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The impact of experimental sedimentation and flooding on the growth and germination of floodplain trees

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Abstract

Land-use changes in a forested floodplain's watershed can lead to incremental changes in the hydrology and sedimentation rates of the floodplain. The impacts of these changes can be difficult to measure due to the slow response time of mature trees. Seedlings and saplings, on the other hand, may show an immediate response. Responses during these early life history stages can have major consequences for regeneration of floodplain forests and ultimately result in community alteration. This study tested the importance of changes in hydrology and sedimentation on the germination and growth rates of three common floodplain tree species: *Acer rubrum*, *Fraxinus pennsylvanica* and *Quercus palustris*. Two-year-old saplings were grown in a greenhouse under two hydrologic regimes, with or without the addition of sediment. Neither periodic flooding with or without sediment nor static flooding on its own affected the growth of the seedlings. With the addition of sediment, static flooding for two weeks lead to a significant decrease in sapling growth. There was a significant species x treatment interaction, suggesting that each species responded differently to the application of flooding and sediment. The timing of germination and the total percent germination for *F. pennsylvanica* and *Q. palustris* seeds were tested under the same conditions. Flooding and sediment acted in an additive manner to delay the germination of both *F. pennsylvanica* and *Q. palustris* and to reduce the total germination rate of *Q. palustris*. There was no difference in the total germination rate of *F. pennsylvanica* seeds under any treatment. During the growth trials, adventitious roots sprouted on saplings grown under sedimentation. Adventitious roots growing into sediment rather than floodwater should be able to utilize the sediment's nutrients and may compensate for some of the stress of flooding. The results of this study suggest that sediment tolerances will vary among species, but will not necessarily correlate with flood tolerances, and that sedimentation may be as important as flooding in determining floodplain plant community composition.

Introduction

Riparian forests are the most extensive class of wetlands in the contiguous United States (Mitsch and Gosselink 2000). They play an important role in providing wildlife habitat, maintaining water quality and preventing catastrophic flooding (Johnson and McCormick 1979; Taylor et al. 1990; Jordan et al. 2003). Riparian forests are part of the hydrogeomorphic class of mainstem floodplains, wetlands whose primary structuring factors are their sedimentation and hydrologic regimes (Golet et al. 1993; Cole et al. 1997; Lenssen et al. 1999). Floodplains in the northeastern United States are situated in historically forested watersheds and have been heavily impacted by land-use conversion for agriculture or urbanization (Gosselink and Lee 1989; Dahl and Johnson 1991). Because the entire contributing watershed is a source of inputs to a floodplain wetland, changes in the watershed are likely to affect the plant community of a floodplain (Mensing et al. 1998; Wardrop and Brooks 1998). Changes in the plant community may in turn impact the functions of floodplain forests. For example, a change in community structure could influence the ability of the floodplain to remove sediment or store floodwater.

In the diverse and variable habitat known as floodplains, there appears to be one unifying factor: the depth, duration, and timing of flooding are the key variables controlling species composition (Tesky and Hinkley 1977; Metzler and Damman 1985; Klimas 1988; Gosselink and Lee 1989; Lugo et al. 1990). However, previous studies indicate that sedimentation may be as important as hydrology in determining plant community composition. The amount and type of sediment influence wetland soil structure, and sediment can be an important input of nutrients (Craft and Casey 2000; Sanchez-Carrillo and Alvarez-Cobelas 2001; Johnston et al. 2001; Saunders and Kalff 2001). Although sediment is a major component of floodplain forests, and one that is likely to be influenced by changes in the contributing watershed (Gosselink and Lee 1989; Hupp 2000), there has been limited research into the specific effects of sedimentation on wetland plant growth (Adamus and Brandt 1990; Ewing 1996; Girel and Manneville 1988; Wardrop and Brooks 1998; Adamus et al. 2001).

When watersheds are converted to agricultural or urban land-use, both the hydrology and the rates of deposition of sediment in their associated wetlands can change (Troendle and Olsen 1994; Ewing 1996; Luo et al. 1997; Ruhlman and Nutter 1999; Tockner and Stanford 2002). Agriculture, land-use conversion and fragmentation are the most obvious landscape scale disturbances to floodplains (McIntyre and Nancy 1991; Cole et al. 1997; Wardrop and Brooks 1998). Timber harvest in a watershed can alter the total flow, peak discharge rate, and the frequency and duration of flows within a stream (Troendle and Olsen 1994), and urbanization has been associated with hydrologic changes in wetlands (Taylor 1993; Ehrenfeld and Schneider 1993; Ewing 1996). On a longer time scale, Hupp et al. (1993) found substantial increases in sedimentation rates in a forested floodplain over the past 50 years, with the highest rates directly downstream from urban-industrialized areas. In addition to altering the rate of sediment deposition in floodplains, human-induced changes in hydrology can alter the nature of sediment, for example, an increase in the ratio of clay to sand in suspended sediment as a result of agriculture (Kleiss 1996).

The slow response time of mature forest communities to incremental changes in environmental parameters makes it difficult to measure the long-term impacts of these changes in a short-term study (Segelquist et al. 1990). Methods such as tree-ring analysis provide an indication of the impacts of environmental conditions on the growth of individual trees (Tardif and Bergerson 1997; Ford and Brooks 2002). However, because mature trees are relatively tolerant of slight environmental variations, including variations in annual flooding, measures of regenerative ability may be more successful at predicting long-term changes in woody plant community structure (Hook and Scholtens 1978; Noble and Slayter 1980; Mitsch and Rust 1984). A number of researchers have found the seedling and sapling phases to be the most sensitive part of a tree’s life cycle (Ewing 1996; Lugo et al. 1990). This suggests that both species and community level responses to changes in hydroperiod or sedimentation level should be easier to measure in young trees. For example, late season floods may preclude the establishment of seedlings, whereas flooding early in the growing season may prevent germination or delay it to the point that the remaining growing season is too short for successful establishment (Klimas 1988). Understanding the impacts of incremental environmental changes on regeneration of forest communities (by studying early life history stages such as germination and sapling growth) can provide a picture of the probable future of floodplain forest communities.

This study addresses current deficiencies in our knowledge of the structuring factors in floodplain forest by testing three specific hypotheses:

1. Common floodplain tree species will experience different growth and germination rates when subject to sedimentation and flooding, as compared to flooding without sedimentation or control.
2. Static flooding for two weeks and static flooding with sedimentation will have a greater impact on growth and germination than periodic flooding or periodic flooding with sedimentation.
3. Responses to flooding and sedimentation will vary among species.

Table 1. Names and relevant classifications of experimental tree species. Wetland indicator status follows USDA, NRCS (2001): FAC = facultative, FACW = facultative wetland. Flood tolerance follows Tesky and Hinkley (1977).

Scientific Name	Common Name	Family	Wetland Indicator Status	Flood Tolerance
Acer rubrum L.	Red Maple	*Aceraceae*	FAC	Tolerant
Fraxinus pennsylvanica Marshall	Green Ash	*Oleaceae*	FACW	Very tolerant
Quercus palustris Muench	Pin Oak	*Fagaceae*	FACW	Intermediately tolerant

A series of controlled experiments in a greenhouse setting allows quantitative assessment of these hypotheses.

Materials and Methods

These experiments tested the relative importance of changes in hydrology versus changes in sedimentation in the germination and growth rates of three common floodplain trees. Table 1 summarizes the scientific and management classifications of the experimental organisms. *Acer rubrum* L. (Red Maple), *Fraxinus pennsylvanica* Marshall (Green Ash) and *Quercus palustris* Muench (Pin Oak) were chosen for both their range of tolerance to flooding and their importance in forested wetland communities in the eastern United States (Chapman et al. 1982; Redington 1994; Golet et al. 1993). These species also were chosen for the different niches they occupy in floodplain forests. *Q. palustris* (and other wetland oaks) are generally found on infrequently flooded terraces at the highest elevations within floodplains (Mitsch and Gosselink 2000). *F. pennsylvanica* and *A. rubrum* are found at lower elevations, where flooding or soil saturation may last up to several months, with *F. pennsylvanica* occupying slightly wetter sites than *A. rubrum* (Fredrickson 1979; Golet et al. 1993).

Two-year-old saplings of *A. rubrum*, *F. pennsylvanica* and *Q. palustris* were grown in a greenhouse under five conditions: control (field capacity moisture level), static flooding, static flooding + sediment, periodic flooding, and period flooding + sediment. The growth of each species was measured as the change in fresh weight and the change in stem length during one growing season. Growth was compared between the various treatments for each species, and also tested for an interaction between species and treatments. The timing of germination and the total percent germination for seeds of the same three species were tested under the same five conditions, to determine the effects of flooding and sedimentation on seed germination.

Two-year-old blare root saplings of *Acer rubrum*, *Fraxinus pennsylvanica* and *Quercus palustris* were purchased from a nursery that specializes in plants for wetland restoration (Ernst Conservation Seeds, Meadville, PA). All saplings were field grown from seed. Seeds used for germination trials were purchased from Ernst Conservation Seeds and Sheffield's Seed Company (Locke, NY). Soil composition was based on soils found in reference wetlands in central Pennsylvania, as described by Bishel (1994). Details on soil preparation are available in Walls (2001). Play sand was selected as the sediment because it is relatively consistent in size, is of intermediate size as compared to the range of size classes present in wetland soils (Bishel-Machung et al. 1996), and sand is the dominant size class of sediments found in mainstem floodplain wetlands in the Ridge and Valley physiographic province (Brooks et al. 1996). Sand was also chosen because it is low in nutrients, and therefore does not confound the sediment treatment with a nutrient treatment

Growth Experiment

Saplings were planted into 15 cm by 15 cm wide by 41 cm tall plots. Six plants of each species were randomly assigned to the five treatments described below. The pots were placed inside 130 L plastic tubs, nine pots per tub. The tubs were placed on the floor in a greenhouse in University Park, Pennsylvania and supplied with supplemental lighting from 7:00 A.M. to 8:00 P.M. The saplings were planted on May 7, 2000, and treatments began on May 30, 2000. On October 5, 2000 the tubs were moved outdoors to induce dormancy, and plants were harvested on December 12, 2000. Harvesting dormant plants allowed for comparable measurements of plant weight before and after treatments, since no leaves were present at either time.

Treatments

Control: The control tubs had drainage holes on the bottom. Plants were watered with tap water every 2 to 4 days as needed to maintain soil moisture at field capacity.

Static flooding: Beginning on May 30, 2000, the tubs were filled with tap water up to approximately 5 cm above the surface of the soil. A drainage hole in the tub maintained the water level. Water was added as needed (one or two times per week) to maintain the water level. After 2 weeks, flooding was ended using a slow drawdown. Small holes were punched in the side of the tubs to lower the water level 5 cm per day for 6 days. For the remainder of the season the water level was maintained by a lower drainage hole (25 cm below the soil surface and 8 cm above the bottom of the pots).

Static flooding + sediment: Before flooding, 450 cm^3 of play sand was spread evenly over the top of each pot, providing approximately 2 cm depth of sediment. The tubs were flooded and drained a per static flooding.

Periodic flooding: Beginning on May 30, 2000, the tubs were filled with tap water to approximately 5 cm above the soil surface. After 2 days, the lower drainage hole was opened and water drained out to 25 cm below soil surface. After 5 days, the tubs were flooded again for 2 days, then drained again. This weekly cycle of flooded for 2 days and unflooded for 5 days was repeated four times. For the remainder of the season the water level was maintained by the lower drainage hole (25 cm from the soil surface and 8 cm from the bottom of the pots).

Periodic flooding + sediment: The tubs were flooded as per periodic flooding. Before each flooding, 112 cm^3 of play sand was spread evenly over the top of each pot, providing approximately 0.5 cm depth of sediment per flooding and a total of 2 cm depth of sediment over 4 weeks.

Growth Measurement and Analysis

The saplings used in the growth experiment were analyzed for their change in fresh weight and their change in stem length.

Change in fresh weight: Each bare root sapling was weighed before planting. After harvest, soil was washed from the roots and any dead leaves that were still attached to the plant (there were very few) were removed. The change in fresh weight was calculated as the weight after harvest minus the weight before planting. Before planting, *A. rubrum* saplings ranged from 1 to 30 g in weight, *F. pennsylvanica* saplings ranged from 6 to 40 g and *Q. palustris* saplings weighed between 20 and 54 g. Because of the large variation in starting weights, linear regression analysis was performed for each species to see if there was a correlation between weight before planting and the change in fresh weight. The mean pre-planting weight for each species and each treatment was analyzed using a one-way ANOVA with Tukey's test to see if there was a significant difference in starting weights by treatment. Normality and homogeneity of variance were tested with the Anderson-Darling normality test and Bartlett's test.

A one-way ANOVA with Tukey's test was used to look for any significant differences in the mean change in fresh weight due to treatment within one species. The Anderson-Darling normality test and either Bartlett's test or Levene's test were used to test for normality within each treatment and homogeneity of variance between treatments. If the data for a species were not normally distributed or had different variances among treatments, the non-parametric Kruskal-Wallis test was also used to look for significant differences between treatments, and the results of the Kruskal-Wallis test were compared to the results of the one-way ANOVA. All statistics were done with Minitab statistical software (Minitab, Inc., State College, PA).

Change in stem length: At the start of treatment, each stem was measured from soil level to the top of the actively growing shoot or upper-most sprouted bud. For plants that were not yet actively growing, stem length was measured to the top of the stem. The length of each stem was measured again on October 4, 2000 (end of treatment), before the plants were moved outside. The change in stem length was calculated as the length at the end of treatment minus the length at the start of treatment. Statistical analysis of the change in stem length was the same as for the change in fresh weight.

Differences between species: To see if different species responded differently to the treatments, a multi-factor ANOVA test was done using the General Linear Model (GLM). The model tested for the effects of species, treatment and species x treatment on the mean change in fresh weight and the mean change in stem length for each species.

Table 2. Mean change in root + shoot fresh weight[1] in g (standard deviation) during one growing season for three floodplain tree species grown under five different treatments. Asteriks indicate a significant difference within one species between treatment and control ($p < 0.05$, Tukey's test).

	control	static flooding	static flooding + sediment	periodic flooding	periodic flooding + sediment
A. rubrum	23.1 (18.8)	21.7 (21.3)	3.9 (2.3)	41.3 (37.6)	30.1 (26.0)
F pennsylvanica	*191.0 (36.9)	128.7 (42.5)	*109.3 (56.9)	118.0 (28.3)	157.7 (76.1)
Q. palustris	11.2 (16.5)	8.0 (10.8)	3.0 (11.9)	6.5 (8.3)	14.2 (10.4)

1. ANOVA p-values for each species (p-values for Kruskal-Wallis test given in parentheses for those species whose data were not normally distributed or had unequal variances): *A. rubrum*: p=0.136 (p=0.055, Kruskal-Wallis test); *F. pennsylvanica*: p=0.047; *Q. palustris*: p=0.550 (p=0.402, Kruskal-Wallis test).

Germination experiment

The soil, sediment, pots and tubs used for germination trials were the same as for the growth experiment. On December 15, 2000, *F. pennsylvanica* and *Q. palustris* seeds were soaked in water over night, wrapped in moist paper towels, placed inside polyethylene bags and put in a cooler to stratify. *Q. palustris* seeds were planted on April 7, 2001, at a depth of 0.6 cm, 22 seeds per pot. After dewinging by hand, *F. pennsylvanica* seeds were planted on April 10, 2001 at a depth of 0.6 cm, 50 seeds per pot. *A. rubrum* seeds received the same treatment, except they began stratification in March 2001 and were planted on July 2, 2001 at a depth of 0.5 cm, 50 seeds per pot.

Treatments for the germination experiment were the same as for the growth experiment, with the following changes. Five replicated (1 pot = 1 replicate) per species per treatment were used, for a total of 75 pots (3 species x 5 treatments x 5 pots). All of the pots for one treatment (10 pots per treatment) were placed into a tub, as described under the growth experiment. All flooding and sedimentation treatments began on April 11, 2001. Periodic flooding followed the same cycle of 2 days flooding and 5 days drained for 4 weeks as described for the growth experiment. Sediment was applied with flooding as described for the growth experiment. The only major difference was that static flooding treatments received 24 days of continuous flooding before draw down, as opposed to 14 days of continuous flooding for the growth experiments.

Germination rates and analysis

The pots were monitored every 3 to 6 days, and the total number of seedlings in each pot was counted. The experiment ended when no additional seedlings had emerged for 1 week. Percent germination was calculated as the total number of seedlings on a given day divided by the total number of seeds planted. Percent germination for all treatments of each species was plotted against time to show how treatment affected the timing of germination.

The total percent germination was calculated as the maximum number of seeds germinated per pot divided by the total number of seeds planted per pot. The total percent germination for each species was analyzed separately for each species. The Anderson-Darling normality test and Bartlett's test were used to test the normality of the data in each treatment and homogeneity of variance of the mean total percent germination for all treatments. A one-way ANOVA with Tukey's test was used to look for any significant difference in the mean total percent germination by treatment within one species. To look for a difference in response to the treatments by different species, a multi-factor ANOVA test was done using the GLM. The model tested for the effects of species, treatment and species x treatment on the mean total percent germination.

Results

Growth experiment

Sediment, when combined with static flooding, negatively impacted sapling growth in all three species, yet the stress of flooding on its own or incrementally applied sediment had no significant effect on sapling growth (Table 2, Table 3). The change in stem length of *A. rubrum* was significantly less under static flooding + sediment as compared to periodic flooding. For *F. pennsylvanica*, there was a significant difference in both the change in stem length and the change in fresh weight between control and static

Table 3. Mean change in stem length[1] in cm (standard deviation) during one growing season for three floodplain tree species grown under five different treatments. Asteriks indicate a significant difference within one species between the two marked treatments or between treatment and control ($p < 0.05$, Tukey's test).

	control	static flooding	static flooding + sediment	periodic flooding	periodic flooding + sediment
A. rubrum	40.0 (25.2)	31.1 (30.6)	*3.0 (2.1)	41.1 (37.6)	*57.2 (36.2)
F. pennsylanica	*54.8 (9.5)	44.6 (20.4)	*24.8 (18.5)	43.7 (12.)	45.4 (10.8)
Q. palustris	14.0 (12.6)	15.0 (18.6)	1.8 (4.0)	28.9 (18.5)	19.8 (16.0)

[1] ANOVA p-values for each species (p-values for Kruskal-Wallis test given in parentheses for those species whose data were not normally distributed or had unequal variances): *A. rubrum:* $p=0.048$ ($p=0.037$, Kruskal-Wallis test); *F. pennsylvanica:* $p=0.031$; *Q. palustris:* $p=0.058$.

flooding + sediment. *Q. palustris* had a weakly significant difference in the change in stem length between periodic flooding and static flooding + sediment ($p=0.058$). In instances where parametric statistics were not valid due to non-normally distributed data or un-equal variances (change in stem length for *A. rubrum* and *F. pennsylvanica* and change in fresh weight for *A. rubrum* and *Q. palustris*), the non-parametric Kruskal-Wallis test confirmed the results of the ANOVA. The pre-planting weight did not influence the change in fresh weight for any species or treatment (for each species, $p > > 0.05$, $r^2 < 0.01$), and there was no significant difference in the mean pre-planting weight between treatments within one species (for each species, $p > > 0.05$).

There was a clear trend for plants grown under static flooding + sediment to have the lowest growth (Table 2, Table 3). Periodic flooding with or without sediment did not significantly affect the growth of any of the species relative to control. Both *A. rubrum* and *Q. palustris* grew slightly better under periodic flooding, although this difference was not significant. *F. pennsylvanica* saplings grew much more vigorously than either *A. rubrum* or *Q. palustris*, as measured by the change in fresh weight. *A. rubrum* and *F. pennsylvanica* had similar changes in stem length, and *Q. palustris* had the lowest growth of all three species as measured by changes in both stem length and fresh weight. Adventitious roots formed at the base of the stem on *F. pennsylvanica* and *A. rubrum* saplings grown under flooding + sedimentation, but not under flooding alone (Table 4).

Table 4. The number of plants with adventitious roots, out of 6 plants per treatment. Adventitious roots sprouted only in the treatments that received sediment.

	static flooding + sediment	periodic flooding + sediment
A. rubrum	4	4
F. pennsylvanica	5	2
Q. palustris	0	0

The results of the GLM indicate a significant influence for treatment ($p=0.008$), species ($p < 0.001$) and treatment x species interaction ($p=0.048$) for the change in fresh weight. For the change in stem length, there was a significant influence from treatment ($p < 0.001$) and species ($p < 0.001$), but no significant interaction between treatment and species ($p=0.427$). The change in stem length was, however, a less accurate measurement of growth, because some of the saplings had been cut off to a uniform length at the nursery, interrupting the normal growth pattern controlled by apical dominance. Plants that sprouted shoots near the base of the stem had to grow up to 40 cm before a positive change in stem length could be measured.

During the growing season, there were visible signs of stress (leaves turned red) in *F. pennsylvanica* saplings subject to static flooding + sediment and to a lesser extent on saplings subject to static flooding without sediment. This symptom disappeared about one week after flooding was removed. In contrast, *A. rubrum* saplings showed the strongest symptoms of stress under control conditions, with mild symptoms under static flooding + sediment. *A. rubrum* control plants and several of the static flooded plants had moderate to severe intervenal chlorosis on young leaves. Control plants also suffered from an infestation of white flies, which eventually spread to the *A. rubrum* trees of other treatments. Young leaves of several *Q. palustris* saplings had mild intervenal chlorosis beginning about 3 weeks after the start of treatment, regardless of the treatment.

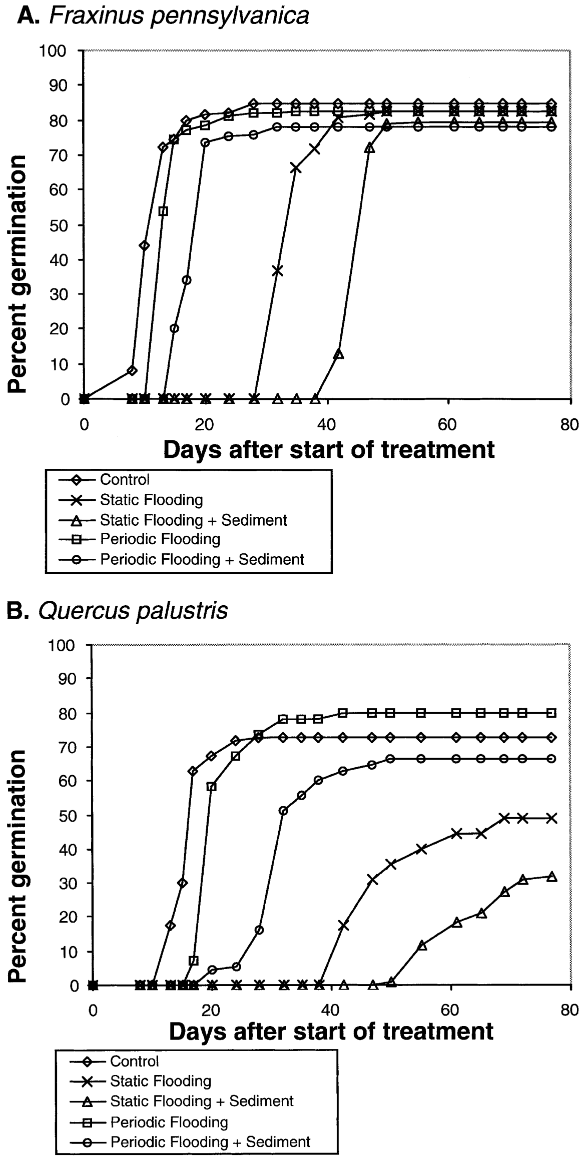

Figure 1. The cumulative percent germination of seeds of (A) *F. pennsylvanica* (B) *Q. palustris* grown under control conditions or static or periodic flooding, with or without the addition of sediment. Each point represents the mean of five replicates. Periodic flooding + sediment, static flooding and static flooding + sediment delayed germination of both species.

Germination experiment

None of the *A. rubrum* seeds in any treatment germinated, so germination data are presented only for *F. pennsylvanica* and *Q. palustris*. The timing of germination of *F. pennsylvanica* and *Q. palustris* was strongly influenced by both flooding and sedimentation (Figure 1). Germination was increasingly delayed as the severity of flooding (from periodic to static) and sedimentation (from absent to present) increased. The effect of flooding and sedimentation on the total germination rate, however, was highly dependent upon the species (Figure 2). Both static flooding and the addition of sediment reduced the total percent germination of *Q. palustris*. The static flooding + sediment treatment had the lowest germination rate, followed by static flooding and periodic flooding + sediment. The pattern was quite different for *F. pennsylvanica*. Despite delays in germination, there were no significant differences in the total germination rate of *F. pennsylvanica* for any treatment. The GLM showed significant differences in the total percent germination for treatment ($p < 0.001$), species ($p < 0.001$) and treatment x species interaction ($p < 0.001$).

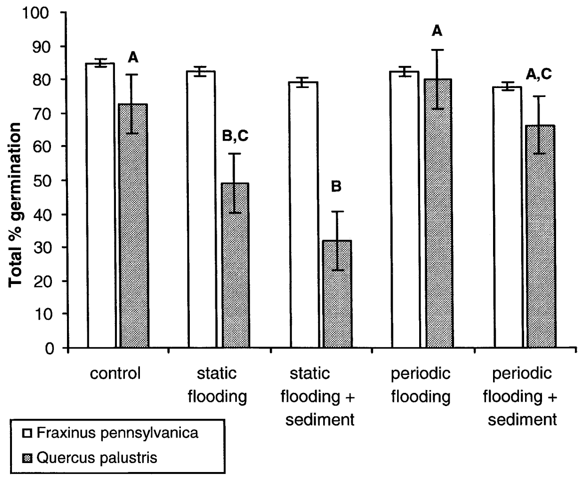

Figure 2. The mean total percent germination ± SE of *F. pennsylvanica* and *Q. palustris* seeds grown under control conditions or static or periodic flooding, with or without the addition of sediment. Letters indicate no significant difference between treatments within one species. There were no significant differences in the total percent germination of *F. pennsylvanica* seeds, regardless of the treatment. *Q. palustris* seeds germinated at a significantly lower rate than control when subject to static flooding, with or without sedimentation.

Discussion

The results of this study suggest that for *A. rubrum*, *F. pennsylvanica* and *Q. palustris* saplings, flooding alone for 2 weeks does not have a significant impact on growth. Similarly, periodic flooding over a period of 4 weeks, with or without applied sediment, did not significantly affect growth. This is consistent with previous studies that have found all three of these species to be tolerant of flooding (e.g., Gill 1970, Chapman et al. 1982, Golet et al. 1993). With the additional stress of sedimentation, however, 2 weeks of flooding did significantly impact the growth of these flood-tolerant trees (Table 2, Table 3). In the germination trials, both sediment and flooding were important variables. For *F. pennsylvanica* and *Q. palustris*, flooding clearly delayed germination (no seeds germinated until stagnant flooding ended). Sedimentation further delayed germination in both stagnant and periodically flooded seeds (Figure 1). For *Q. palustris*, the negative effect of sediment on the final germination rate compounded that of flooding. Sedimentation reduced the germination rate an additional 8% over periodic flooding and 18% over static flooding. For *F. pennsylvanica*, the percent germination was slightly lower for the sediment treatments than for the same flood levels without sediment, but this difference was not significant.

Small, incremental changes in floodplain hydrology and sedimentation rates – such as those tested here – are the kind of changes that often accompany land use conversion within a watershed (Gosselink and Lee 1989). While the 'depth, duration and frequency of flooding' may be the master variables controlling composition of flood plain forests, it was the interaction of sediment and flooding that significantly affected growth and germination in this study. Clearly, sediment can have a profound and variable impact on the regeneration of floodplain trees and the composition of floodplain forests.

Despite limitations in statistical power due to small samples sizes and large variances, there was support for all three of the original hypotheses. The static flooding + sediment treatment consistently had the lowest mean growth, regardless of the species or measure of growth. The variable but consistent decrease in growth or germination associated with the addition of sediment provides strong evidence for the negative impact of sediment on tree regeneration. The striking differences in germination rates under sedimentation, and the less striking, but nonetheless statistically significant treatment x species interaction in the change in fresh weight support the hypothesis that different species will respond differently to the stress of sediment.

Few studies have tested the affects of flood-deposited sediment on tree growth, as opposed to intense sediment loads such as those caused by the placement of fill (Adamus and Brandt 1990, Adamus et al. 2001). Ewing (1996) found reduced growth in wetland trees and herbs under sedimentation, but the levels of sediment used in that study (10 to 18 cm) were considerably higher than most published rates of sedimentation in floodplains (i.e., Lugo et al. 1990; Neely and Wiler 1993; Kleiss 1996). Other studies have shown that flooding alone may delay germination, but does not reduce the germination rates of floodplain trees (Hosner 1957; Neely and Wiler 1993). In fact, *A. rubrum* seeds have been known to germinate in standing water (Hosner 1957). Sediment, on the other hand, has delayed germination of seeds from an emergent wetland seed bank in the greenhouse (Neely and Wiler 1993) or reduced germination in some herbaceous species (Wardrop and Brooks 1998). Delayed germination may be a coping mechanism under flooding or sedimentation (Neely and Wiler 1993), but it could also prevent the successful establishment of seedlings before the end of the growing season (Klimas 1988; Jones et al. 1997).

Odum (1978) proposed that the benefits of flooding (increased water and nutrient supply) may out-weigh the metabolic costs for flood-adapted species. This appeared to be the case with *A. rubrum* and *Q. palustris* saplings, which actually had greater gains in fresh weight and stem length under periodic flooding than under control conditions. Young leaves of *A. rubrum* and *Q. palustris* saplings had intervenal chlorosis, primarily in non-flooded plants. Given the relatively high pH of the soils (7.5-8.3), and the low availability of iron under high pH, iron deficiency was the likely cause of chlorosis. The reducing conditions of flooded soils tend to increase the availability of iron (Marschner 1995). This probably explains why the leaves of flooded plants remained green and may account for the improved performance in periodically flooded plants.

Plants that are adapted to flooding undergo both physiological and morphological changes in response to root inundation, all of which can lead to reduced growth. Physiological changes include alteration of root metabolic pathways and stomatal closure, with accompanying reductions in transpiration, photosynthesis and water uptake (Hook and Scholtens 1978; Lugo et al. 1990; Will et al. 1995; Ewing 1996; Megonigal et al. 1997; Lenssen et al. 1999). While these physiological processes were not measured in this study, several morphological changes typical of flooded trees were apparent (Walls 2001). These include a decrease in root biomass (Megonigal et al. 1997), hypertrophied lenticles at the base of stems (Armstrong 1978), and the formation of adventitious roots (Gill 1975; Hook and Scholtens 1978; Vartapetian and Jackson 1997).

The growth of adventitious roots appears to be a response to increased ethylene production and auxin accumulation at the base of the stem and may or may not provide a benefit to flooded plants (Gill 1975; Hook and Scholtens 1978; Jackson 1990). Adventitious roots are often found growing directly into the floodwater, yet in this study, only plants that received sediment formed adventitious roots, and all adventitious roots grew directly into the sediment (Table 4). Adventitious roots growing into sediment rather than water are able to utilize the nutrients available there. The sediment used in this study was low in nutrients, but sediments deposited on floodplains often carry high levels of both inorganic and organic nutrients (Odum 1978; Khoshmanesh et al. 1999; Steiger and Gurnell 2002). Being at the surface of the soil, newly deposited sediments are also better aerated than lower soil layers, so that adventitious roots could survive and grow. Under this scenario, adventitious roots could be beneficial to the growth and survival of flooded plants.

While the presence of adventitious roots in sediment may serve as a coping mechanism for some floodplain plants, sediment nonetheless had an overall detrimental effect on the growth and germination of the trees in this study. These plants were grown in a greenhouse under controlled conditions, but in actual floodplains, there is a host of pathogenic and predatory organisms that may attack plants weakened by anaerobic soil conditions. Similarly, while the growth of plants subject to static flooding without sediment and plants subject to periodic flooding + sediment was not significantly lower than control in this experiment, there was a trend of slightly reduced growth under these two conditions (Table 2, Table 3). This may be important in natural settings where plants suffer from multiple stresses and competitive interactions.

Conclusions

It is clear that sediment, when acting in combination with flooding, can negatively influence the growth or germination of floodplain tree saplings. It is not yet clear how or if this variable reduction in growth and germination will affect the composition or structure of a floodplain forest subject to increased sedimentation. If the detrimental effects of sedimentation are similar to the effects of flooding, species that are the least tolerant of flooding should also be the least tolerant of sediment. However, sediment probably does not always act in the same manner as flooding. For example, the least flood tolerant tree in these experiments (*Q. palustris*) had the strongest germination response to sediment, but the weakest growth response. Responses to sediment are also likely to vary over time. Sedimentation could at first have the greatest affect on the least flood tolerant species, but eventually have more impact on more flood tolerant species, as low spots fill in with sediment and become more upland in nature. The early stage of impact – during which less tolerant plants that occupy transitional positions between wetland and upland are more heavily affected – has been demonstrated for changes in hydrologic regimes such as those that accompany urbanization of a watershed (Taylor 1993).

To relate the data from growth and germination trials to community changes in floodplains, field studies of floodplain forests that examine landscape scale disturbance, rates of sedimentation and woody plant community structure are needed. Because of the slow response time of woody plant communities, it may be most productive to survey the seedling and sapling populations, or to survey floodplains in watersheds that have been subject to land-use conversion for different lengths of time. Studies of the functions of wetlands subject to varying levels of sedimentation could provide insight into the functional responses of wetlands to sedimentation. Major changes in a stream's watershed should change the nature of the riparian community, but just what those changes are, the vectors of change, and how the changes affect the ecological functions of the floodplain is still an open question. Given the importance of floodplains and riparian plant communities in protecting water supply, providing wildlife habitat and controlling floods, it is a question worth answering.

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