
	20	5.7 (0.3)	3.4 (0.3)	6.0 (0.8)
	30	2.4 (0.2)	1.9 (0.5)	4.0 (0.5)
	40	1.5 (0.5)	1.0 (0.4)	6.5 (0.4)
Shade	10	3.6 (1.0)	3.5 (1.0)	4.1 (1.0)
	20	4.5 (0.9)	1.5 (0.3)	7.1 (1.1)
	30	3.2 (0.1)	2.0 (0.8)	4.1 (1.1)
	40	2.7 (0.4)	1.8 (0.4)	4.3 (0.4)

TABLE 2.—Transpiration rates (g $H_2O dm^{-2} hr^{-1}$) of submersed and nonsubmersed silver maple seedlings under two light regimes. Seedlings were 1 month old at start of treatments. 1 SE of the mean is indicated in parentheses

Light regime	Days of treatment	Submersed: Clear water	Submersed: Muddy water	Nonsubmersed
Full sun	10	3.0 (0.7)	2.7 (0.2)	2.0 (0.3)
	20	2.2 (0.2)	2.3 (0.2)	2.6 (0.2)
	30	2.6 (0.4)	2.4 (0.4)	1.7 (0.3)
	40	2.0 (0.4)	1.5 (0.1)	2.7 (0.3)
Shade	10	2.6 (0.3)	2.8 (0.3)	2.1 (0.3)
	20	2.5 (0.3)	1.8 (0.1)	2.0 (0.4)
	30	2.1 (0.3)	2.8 (0.3)	1.3 (0.1)
	40	2.5 (0.4)	2.1 (0.2)	1.5 (0.1)

flooding because of their ability to regain photosynthetic function rapidly following cessation of flooding (Regehr *et al.,* 1975). In the floodplain environment, silver maple seedlings must compete with a well-developed herbaceous stratum for light and nutrients (Peterson and Rolfe, 1982a). Silver maple seedlings that have a rapid rate of photosynthetic recovery following flooding should have a competitive advantage over individuals that are slow to recover. This study has shown that 2-year-old seedlings had a greater capacity for photosynthetic recovery than recently germinated seedlings.

FLOODING RESPONSES AND LIFE HISTORY OF SILVER MAPLE

Flooding is the most important environmental variable in the life history of silver maple. Germination occurs only on soils with favorable soil moisture and microclimate (Sigafoos, 1964; Lewis, 1975). These conditions, which typically exist during a postflood drydown period, must occur shortly after fruitfall. Flooding that occurs soon after germination can physically damage seedlings by water movement or sedimentation (Petersen, pers. observ.).

Light conditions apparently have minimal effect on the growth of silver maple seedlings. Seeds germinate in light gaps as well as in dense shade. This study has shown that seedlings grown under low light conditions develop a "shade plant" morphology with only a slight reduction in root biomass. Silver maple can maintain relatively high rates of net photosynthesis over a broad range of photosynthetically active photon flux density.

TABLE 3.—Photosynthetic rates (mg CO_2 $dm^{-2}hr^{-1}$) of 2-month-old and 2-year-old silver maple seedlings following the end of submersion treatments. Rates significantly less than that of control seedlings are indicated (*). 1 SE of the mean is indicated in parentheses

Seedling age	Submersion treatment (days)	Days after end of submersion 1	7	14
2 months old	3	8.8 (0.4)*	7.7 (0.8)*	8.2 (1.3)
	11	4.1 (0.6)*	8.0 (1.5)*	11.7 (0.5)
	21	0.5 (0.5)*	2.3 (2.9)*	2.0 (2.0)*
2 years old	3	8.2 (0.5)	10.0 (0.6)	8.6 (0.3)
	11	6.8 (0.3)*	10.0 (0.9)	10.8 (1.2)
	21	5.2 (0.7)*	8.9 (1.2)	9.8 (0.7)

TABLE 4.—Transpiration rates (g H_2O $dm^{-2}hr^{-1}$) of 2-month-old and 2-year-old silver maple seedlings following the end of submersion treatments. Rates significantly less (*) and greater (**) than that of control seedlings are indicated. 1 SE of the mean is indicated in parentheses

Seedling age	Submersion treatment (days)	Days after end of submersion 1	7	14
2 months old	3	2.1 (0.1)	1.8 (0.2)	1.8 (0.2)
	11	1.4 (0.3)*	1.8 (0.4)	2.6 (0.1)**
	21	0.9 (0.2)*	1.0 (0.4)*	1.0 (0.4)*
2 years old	3	2.3 (0.2)	2.2 (0.1)	1.9 (0.1)
	11	2.0 (0.1)*	2.0 (0.6)	2.4 (0.1)**
	21	1.3 (0.6)*	2.2 (0.2)**	2.0 (0.1)

Survival and establishment of silver maple seedlings are almost entirely dependent on patterns and duration of flooding. Since dormant season flooding is not deleterious to deciduous trees (Teskey and Hinckley, 1977a), only floods that occur after budbreak affect silver maple growth. The effect of timing of flooding is not clear. In this study, the decrease in photosynthesis in spring-flooded and summer-flooded treatments was similar, although plants flooded in the spring had lower water use efficiency. Duration of flooding had a strong inverse correlation with rate of photosynthesis and biomass production, which indicates that long periods of flooding can severely restrict the growth and competitive ability of silver maple seedlings.

The capacity for recovery of normal physiological functions following cessation of flooding is critical for floodplain species. In this study, silver maple seedlings that had previously experienced flooding had a greater capacity for recovery of preflood photosynthetic and transpiration rates than seedlings inundated for the first time. Even a small difference in seedling age appears to affect postflood survival and growth. The ability to regain normal levels of photosynthesis and transpiration may be an important characteristic in the natural selection of silver maple and other floodplain species, and should be considered in the selection of individuals for floodplain silviculture.

Acknowledgments.—We thank Pam Brodsky for help with the physiological measurements, and Alan Drew and Roger Carlson for assistance with statistical analyses. Helpful comments on the manuscript were provided by William E. Williams, Ed Reekie and Keith Garbutt.

LITERATURE CITED

BACONE, J., F. A. BAZZAZ AND W. R. BOGGESS. 1976. Correlated photosynthetic responses and habitat factors of two successional tree species. *Oecologia,* **23**:63-74.

BAZZAZ, F. A. AND J. S. BOYER. 1972. A compensating method for measuring carbon dioxide exchange, transpiration, and diffusive resistances of plants under controlled environmental conditions. *Ecology,* **53**:343-349.

BELL, D. T. 1974. Tree stratum composition and distribution in the streamside forest. *Am. Midl. Nat.,* **92**:35-46.

BJORKMAN, O. AND P. HOLMGREN. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes of exposed and shaded habitats. *Physiol. Plant.,* **16**:889-914.

DREW, A. P. AND F. A. BAZZAZ. 1979. Response of stomatal resistance and photosynthesis to night temperature in *Populus deltoides. Oecologia,* **41**:89-98.

FOWELLS, H. A. (ED.). 1965. Silvics of forest trees of the United States. *U.S. Dep. Agric., Agric. Handb. 271.* Forest Service, U.S. Department of Agriculture, Washington, D. C. 762 p.

FRANZ, E. H. AND F. A. BAZZAZ. 1977. Simulation of vegetation response to modified hydrologic regimes: a probabilistic model based on niche differentiation in a floodplain forest. *Ecology,* **58**:176-183.

HOSNER, J. F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. *For. Sci.,* **6**:246-251.

KEELEY, J. E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica. Ecol. Monogr.,* **49**:89-108.

KOZLOWSKI, T. T. AND S. G. PALLARDY. 1979. Stomatal responses of *Fraxinus pennsylvanica* seedlings during and after flooding. *Physiol. Plant.,* **46**:155-158.

KRAMER, P. J. AND T. T. KOZLOWSKI. 1979. Physiology of woody plants. Academic Press, New York. 811 p.

LEWIS, K. P. 1975. Community analysis and the dynamics of establishment of *Acer saccharinum* on flood plains of the unglaciated Appalachian Plateau. Ph.D. Thesis, Ohio University, Athens. 111 p.

McGEE, A. B., M. R. SCHMIERBACH AND F. A. BAZZAZ. 1981. Photosynthesis and growth in populations of *Populus deltoides* from contrasting habitats. *Am. Midl. Nat.,* **105**:305-311.

ORMSBEE, P., F. A. BAZZAZ AND W. R. BOGGESS. 1976. Physiological ecology of *Juniperus virginiana* in oldfields. *Oecologia,* **23**:75-82.

PEREIRA, J. S. AND T. T. KOZLOWSKI. 1977. Variation among woody angiosperms in response to flooding. *Physiol. Plant.,* **41**:184-192.

PETERSON, D. L. AND G. L. ROLFE. 1982a. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *Am. Midl. Nat.,* **107**:325-339.

______ AND ______. 1982b. Seasonal variation in nutrients of floodplain and upland forest soils of central Illinois. *Soil Sci. Soc. Am. Proc.*, **46**:1310-1315.

REGEHR, D. L., F. A. BAZZAZ AND W. R. BOGGESS. 1975. Photosynthesis, transpiration and leaf conductance of *Populus deltoides* in relation to flooding and drought. *Photosynthetica*, **9**:52-61.

SENA GOMES, A. R. AND T. T. KOZLOWSKI. 1980. Growth responses and adaptations of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiol.* **66**:267-271.

SIGAFOOS, R. S. 1964. Botanical evidence of floods and floodplain deposition. *U.S. Geol. Surv. Prof. Pap. 485-A*. Washington, D.C. 35 p.

TANG, Z. C. AND T. T. KOZLOWSKI. 1982. Physiological, morphological and growth responses of *Platanus occidentalis* seedlings to flooding. *Plant Soil*, **66**:243-255.

TESKEY, R. O. AND T. M. HINCKLEY. 1977a. Impact of water level changes on woody riparian and wetland communities. Vol. 1, Plant and soil responses to flooding. U.S. Fish and Wildlife Service, Washington, D.C. 30 p.

______ AND ______. 1977b. Impact of water level changes on woody riparian and wetland communities. Vol. 3, The central forest region. U.S. Fish and Wildlife Service, Washington, D.C. 36 p.

SUBMITTED 31 MAY 1983 ACCEPTED 3 OCTOBER 1983