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Effects of flooding on pitch pine *(Pinus rigida* Mill.) growth and survivorship'

Stephen I. Craine [2,3] and Colin M. Orians

Department of Biology, Tufts University, Medford MA 02155, USA

CRANE S. 1. AND ORIANS C. M. (Tufts University, Medford, Mass.). Effects of flooding on pitch pine *(Pima rigida* Mill.) growth and survivorship. J. Torrey Bot. Soc. 133(2): 289-296. 2006.—Pitch pines *(Pinus rigida* Mill.) colonize the shores of Cape Cod coastal plain ponds in periods of low water and, once established, inhibit the growth of resident herbaceous species, including rare endemics. The effects of flooding on *P. rigida may* vary with plant age and may be affected by previous exposure to flooded conditions. To determine the effects of flooding on pitch pine survivorship, we performed three sets of experiments. First, we examined the effects of relative flood depth--root flooding versus total submersion—on three-month-old seedlings. Second, we determined whether prior exposure to root flooding enhanced subsequent survivorship in flooded conditions one year later. Lastly, we compared the effects of root flooding on pines of different ages—three months, 15 months, and five years. We found that three-month-old *P. rigida* succumbed to total submersion in two to four weeks but tolerated root flooding for up to one year. Fifteen-month-old seedlings that had survived eight weeks of root flooding one year earlier were significantly more flood-tolerant than members of the same cohort that had never been flooded. Fifteen-month-old seedlings, as well as five-year-old saplings, suffered significantly more mortality after four months of root flooding than did three-month-old seedlings. The ability of young *P. rigida,* normally an upland plant, to survive in waterlogged soil appears to be due, in part, to morphologic modifications acquired in response to flooded conditions, including hypertrophy of lenticels on the stem and plagiotropism. Both these acquired modifications are known to help oxygenate root tissues through internal channels, avoiding cellular anoxia despite reduced oxygen availability in the rhizosphere. Overall, our results suggest that periodic flooding has historically played a role in preventing the colonization of *P. rigida* on coastal plain pond shores and that reduced flooding intensity may lead to more frequent encroachment of *P. rigida* in this habitat.

Key words: coastal plain ponds, flood hardening, flood tolerance, phenotypic plasticity, *Pinus rigida,* pitch pine.

Coastal plain ponds, with their gently sloping, sandy shores and irregularly fluctuating water levels, support a large number of rare plant species (Barbour et a]. 1998, Sorrie 1994) that have evolved adaptations to survive frequent but unpredictable flooding (Wilson and Keddy 1986, Schneider 1994). These species are generally poor competitors in more stable environments (Wisheu and Keddy 1994), and if frequency and intensity of flooding decrease, upland plants that were once excluded may begin to colonize these habitats, competing with pondshore endemics (Keddy and Reznicek 1982, Schneider 1992). For example, increasing human exploitation of underground water resources has led to lower water levels and reduced hydroperiod in ponds of Cape Cod, Massachusetts (McHorney 1998), and, coincidentally, large numbers of pitch pines (Pinus rigida Mill.) have colonized the shores of these ponds (Simmons 1996). Once established, dense stands of young pines are capable of excluding resident herbaceous species (Craine and Orians 2004). The extent and duration of flooding required to exclude upland species from these pond shores is not well known.

This is of concern to conservationists since some ponds that were extensively colonized by pitch pines in the 1990s, especially those in the Hyannis Ponds Wildlife Management Area, support exemplary populations of rare coastal plain herbs (Sinnott 1912, McGuire and McHorney 1998). These ponds went completely dry in 1991, during a period of low rainfall and intensive pumping from municipal wells close to the ponds (McHorney 1998). That year, the nearest USGS groundwater monitoring well recorded its lowest reading since it was established in 1958 (McHomey 1998). A cohort of P. rigida seedlings became established in this period on shores of the Hyannis ponds and survived until two consecutive summers of abnormally high water in 1997-98. A few years later, stands of dead saplings as tall as 2-3 m and as dense as 4.7 stems m^{-2} remained on the shores of several of these ponds (Craine and Orians 2004).

The present experiments were motivated by

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[3] E-mail: stevecraine@yahoo.com .

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conservation concerns posed by the colonization of large numbers of pitch pines on these pond shores. Given the lack of experimental data on *P. rigida* response to flooding, we performed a series of experiments on potted seedlings and saplings as an aid to designing water-use guidelines in the area. Our experiments addressed the following four questions: 1) How detrimental to *P. rigida* seedlings are total submersion and root flooding? 2) Can young seedlings develop morphological adaptations to soil anoxia and hypoxia that increase survival? 3) Can *Pinus rigida* individuals become flood hardened, that is, does exposure to flooding at one stage of life increase the ability of the individual to survive if it *is* flooded again? and 4) Are younger seedlings more or less tolerant of root flooding than older seedlings and saplings?

Materials and Methods. THE STUDY ORGAN-
Pinus *rigida* Mill. is a diploxylon pine that is common along the Atlantic coastal plain from New England to Virginia (Little and Garrett 1999). It is most abundant in the Pine Barrens of south central New Jersey. For an essentially mesophytic species, pitch pine is remarkable for the ability of its roots to grow below the water table (McQuilkin 1935). In the Pine Barrens, *P. rigida* is frequently found in wet sites, but on Cape Cod, it is known as an upland species, growing mainly on very well drained, glacial outwash, often in association with oaks (Ledig and Little 1979). Once established on coastal plain pond shores, pitch pines may *cause* profound changes in the herbaceous plant community (Craine and Orians 2004).

For experiments with seedlings, *P. rigida seeds* were collected in October 1999 from several dozen, widely separated trees in an upland area of the Hyannis Ponds Wildlife Management Area. All seeds were combined and stored at 5° C until germinated (Dirr and Heuser 1987). For experiments with saplings, 20 *P. rigida* saplings were purchased from a commercial nursery. These originated from seed collected from an unknown pitch pine population in New Jersey. They were growing in 3.7 L pots, were believed to be about five years old, and averaged 1.37 m tall (range: 1.15-1.55 m).

EFFECT OF FLOODING DEPTH AND DURATION ON FLOOD TOLERANCE. *Pinus rigida* seeds were germinated in December 1999 in potting soil. After two months, approximately 220 seedlings were transplanted into 10 cm diameter pots filled with a mixture of commercial potting soil and washed sand (1:1 by volume).

On March 1, 2000, when seedlings were 5-8 cm tall and most were beginning to develop secondary (true) needles, 180 seedlings were chosen and randomly assigned to each treatment as follows: 20 controls, 80 totally submersed, and 80 root flooded. (Other seedlings of this cohort not used in this experiment were maintained with normal watering and used the in flood hardening experiment a year later [see next section].) All pots were placed in clear plastic tubs (61 X 35 X 29 cm), 10 pots per tub. The two tubs that held control seedlings had drainage holes drilled in the bottoms. The others were filled with water—eight filled to cover the seedlings entirely, and eight filled to about 1 cm above the soil surface. The tubs were kept on two parallel benches in a greenhouse at Tufts University, Medford, Massachusetts.

Each week, seedlings were visually inspected, without disturbing them, for signs of morphological changes that may have been induced by flooding. At two, four, and eight weeks, 20 seedlings from each flooded treatment were chosen at random and removed from the water. Each group of pots removed was allowed to drain and then watered daily to field capacity for three weeks to allow for possible recovery before being scored for survivorship.

After 12 weeks, 10 individuals were randomly selected from the remaining 20 seedlings in each treatment to determine treatment effects on growth. Mean stem mass, stem height, stem diameter, root mass, total mass, and root-to-stem mass ratios were compared among the surviving seedlings (in the root flooded and control groups) using a two-tailed, pooled variance t-test. The remaining root-flooded and control plants, all of which were still alive, were maintained under their respective experimental conditions for an additional 10 months.

EFFECT OF PRECONDITIONING ON FLOOD TOLERANCE. Two groups of 15-month-old seedlings from the cohort germinated in December 1999 were used for this experiment in spring-summer, 2001. The not-previously flooded (NPF) group consisted of 20 seedlings that had not been used in the 2000 experiment. The previously flooded (PF) group consisted of 17 that had survived 8 weeks of root flooding in 2000 and had been watered normally since then. The only difference in the growth histories of these two groups was the eight weeks that the latter group had spent in waterlogged soil. For baseline data, we measured stem height and stem diameter, counted the number of branches, and estimated the percent of needles that were green. Seedlings within each group were randomly assigned to two treatments: root flooding and normal watering. Each 10 cm pot was placed in a 1 L plastic deli container, either with or without a drainage hole in the bottom. All pots were watered daily. Water in the flooded treatments was kept at about I cm above the soil surface. Treatments were interspersed on a bench in the greenhouse at Tufts University, and their positions were rotated several times during the course of the experiment to minimize placement effects.

Observations of the seedlings' condition *were* recorded weekly. Death was defined conservatively as the complete loss of live (green) leaf tissue (Williams et al. 1998). The experiment continued for 17 weeks. Differences in average time to death within treatments and groups were compared statistically using the Mantel-Haenszel logrank test (GraphPad 1999), which tests the similarity between survival curves using the x^2 distribution (Daniel 2005). The logrank test calculates a hazard ratio, which is the probability of an event (in this case, seedling mortality) occurring to an individual in one treatment group divided by the probability of it occurring to an individual in a comparator group (Daniel 2005).

EFFECT OF AGE ON FLOOD TOLERANCE. We compared root flooding versus normal watering across experiments in *P. rigida* three-month-old seedlings, 15-month-old seedlings, and five-year-old saplings. The experimental designs used for each of these age classes were intended to be as similar as possible to allow for general comparisons across age groups, as described below. Survival curves for the two treatments in each of the three age classes were compared using the Mantel-Haenszel logrank test.

Three-month-old Seedlings. In spring 2003, 30 seedlings grown from the same stock of seeds described above were transplanted into 10 cm round pots filled with a 1:1 mixture of potting soil and washed sand. When seedlings were three months old and about 6 cm tall, half were assigned to be root flooded and half to be watered normally. Each pot was placed in a I L plastic deli container, with or without holes, as described in the previous section.

All pots were watered daily. Water in the flooded treatments was kept at about 1 cm above the soil surface. Seedlings were inspected and their condition and survivorship noted weekly. After 17 weeks, 10 seedlings from each group were measured (stem height and diameter), removed from the soil (with the distribution of roots noted), dried, and weighed.

15-month-old Seedlings. To evaluate flood tolerance of older seedlings, data were used from the not-previously flooded group from the flood tolerance experiment. These seedlings experienced the same experimental environment as the three-month-old seedlings.

Five-year-old Saplings. This experiment with 20 saplings was conducted in spring-summer 2001 in an enclosure in an open field at the University of Massachusetts Agricultural Extension Service at Waltham, Mass. Each 3.7 L pot was placed inside a larger pot (approximately 20 L). For the flooded treatments, the outer pots were lined with plastic; the others had large drainage holes. All pots were watered with an automatic watering system that delivered about 1.5 L of water once a day to the control saplings and about 4.5 L once a day to the flooded treatment. This was more than adequate watering for the well-drained saplings and was sufficient to fill the plastic-lined pots to the brim (about 20 cm above the soil surface), even after considerable evaporation between waterings. During the 17 weeks of the experiment, survivorship and the condition of each sapling were recorded weekly. Death was defined conservatively as the complete loss of live (green) leaf tissue.

STATISTICAL SOFTWARE. All statistical calculations were performed using SYSTAT Version 10 (SPSS 2000) except for the logrank tests, which were done in Prism statistical software (GraphPad 1999).

Results. EFFECT OF FLOODING DEPTH AND DURATION ON FLOOD TOLERANCE. Of the three-month-old pitch pines that were totally submersed, 90% survived two weeks, but only 5% survived four weeks of flooding. None of those totally submersed for eight or 12 weeks survived. (No seedlings that appeared dead when removed from the water recovered after three weeks of normal watering.) Root flooding, by contrast, caused no mortality in the 12 weeks of this experiment (Table I). In fact, 11 root-flooded seedlings that were not sacrificed for growth measurements at the end of the 2000 experiment were maintained in this experimental condition

Table 1. Percent of three-month-old seedlings surviving in each of three treatments after four time periods.[a]

Treatment	2 weeks	4 weeks	8 weeks	12 weeks
Total submersion	90%	5%	0	0
Root flooded	100%	100%	100%	100%
Normal watering	100%	100%	100%	100%

[a] N = 20 per treatment, except N = 19 for root flooded × 2 weeks.

in the greenhouse for an additional 10 months (13 months total) without any mortality.

Hypertrophied lenticels were observed on the stems of some root-flooded seedlings beginning in the seventh week. By the 12'k week, all root-flooded individuals had visible !entice] expansion. None of the control seedlings had visible lenticels. On some root-flooded plants, but on none of the controls, one or more roots grew at or above the soil surface.

After 12 weeks of the experiment, all totally submersed plants had been dead and decaying for eight to 10 weeks. Consequently, all measurements taken on these seedlings were far lower than in the other two groups (data not shown). Therefore, a two-sample t-test comparing the two groups of survivors—root flooded and normal watering—was more revealing of the impact of flooding on growth than an ANOVA comparing all three treatments. Mean stem height and stem mass did not differ significantly between the root-flooded and normally watered seedlings (Table 2). Normally watered seedlings, however, had significantly greater root mass (and therefore greater total mass and higher root-to-stem mass ratios) than did the root-flooded seedlings (Table 2). Moreover, the distribution of roots differed between the two treatments. Roots of normally watered seedlings were concentrated in the lower 25% of the pot, while the majority of live roots on the root-flooded seedlings were in the top 25% of the soil, with some at or above the surface. Finally, mean stem diameter in the root-flooded group was significantly greater than in the normally watered group (Table 2).

EFFECT OR PRECONDITIONING ON FLOOD TOLERANCE. There were no significant differences in baseline stem height, number of branches, or overall percent green needles between the previously flooded (PF) and not-previously flooded (NPF) groups ($P > 0.18$; data not shown). Only stem diameter differed significantly. The mean baseline diameter for PF seedlings was 3.83 mm (± 0.17 SE), and for NPF it was 3.26 mm (± 0.09) (t 3.09, df 35, p= 0.004).

Root-flooded seedlings had much lower survivorship than normally watered controls in both the PF and NPF groups (Figure 1). In both groups, normally watered plants suffered no mortality in the course of the 17-week experiment. Between the two root-flooded treatment groups, *P. rigida* seedlings that had experienced eight weeks of root flooding one year earlier survived significantly longer than those that had not previously grown in waterlogged soil (logrank test: $x2 = 6.851$, df = 1, hazard ratio: 3.069, 95% CI = 1.496 to 16.48; p = 0.009 In the flooded treatments, NPF seedlings reached 50% mortality between weeks nine and 10, and 90% were dead by week 13. The first mortality in the PF group came at week 12 and mortality reached 50% only after 16 weeks.

EFFECT OF AGE ON FLOOD TOLERANCE. Three-month-old root-flooded seedlings exhibited less mortality than 15-month-old seedlings or 5-year-old saplings (Figure 2). As in experiment 1, neither root-flooded nor normally watered three-month-old seedlings suffered any mortality in 17 weeks. As in experiment 1, flooded seedlings had significantly thicker stems, reflecting the observed hypertrophy of lenticels (root flooded:

Table 2. Comparative growth of root-flooded and normally watered seedlings after 12 weeks.[a]

Measurement	Root flooded[b]	Control[b]	t[c]	P
Stem height (mm)	78.5 ± 5.7	86.6 ± 4.4	1.129	0.274
Stem mass (g)	0.655 ± 0.059	0.644 ± 0.045	0.148	0.884
Root mass (g)	0.327 ± 0.045	0.731 ± 0.039	6.791	<0.0001
Total mass (g)	0.982 ± 0.098	1.375 ± 0.068	3.301	0.004
Root-to-stem ratio	0.50 ± 0.04	1.16 ± 0.07	8.144	<0.0001
Stem diameter (mm)	3.85 ± 0.28	2.32 ± 0.12	5.020	<0.0001

[a] N = 10 per treatment.
[b] Mean (± standard error).
[c] Two-tailed t-test, pooled variance.

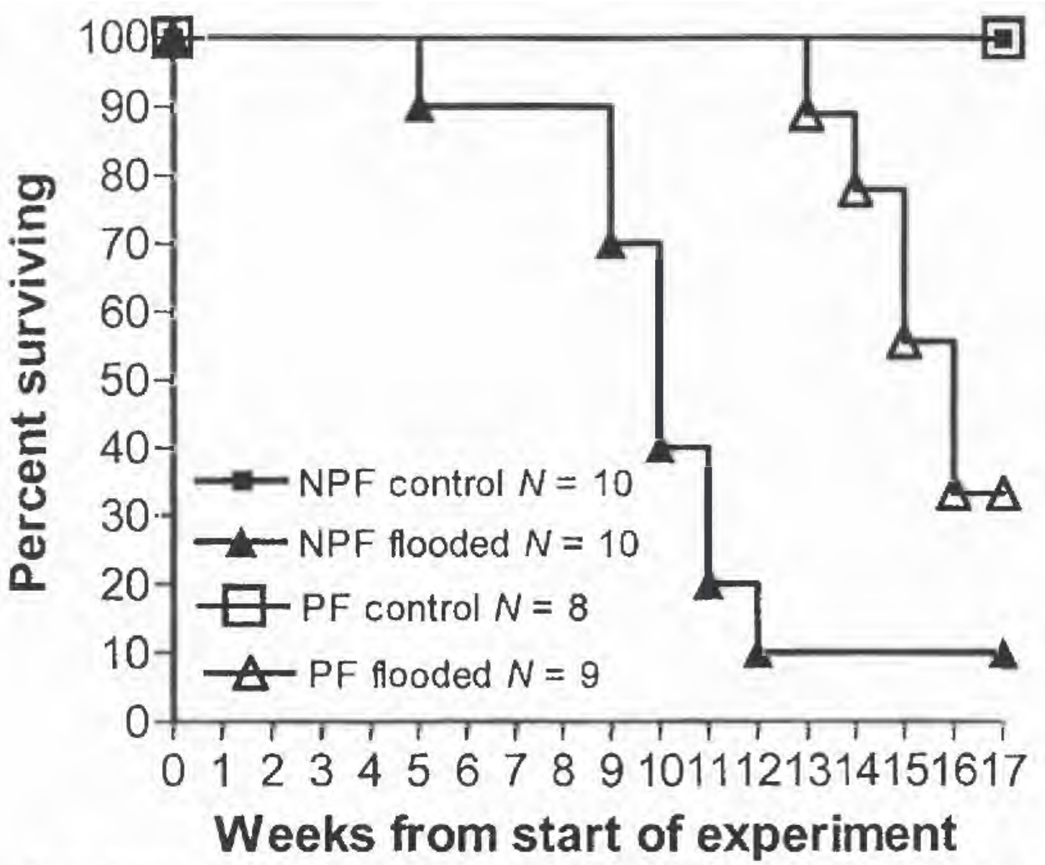

FIG. 1. Survivorship curves for 15-month-old *Pinus rigida* seedlings in two groups—previously flooded (PF, open symbols) and not-previously flooded (NPF, solid symbols)—treated with root flooding (triangles) and normal watering (squares) for 17 weeks. Each symbol represents a week in which new mortality was observed. Mortality was significantly greater in the root-flooded NPF group than in the root-flooded PF group (logrank test: $\chi^1 = 6.851$, df = 1, hazard ratio: 3.069, 95% CI = 1.496 to 16.48; $P = 0.009$).

4.0 ± 0.2 mm, normally watered: 2.9 ± 0.1 mm; t = 4.77, p=0.0002). Seven of 10 flooded seedlings removed from the soil had one or more roots growing at the soil surface; none of the normally watered seedlings had roots at the surface, rather, most of their roots were near the bottoms of the pots.

As reported above, normally watered 15-month-old seedlings that had never been flooded previously had no mortality in the course of this 17-week experiment. Not-previously flooded seedlings that were root flooded in this experiment experienced 50% mortality by week 10, and 90% were dead by week 12.

Among the five-year-old saplings, there was also no mortality in the normally watered group in the course of the experiment. Neither flooded mar control saplings were visibly affected by herbivores or pathogens during this outdoor experiment. For root-flooded saplings, 50% mortality was reached by week 11 and 90% by week 16. Mortality among five-year-old flooded saplings was not significantly different from that of 15-month-old flooded seedlings (logrank test: t = 1.332, df 1, hazard ratio: 1.6, 95% CI = 0.64 to 5.60; p= 0.249).

Discussion. These experiments indicate that young *Pinus rigida* seedlings have considerable ability to survive root flooding and suggest that tolerance to root flooding decreases after the first several months of age. Furthermore, flood hardening appears possible, since seedlings exposed to root flooding in their first season were more tolerant of flooding in the following year than equal-aged seedlings that had never grown in flooded soil.

Induced flood tolerance varies among species

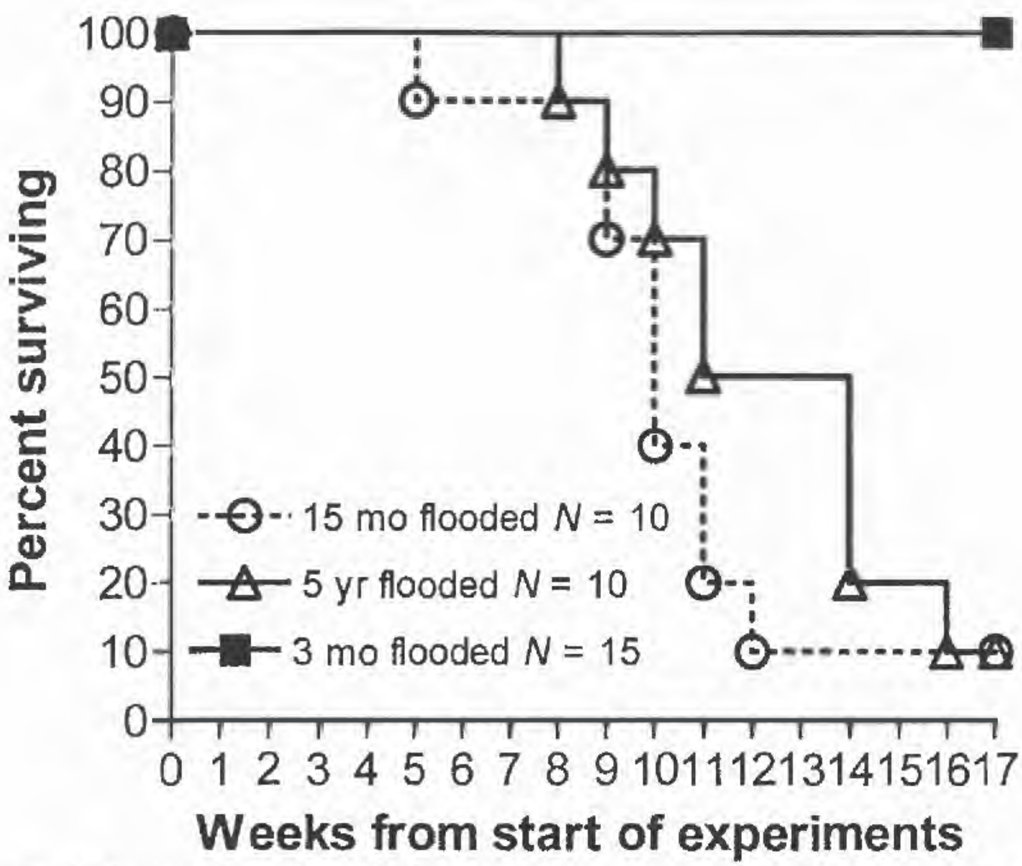

FIG. 2. Survivorship curves for root-flooded *Pinus rigida* three months, 15 months, and five years old. Each symbol represents a week in which new mortality was observed. Root-flooded three-month-old seedlings and normally watered controls in each age group experienced no mortality in the 17-week experiments. The difference in mortality rates between 15-month-old and five-year-old root-flooded groups was not statistically significant (logrank test: $\chi^2 = 1.332$, df = 1, hazard ratio: 1.6, 95% CI = 0.64 to 5.60; $P = 0.249$).

but is known to involve both physiologic and morphologic changes (Gill 1970, Hook et al. 1970, Hook and Scholtens 1978, Justin and Armstrong 1987, Vartapetian and Jackson 1997). Principal physiologic changes involve alterations in metabolic pathways allowing anaerobic generation of ATP (Drew 1997). Morphologic modifications include hypertrophy of lenticels, plagiotropism, aerenchyma, and other changes making internal tissues more porous to oxygen (McKelvin et al. 1987). The role of lenticels in gas exchange has been confirmed in several pine species, including *P. contorta* Dougl. ex Loud. (Philipson and Coutts 1978), *P. clausa* (Chapm.) Vasey, *P. serotina* Michx., and *P. taeda* L.(Topa and McLeod 1986), and *P. sylverstris* L. (Aronen and Haggman 1994).

In our experiments, root-flooded pitch pine seedlings exhibited two visible morphologic changes that could relieve cellular anoxia in waterlogged roots and help explain their ability to survive—expanded lenticels on the stem and a proliferation of roots near or above the soil surface. Soft, spongy lenticels extended outward from the epidermis of flooded pine seedlings. When covering the entire stem of a pine seedling, they added significantly to its diameter. Even one year later, the mean stem diameter of previously flooded seedlings was significantly greater than that of equal aged seedlings that had never been flooded.

It was notable in these experiments that young seedlings subjected to flooding in one year were significantly more resistant to flooding in the following year than were members of the same cohort that had never been flooded. This differential in survival, along with the observed differences in root form and lenticel expansion, suggest that the facultative changes occurring during the first season of flooding continued to confer increased flood tolerance one year later. Flood preconditioning has been found to have no influence on survival in subsequent floods for 10 woody wetland species, including baldcypress *(Taxodium distichum* [L.] Rich.), Atlantic white cedar *(Chamaecypris thyodies [L.]* BSP), and swamp tupelo *(Nyssa aquatica* L.) (McIninch et al. 1994) and for seedlings of three bottomland tree species, baldcypress, nuttall oak *(Quercus nuttallii* Palmer), and swamp chestnut oak *(Q. michauxii* Nutt.) (Anderson and Pezeshki 2001). Anderson and Pezeshki (2001) state that flood hardening in bottomland woody species has not been reported. Perhaps upland species are more amenable to flood hardening, since hardening implies facultative modifications induced only after exposure (Aronen and Haggman 1994, Pigliucci and Kolodynska 2002). In wetland species, flood tolerance is a constitutive adaptation (Drew 1997), leaving less room for phenotypic plasticity in response to conditions experienced in an individual's lifetime.

In the present flood hardening experiment, the likelihood of mortality was three times greater for the not-previously flooded pitch pines (hazard ratio 3.069). The group of pre-exposed seedlings did not surpass 50% mortality until the Le week of flooding, white half of the seedlings not-previously flooded died within 10 weeks. In their natural environment, where spring flooding usually is followed by falling water levels by early summer (Letty 1984, McHorney 1998), the difference between surviving 16 weeks and surviving 10 weeks might determine whether a pitch pine cohort continues to grow and compete with other species on a pond shore.

Our experiments occurred in different years and under slightly different conditions and we were unable to replicate in experimental conditions the exact oxygen content and chemistry of pond water, which is itself highly variable. Nevertheless, root flooding was clearly more detrimental to older seedlings and saplings in this study. This result is consistent with a study of black gum *(Nyssa sylvarica* Marsh.), a wetland hardwood, in which the ability to survive root flooding was found to be greatest in younger seedlings (Keeley 1979). The thicker bark of a sapling, or even a one-year-nld seedling, may limit the effectiveness of lenticels in helping air penetrate into internal tissues, Furthermore, the distance from above-water tissues to the waterlogged roots is greater in taller plants.

Both of the mechanisms observed in these experiments—lenticels and surficial roots (along with other acquired morphologic adaptations which were not evaluated, such as aercnchyma in stems and roots and a more porous Casparian strip)—rely on passive diffusion of gasses and thus can *be effective* only over relatively short distances within the plant (Hook and Scholtens 1978, Vartapetian and Jackson 1997). As roots grow deeper in the soil or as the water level rises higher on the stem, the distance between this source of oxygen and the roots that need it may become too great for diffusion to operate efficiently. This would make it more difficult for larger trees to cope with root flooding than smaller ones, possibly accounting for the differences detected in the present experiments. Hook and Scholtens (1978) report that, while lenticels have been shown to enhance gas exchange in seedlings of woody plants, this has never been clearly demonstrated in mature trees.

Overall, our results suggest that young seedlings, especially those previously exposed to a flooding event, will exhibit higher survival when standing in very shallow water on temporarily flooded coastal plain pond shores. Because increasing human exploitation of underground water resources has been shown to lead to lower water levels and reduced flooding duration (McHorney 1998), we expect pitch pines colonization rates to increase in this habitat. This is of concern since pitch pines can reduce species richness and total herbaceous cover of coastal plain ponds (Craine and Orians 2004).

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