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# Photosynthetic Response to Flooding of Acer rubrum Seedlings from Wet and Dry Sites

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ABSTRACT.—Seeds were collected from three red maple swamps (wet sites) and three uplands (dry sites) near Ithaca, New York, and the resulting seedlings were used in flood tolerance studies to investigate if red maple's broad habitat range is due to ecotypic differentiation. One-year-old seedlings were flooded while still dormant (spring flooding study) and net photosynthesis, growth and chlorophyll levels were measured at 1 mo intervals for 3 mo. Flooding reduced net photosynthesis, growth and chlorophyll levels in seedlings from both sites, but survival of both wet and dry site seedlings was near 100%. After 1 mo of flooding net photosynthesis of wet and dry site seedlings were similar, but after 3 mo, flooded wet site seedlings had higher photosynthetic rates than did dry site seedlings. Control wet site seedlings were significantly larger than dry site seedlings and had significantly higher photosynthetic rates and chlorophyll levels. These differences suggest either genetic variation between seedlings from the two habitats in response to the growing conditions or the influence of seed size differences and confound the spring flooding study results. Flooded wet site seedlings had higher, final, net photosynthetic rates than did dry site seedlings, but the response to flooding was greater for wet site seedlings than it was for dry site seedlings.

In a second study (summer flooding study), 1-y-old seedlings in full leaf were flooded for 22 d and then drained to determine if recovery from flooding stress differed for wet and dry site seedlings. Again, flooding decreased net photosynthesis for seedlings from both habitats but, when the trees were drained, net photosynthesis for wet site seedlings recovered more quickly and to a higher level than it did for dry site seedlings. Flooding also caused a drop in chlorophyll levels for seedlings from both habitats, but chlorophyll levels of seedlings from neither habitat recovered when the seedlings were drained. There were no significant differences between wet site and dry site control seedlings for net photosynthesis; therefore, the quicker and larger recovery of photosynthetic potential in wet site seedlings in the summer flooding study suggests that ecotypic differentiation has occurred and that genetic differences, in part, account for red maple's occurrence on contrasting edaphic sites.

## INTRODUCTION

Although trees differ in their response to flooding, rapid declines in stomatal conductance and net photosynthesis are common responses to soil anoxia. The rates of decline (Pezeshki and Chambers, 1986; Dreyer *et al.*, 1991), ability to acclimate and thereby recover lost photosynthetic potential while still flooded (Sena Gomes and Kozlowski, 1980a, b) and recovery after flooded conditions have subsided (Kozlowski and Pallardy, 1979; Peterson and Bazzaz, 1984; Harrington, 1987; Osonubi and Osundina, 1987) have all been used to investigate mechanisms of, and rank species for, flood tolerance. Flood tolerant tree species recover net photosynthetic potential after acclimating to anoxic soil conditions, and net photosynthesis recovers more quickly and to a higher extent for flood tolerant tree species when drained compared to flood intolerant tree species.

Most researchers have examined a single species or compared species to examine flood tolerance (Regehr *et al.*, 1975; Topa and Cheeseman, 1992; Topa and McLeod 1986a, b;

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Pezeshki *et al.*, 1996), but relatively few have examined intraspecific variation (Keeley, 1979; Will *et al.*, 1995). The purpose of this study was to examine differences in photosynthesis and growth between upland and wetland populations of red maple (*Acer rubrum*) to determine if ecotypic differentiation contributes to red maple's occurrence in wetlands and dry uplands. Is red maple a generalist species (Abrams and Kubiske, 1990; Abrams, 1998) able to acclimate to the stresses encountered in upland and wetland soils or have genetically distinct ecotypes evolved that differ in their ability to tolerate flooding?

## METHODS

*Plant source.*—Red maple seeds were collected from three wet and three dry sites near Ithaca, New York in May 1995. Sites were chosen to represent the extremes of red maple's hydrologic range: a wet site (WS) was defined by poorly drained soils that were saturated in the spring during seed development (a wetland or swamp), and a dry site (DS) was defined by well drained upland soils (Table 1). Samaras were collected from four trees at each site just before dispersal, stored in plastic bags and refrigerated until sown. Seeds were sown in trays within 1 wk of collecting and trays were placed on a greenhouse bench. Trays were filled with greenhouse soil mix (1 part loam, 2 parts peatmoss, 1 part perlite) with the following additions: 0.49 g $L^{-1}$ magnesium sulfate, 1.22 g $L^{-1}$ gypsum, 0.58 g $L^{-1}$ triple super phosphate, 0.88 g $L^{-1}$ Micromax (Scotts-Sierra Horticultural Products Company, Marysville, Ohio), 0.28 g $L^{-1}$ calcium nitrate, 0.28 g $L^{-1}$ potassium nitrate and 0.42 $gL^{-1}$ ferrous sulfate. Once true leaves developed seedlings were transplanted individually to 10 cm plastic pots and grown for the remainder of the season in a greenhouse. After fall senescence the potted seedlings were stored in a dark cooler at 4 C.

*Spring flooding study.*—One-year-old red maple seedlings derived as described above were transplanted into large tubs while still dormant. The tubs measured 120 × 90 × 42 cm (length, width and depth, respectively) and were filled with approximately 350 L of greenhouse soil mix (described above). Treatments were randomly assigned to tubs placed in rows approximately 1 m apart, out-of-doors on a gravel pad in full sun. Control tubs had holes on the bottom; flooded tubs were lined with 8 mil (0.2 mm) plastic sheeting.

Each tub contained six seedlings, one from each of the three wet and three dry sites. Three different half-sib families (randomly selected from the collection of 4 half-sib families) from each site were used and each half-sib family was represented in one control and one flooded tub per harvest. This design resulted in a total of 108 seedlings [three half-sib families per site × three sites per habitat × two habitats (wet and dry sites) × three harvests × two treatments (control and flooded)]. A total of 18 tubs were used in the study, nine control and nine flooded. Tubs were harvested 1, 2 and 3 mo after the initiation of treatments, with three control and three flooded tubs harvested each period.

Dormant seedlings were removed from the cooler on 9 May 1996 and transplanted the following day into tubs. Ten d later (20 May 1996) the flooding treatment was initiated by filling the appropriate tubs with tap water 5 to 8 cm above the soil surface. The water level was maintained as close to constant as possible by adding water daily or removing water after rain. Control tubs were watered daily.

Net photosynthesis was measured at the end of each harvest period for seedlings harvested during that period (30, 60 and 90 d after the initiation of treatments) with a LI-6200 Portable Photosynthesis System (LI-COR, Lincoln, Nebraska). Two fully expanded leaves on each seedling were measured between 10 AM and noon under natural light at a minimum of 1500 $\mu mol\ m^{-2}\ s^{-1}$, well above red maple's saturation point of 360 $\mu mol\ m^{-2}\ s^{-1}$ (Jurik *et al.*, 1988).

The temperature between 10 AM and noon on day 30 (harvest 1) ranged from 18.9 to

TABLE 1.—Description of red maple seed collection sites. Designation indicates whether the site was considered a wet or dry habitat for the purpose of this study

| Descriptor | Location | Designation | Soil series | Drainage class* | Latitude, longitude | Elevation (m) |
|---|---|---|---|---|---|---|
| MZ | Montezuma National Wildlife Refuge, Seneca County, New York | Wet | Muck | VPD | 42°57′30″N, 76°45′00″W | 119 |
| VE | Spencer-Van Etten Swamp, Chemung County, New York | Wet | Papakating | VPD | 42°12′15″N, 76°32′35″W | 308 |
| CL | Cayuta Lake, Schuyler County, New York | Wet | Carlisle Muck | VPD | 42°22′35″N, 76°44′00″W | 402 |
| FLT | Finger Lakes Trail, Schuyler County, New York | Dry | Valois | WD | 42°22′00″N, 76°46′10″W | 564 |
| BH1 | Bald Hill, Tompkins County, New York | Dry | Mardin | MWD | 42°21′45″N, 76°22′50″W | 518 |
| BH2 | Bald Hill, Tompkins County, New York | Dry | Mardin | MWD | 42°22′10″N, 76°22′50″W | 442 |

* Drainage classes: MWD = Moderately Well Drained, WD = Well Drained, VPD = Very Poorly Drained

21.1 C, on day 60 (harvest 2) from 24.4 to 27.2 and on day 90 (harvest 3) from 20.5 to 23.9. Relative humidity averaged 84, 71 and 74% between 10 AM and noon for days 30, 60 and 90, respectively.

Results were analyzed using a mixed-model performed with SAS (SAS Institute Inc., Cary, North Carolina). Random effects, fixed effects, interactions between fixed effects and a series of preplanned contrasts were performed. The random effects were family nested within site and site nested within habitat; however, random effects were never statistically significant and were removed from the model. The fixed (main) effects were harvest, habitat and treatment. Four preplanned contrasts were performed: control WS vs. control DS (across all harvests); flooded WS vs. flooded DS (across all harvests); control WS vs. control DS (change from harvest 1 to harvest 3); flooded WS vs. flooded DS (change from harvest 1 to harvest 3).

*Summer flooding study.* –One-year-old seedlings in full leaf from three wet sites and three dry sites (Table 1) were randomly selected and randomly assigned to flooded or drained treatments. Trees were planted as described above with one tree from each of three wet sites and one tree from each of three dry sites in each tub. The seedlings were allowed to acclimate for 1 wk and on 26 July 1997 (Day 0) three tubs were flooded and three tubs were left freely draining as a control. Flooded tubs were filled to 5 cm above the soil surface and were topped off daily with tap water. The tubs were flooded for 22 d (flooded period) and then drained by cutting holes in the plastic lining (drained period). Control tubs, and tubs drained after day 22, were watered daily.

Net photosynthesis was measured with the LI-6200 Portable Photosynthesis System on days 1, 3, 6, 11, 16 and 22 (flooded period) and days 23, 27, 30 and 32 (drained period). The same two fully expanded leaves on each tree were measured throughout the experiment between 10 AM and noon under natural light at a minimum of 1500 $\mu$mol $m^{-2}$ $s^{-1}$, well above red maple's saturation point of 360 $\mu$mol $m^{-2}$ $s^{-1}$.

Relative chlorophyll content was measured on the same leaves used to measure photosynthesis using a Chlorophyll Meter SPAD-502 (Minolta Camera Co., Japan). Three chlorophyll readings per leaf were taken on days 3, 6, 11 and 16 (flooded period) and on days 23, 25, 28 and 32 (drained period).

Results were analyzed using a mixed-model, repeated-measures procedure performed with SAS (SAS Institute Inc., Cary, North Carolina) for random effects, fixed effects, interactions between fixed effects and a series of preplanned contrasts. The random effects were family nested within site and site nested within habitat; however, random effects were never statistically significant and were removed from the model. The fixed (main) effects were harvest, habitat and treatment. The following preplanned contrasts were performed separately for control trees and for flooded trees: WS vs. DS for all days; WS vs. DS on day 32; and WS vs. DS rate of recovery (change from day 23 to 32).

## RESULTS

*Spring flooding study.*—Survival was high for all treatments during the study; one WS and two DS flooded seedlings died during the experiment. Control seedlings grew throughout the experiment but flooding caused a near cessation of growth for both WS and DS seedlings. Control WS seedlings were larger than DS seedlings leading to a larger decrease in WS leaf area, shoot dry weight and root dry weight when flooded and a significant habitat by treatment interaction for all growth parameters ($P < 0.001$; Table 2). Net photosynthesis, stomatal conductance and chlorophyll levels (SPAD) were also higher ($P < 0.0001$) for control WS seedlings compared to DS seedlings.

Flooding caused a sharp decline in net photosynthesis for both WS and DS seedlings.

TABLE 2.—Mean (SD) total leaf area, shoot dry weight and root dry weight for control and flooded red maple seedlings in the spring flooding study. Trees were harvested 30, 60 and 90 d after the initiation of treatments (3 seedlings per habitat averaged by tub × 3 tubs)

| Treatment harvest | Total leaf area ($cm^2$) | | Shoot dry weight (g) | | Root dry weight (g) | |
|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD |
| Wet site control | | | | | | |
| 30 days | 642 | 122 | 8.4 | 2.4 | 3.6 | 1.2 |
| 60 days | 1640 | 958 | 20.2 | 13.2 | 6.8 | 2.4 |
| 90 days | 4688 | 1093 | 75.0 | 22.0 | 23.4 | 7.3 |
| Dry site control | | | | | | |
| 30 days | 240 | 85 | 2.4 | 0.81 | 1.2 | 0.4 |
| 60 days | 1016 | 470 | 10.1 | 5.0 | 2.6 | 0.8 |
| 90 days | 2953 | 563 | 32.1 | 7.4 | 9.6 | 9.4 |
| Wet site flooded | | | | | | |
| 30 days | 477 | 124 | 8.0 | 2.6 | 3.2 | 0.7 |
| 60 days | 561 | 123 | 11.0 | 2.4 | 3.2 | 0.5 |
| 90 days | 512 | 109 | 12.4 | 3.6 | 3.4 | 1.3 |
| Dry site flooded | | | | | | |
| 30 days | 201 | 51 | 2.5 | 0.8 | 0.9 | 0.3 |
| 60 days | 204 | 65 | 3.3 | 1.1 | 1.1 | 0.3 |
| 90 days | 198 | 63 | 3.2 | 1.0 | 1.0 | 0.3 |

The significant habitat by treatment interaction ($P < 0.0001$) indicates that flooding caused a larger decline in net photosynthesis for WS than DS seedlings (Fig. 1).

At day 30 there was no significant difference between flooded WS and DS net photosynthesis; however, at day 90 flooded WS net photosynthesis measured 3.54 $\mu mol\ m^{-2}\ s^{-1}$, three times higher than flooded DS net photosynthesis of 1.14 $\mu mol\ m^{-2}\ s^{-1}$ (Fig. 1). The change in net photosynthesis from day 30 to day 90 was significantly different ($P < 0.02$) for flooded WS and DS seedlings; WS seedlings had a more positive rate of increase.

The results for stomatal conductance (Fig. 2) were similar to those reported for net photosynthesis with harvest, habitat and treatment as significant main effects ($P < 0.0001$), a significant habitat by treatment interaction ($P < 0.0001$) and a significant difference between control WS and DS seedlings ($P < 0.0001$). At day 60 stomatal conductance was near zero for flooded WS and DS seedlings but at day 90 WS stomatal conductance was four times higher than DS stomatal conductance.

SPAD readings, which give a relative indication of chlorophyll concentration, were always higher for WS than DS seedlings within a treatment (Fig. 3). At day 30 control WS SPAD measured 25.2 and rose to 35.9 at day 90 compared to control DS levels which started at 17.8 and rose to 32.1. At day 30 flooded seedlings had slightly higher SPAD readings than their respective controls, but with time SPAD readings for flooded seedlings declined with flooded wet and dry site seedlings measuring 18.0 and 14.8, respectively, at day 90. Decline in SPAD due to flooding and time was similar for each habitat and therefore neither of the interaction terms were significant.

*Summer flooding study.*—Control WS and DS net photosynthesis were not significantly different in this experiment (Fig. 4). Flooding caused DS net photosynthesis to decline by

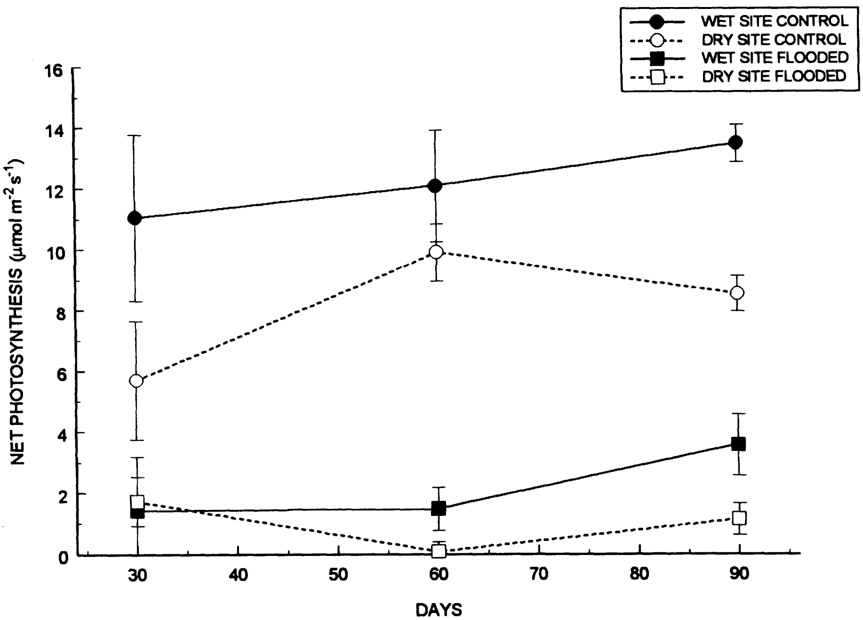


FIG. 1.—Net photosynthesis of flooded and control red maple seedlings after 30, 60 and 90 d of treatment (harvests 1, 2 and 3, respectively). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

day 3 and it continued to decline during the entire flooding period, but WS net photosynthesis did not decline until after day 6. By day 22 flooded WS net photosynthesis reached a low of 1.6 µmol $m^{-2}$ $s^{-1}$ compared to a low of 1.2 µmol $m^{-2}$ $s^{-1}$ for flooded DS seedlings. On day 22 the flooded tubs were drained and by day 27 recovery of net photosynthesis was apparent in both wet and dry site seedlings. The rate of recovery, measured from days 23 to 32, was faster for WS seedlings than for DS seedlings ($P < 0.01$), as was the absolute value on day 32 (7.2 µmol $m^{-2}$ $s^{-1}$ for drained WS seedlings and 4.2 µmol $m^{-2}$ $s^{-1}$ for drained DS seedlings; $P < 0.001$). Analysis across all days revealed a significant habitat by treatment interaction, showing that flooding caused a greater decline in DS net photosynthesis.

There was no significant difference in control WS and DS stomatal conductance (Fig. 5). The habitat by treatment interaction was significant ($P < 0.01$) indicating a greater decline in DS stomatal conductance. Stomatal conductance on day 32 was higher for WS seedlings than DS seedlings ($P < 0.0001$), as was the WS rate of recovery ($P < 0.0005$).

Control WS SPAD readings were significantly higher than control DS SPAD readings ($P < 0.0001$). Flooding caused SPAD readings to decline but chlorophyll levels failed to recover when the trees were drained (Fig. 6). Interaction terms were non significant, indicating that treatment had a similar effect on WS and DS chlorophyll levels.

## DISCUSSION

To delineate differences in flood tolerance between putative ecotypes it is important to design experiments of sufficient duration to allow morphological and physiological acclimation responses to have an effect. With experiments of sufficient duration, differences in

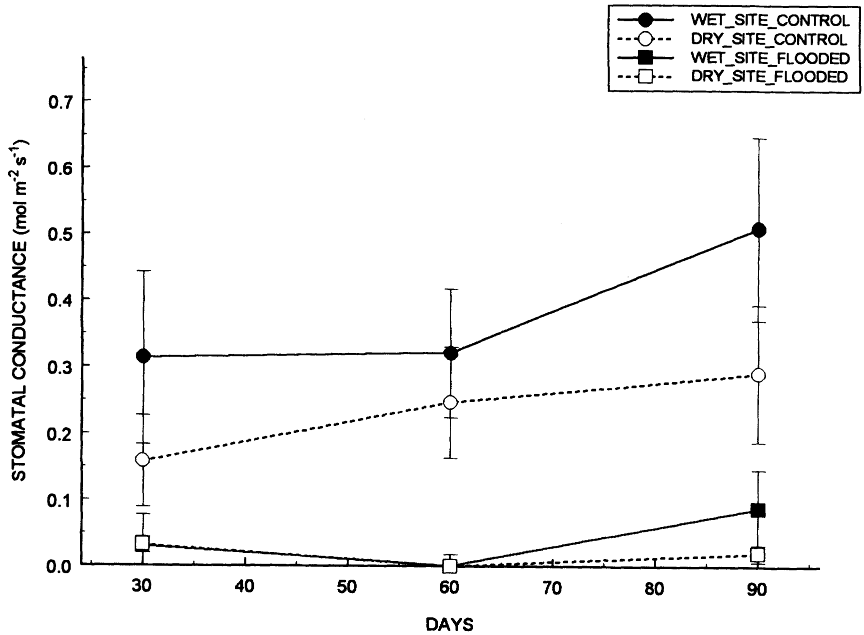


FIG. 2.—Stomatal conductance of flooded and control red maple seedlings after 30, 60 and 90 d of treatment (harvests 1, 2 and 3, respectively). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

physiology or different degrees of phenotypic plasticity in response to flooding can be used as evidence of genetic differentiation (Bradshaw and Hardwick, 1989).

Phenotypic plasticity and ecotypic differentiation are not mutually exclusive as is suggested by many studies examining intraspecific variation (Abrams and Kubiske, 1990; Will *et al.*, 1995). Phenotypic plasticity, as defined by Bradshaw and Hardwick (1989), is a genetically controlled response to a temporary or fluctuating stress; therefore, different degrees of phenotypic plasticity in response to a stress (in this case flooding) is evidence of ecotypic differentiation. Schlichting and Pigliucci (1998) listed four attributes of plastic responses to the environment that can be modified by selection: amount, pattern, rapidity and reversibility. We focused on the amount of plasticity displayed by wet and dry site trees to investigate ecotypic differentiation.

Interpretation of the spring flooding study is confounded by the size and physiological differences between the WS and DS control seedlings. Wet site control seedlings were larger, had higher net photosynthetic rates, higher stomatal conductance and higher SPAD readings than DS seedlings. Since flooding caused a sharp decline in growth, net photosynthesis and stomatal conductance, WS seedlings were more affected by flooding than were DS seedlings. However, since flooding caused net photosynthesis to fall to near zero, the fact that at day 90 flooded WS net photosynthesis was three times higher than flooded DS net photosynthesis has important biological significance. Survival will depend on a positive net carbon balance and where that balance is struck cannot be determined with instantaneous photosynthetic measurements. The seedlings would have to be studied for a longer time or through subsequent growing seasons to determine the biological significance of the higher

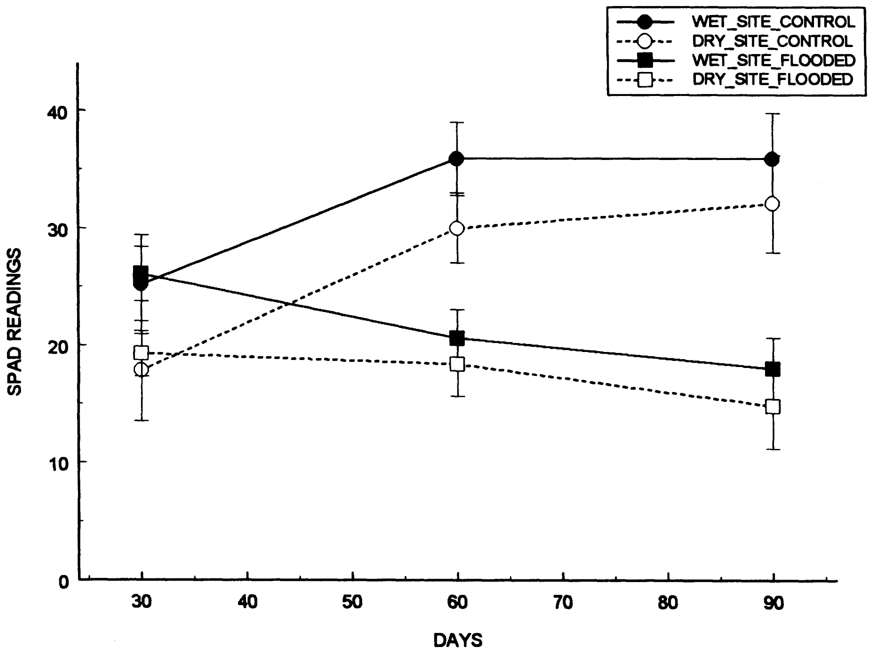


FIG. 3.—SPAD readings for flooded and control red maple seedlings after 30, 60 and 90 d of treatment (harvests 1, 2 and 3, respectively). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

net photosynthetic rate. Due to the confounding effects of size and physiology, it is not possible to conclude from the spring flooding study that ecotypic differentiation accounts for red maple's occurrence on upland and wetland sites. Will *et al.* (1995) also reported a decline in photosynthesis for flooded red maple seedlings from wet and dry sites and concluded that there were no significant differences in response and therefore no evidence for ecotypic differentiation in response to flooding.

It is important to note that in the spring and summer studies, the random effects, family nested within site and site nested within habitat, were never statistically significant indicating little variation within habitat compared to significant differences between habitats. Differences between habitats occurred not only in response to flooding but were also apparent between control seedlings from each habitat. Control photosynthetic rates and chlorophyll levels clearly indicated differences in WS and DS red maple physiology. These differences may have been due to genetically controlled responses to the growing conditions (ecotypic differentiation) or a seed size effect on growth and development. Wet site seeds were significantly larger than DS seeds (Anella and Whitlow, 1998).

Red maple swamps are often characterized by a period of flooding in the spring followed by lower water levels during the summer and perhaps even summer drought (Golet *et al.*, 1993) suggesting that an ability to tolerate a period of temporary stress may be advantageous since the stress will eventually subside. Therefore, examining recovery after flooding is important. The ability to recover lost photosynthetic potential upon draining indicates an ability to tolerate or avoid anoxia without incurring damage to the photosynthetic apparatus (Pezeshki and Chambers, 1985; Kozlowski and Pallardy, 1979). The recovery study showed

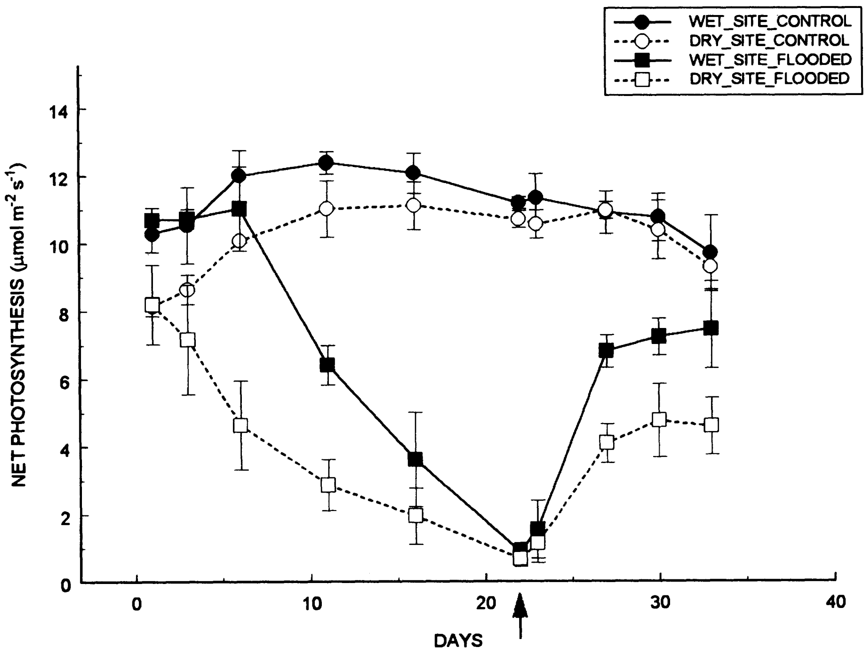


FIG. 4.—Net photosynthesis of control and flooded red maple seedlings. Flooded treatment began on day zero and trees were drained on day twenty-two (arrow). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

that WS seedlings were affected less than DS seedlings by a short-term flooding stress (22 d). Although flooding resulted in the cessation of growth and low rates of photosynthesis for seedlings from each habitat, upon draining the WS seedlings had a faster rate of recovery and regained more of their photosynthetic potential by the experiment's end then did the DS seedlings. The same was true for stomatal conductance. Contrary to the spring flooding study, the summer flooding study did give evidence of ecotypic differentiation in response to flooding stress between WS and DS red maple seedlings from near Ithaca, New York.

Recovery of photosynthetic potential by red maple seedlings in drained soils was also reported by Will *et al.* (1995), but they did not find differences between wet and dry site seedlings. Flood tolerance depends on duration of flooding, time of year and age of tree (Kozlowski *et al.*, 1991), and these factors may account for discrepancies between the spring and summer studies and between these studies and those conducted by Will *et al.* (1995).

Trees that are flooded and drained do not usually recover 100% of their lost photosynthetic potential. This lack of complete recovery has been attributed to a lack of stomatal opening, damage to the photosynthetic apparatus and loss of chlorophyll (Kozlowski *et al.*, 1991). With the onset of flooding, chlorophyll levels dropped similarly for WS and DS seedlings but there was no recovery in chlorophyll level once the seedlings were drained, indicating chlorophyll degradation could account for the incomplete recovery of net photosynthesis. This hypothesis agrees with the findings of Sena Gomes and Kozlowski (1986), who reported that the leaves of *Theobroma cacao* var. *catongo* seedlings were very chlorotic after 60 d of flooding. However, our results conflict with the report of Pezeshki *et al.* (1996) who concluded that flooding had no effect on leaf chlorophyll concentration for flooded

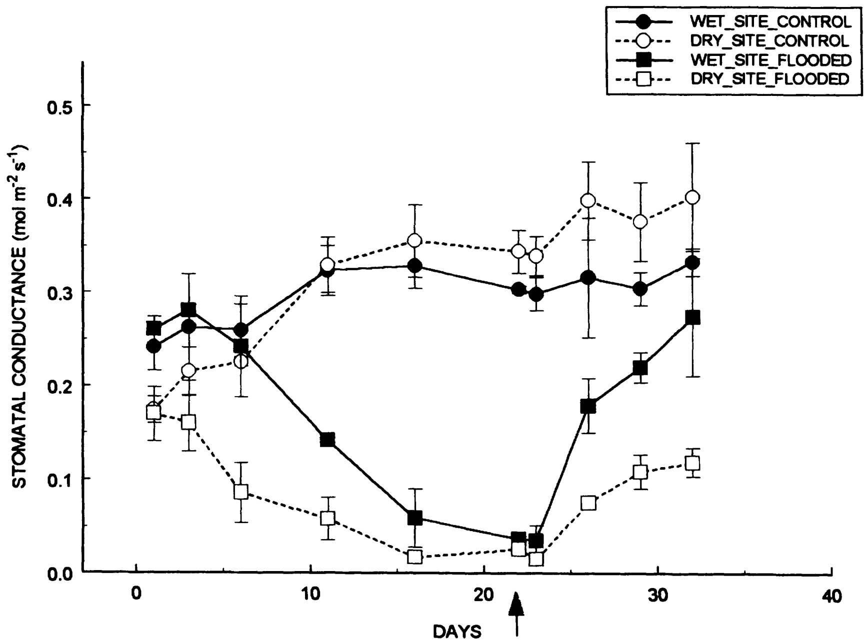


FIG. 5.—Stomatal conductance of control and flooded red maple seedlings. Flooded treatment began on day zero and trees were drained on day twenty-two (arrow). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

*Taxodium distichum, Quercus lyrata* and *Q. falcata* var. *pagodaefolia*. Sibley *et al.* (1996) have shown that SPAD readings correlate well with actual chlorophyll extractions from red maple leaves.

Differences in chlorophyll level suggest that WS seedlings were genetically different from DS seedlings either in their natural level of chlorophyll or in response to growing conditions such as nutrient level or pH in the nursery. This may be an important area for further investigation since ecotypic differentiation for nutrient use and/or uptake is also a possibility.

The differences between WS and DS control seedlings in size, photosynthesis rate and chlorophyll level, along with the fact that there was no significant variation within a site or within a habitat, suggest that either ecotypic differentiation has occurred or that maternal environment effects had an influence on seedling characteristics. These possibilities cannot be separated with the data presented. Response to flooding is confounded by these initial differences in seedling characteristics in the spring flooding study. However, the quicker and larger recovery of photosynthesis during the summer flooding study (when there were no significant differences in control net photosynthetic rates to confound the results) do suggest ecotypic differentiation between wet site and dry site populations of red maple near Ithaca, New York.

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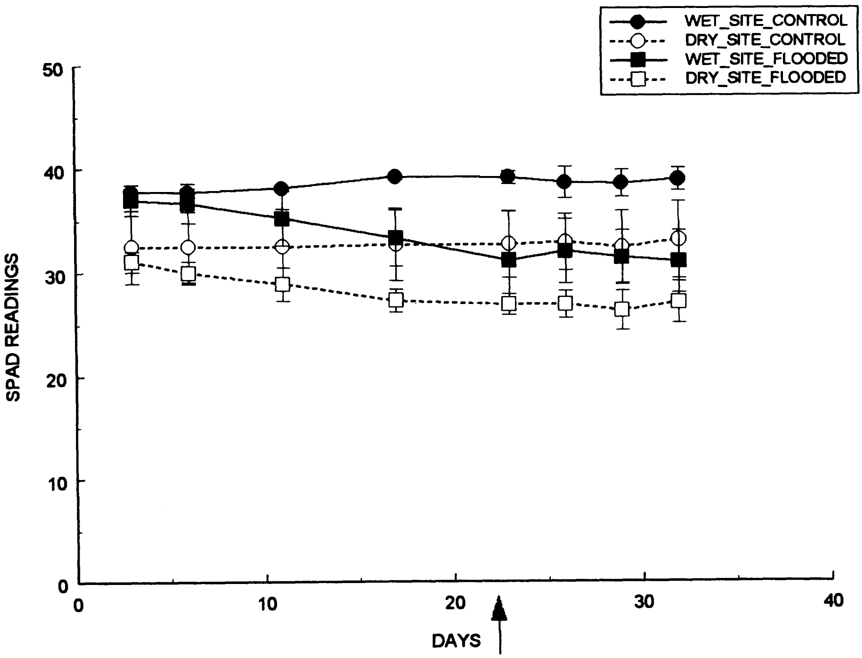


FIG. 6.—SPAD readings for control and flooded red maple seedlings. Flooded treatment began on day zero and trees were drained on day twenty-two (arrow). Error bars represent standard deviation (3 seedlings per habitat averaged by tub × 3 tubs)

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