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EFFECTS OF SOIL MOISTURE REGIMES ON GROWTH AND SURVIVAL OF BLACK WILLOW (*SALIX NIGRA*) POSTS (CUTTINGS)

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Abstract: A study was conducted under greenhouse conditions to examine the effects of various soil moisture regimes on black willow (*Salix nigra*) posts (cuttings). Five treatments representing a range of soil moisture regimes, from continuous flooding to mild drought, were imposed separately. A well-watered, well-drained treatment served as the control. Leaf gas exchange (stomatal conductance and net photosynthesis), survival, and biomass production of posts were evaluated. The stomatal conductance and net photosynthesis data clearly demonstrated the sensitivity of willow posts to low oxygen conditions (under flooded treatments) as well as to soil drought. Growth and biomass were also adversely affected by flooding and drought treatments. The patterns of root development along the posts seemed to be associated with the watering regime. Root biomass was depressed in zones subjected to flooding and low soil redox potential. In addition, leaf area, leaf biomass, and shoot (leaf+branch) biomass were significantly lower in the continuously-flooded and drought treatments as compared to control plants. Results indicated that maximum photosynthesis and growth in willow posts required ample soil moisture (but non-waterlogging conditions) and adequate drainage in the top 60 cm of soil. The use of willow posts for streambank restoration remains as a viable strategy; however, considerations should be given to water-table elevations, soil Eh conditions, soil moisture regime, and soil texture in order to improve the prospect for successful results.

Key Words: bioengineering, erosion control, flooding, gas exchange, hydrology, restoration, soil stabilization, wetlands

INTRODUCTION

Willow (*Salix spp.*) posts (cuttings) have been used extensively as a restoration technique to control river bank erosion and to improve natural habitat (Grissinger and Bowie 1984, Shields et al. 1995a, b, Watson et al. 1995). While the practice has proved to be successful in Illinois (Frazee and Roseboom 1997) and Wisconsin, USA (Pingry et al. 1997), in certain other areas the posts have displayed high mortality rates. For instance, in Harland Creek, Mississippi, USA, willow post survival rates were less than 40% by the end of the first growing season (Shields et al. 1995a). Wolfe (1992) reported two-year survival of less than 6% for small willow cuttings planted on unstable, eroding streambanks. Such low rates of success have been attributed to many factors, including soil flooding and drought. However, to date, the exact cause of such poor performance remains unknown. Preliminary field observations and limited physiological data from willow posts planted at Harland Creek site, Mississippi, suggested that soil reducing conditions on lower slopes close to the river bed may be the primary cause of failure of willow posts planted on lower part of slopes (Abt et al. 1996). In addition, periodic soil drought in the sandy upper slope soils may contribute to low willow post survival (Shields et al. 1998). Recent studies have provided additional evidence indicating the influence of soil characteristics (texture) on survival and growth of willow posts (Shields et al. 1998). However, the major influence of soil conditions on posts, at least during the initial establishment phase, seems to be closely related to soil moisture. Water availability for plant use is governed by water-table elevation and soil texture. Further, soil chemistry (e.g., oxidation-reduction potential (Eh)) is also governed by soil moisture and texture, among other variables. Establishment of cuttings in other species within Salicaceae also depends on water table and soil texture (Decamps 1996 after Mahoney and Rood 1992). In the present study, soil texture was maintained constant while imposing various soil moisture regimes. We tested the hypotheses that soil moisture regime (i.e., flooding (and the subsequent low soil Eh)) and soil drought, are primary factors adversely affecting (a) the leaf gas exchange capacity and net carbon fixation; (b) root production and growth; and (c) other biomass components thus altering normal biomass partitioning ratios. Major objectives of this study included evaluation of the effects of static and dynamic flooding regime and drought on (a) root and shoot development in willow posts; (b) patterns of root distribution and biomass production along the buried portion of the posts; and (c) changes in biomass allocation patterns.

MATERIALS AND METHODS

Black willow (*Salix nigra* Marshall) posts were collected from a small, localized population on the Loosahatchie River floodplain in western Tennessee, USA, in late February, 1997 while plants were dormant. Each post was cut so that it was 3.8 cm in diameter at the base, and 1.83 m in length. The existing branches were removed from each post to conform with common planting practices. Prior to planting, the posts were kept in a cold dark storage area with the bottom half placed in moist commercial soil mixture. The time lag between cutting and planting was 4 days. Pots 1.21 m long and 10.2 cm diameter were constructed of PVC pipe and filled with two parts washed sand mixed with one part field soil (v/v). The field soil was Sharkey Clay Series collected from the main floodplain of the Mississippi River in Dyer County, Tennessee. Caps were glued to the bottom of each pot, and holes were drilled on the side to allow control of water regime. Posts with a mean fresh biomass of 1.11 kg (standard error = 0.035) were planted to a depth of 1.17 m in each pot, leaving 0.66 m of post above the soil level. The study was conducted in an air-conditioned greenhouse with an average daily low temperature of 17.2 °C and average daily high temperature of 31.4 °C. Temperatures ranged from a daily low of 11.1 °C in March, to a high of 37.8 °C in May. The only light source in the greenhouse was from the natural light that provided a daily maximum photosynthetic active radiation (PAR) around 1700–1800 μ mol m $^{-2}$ s $^{-1}$ at the top of plant canopy during sunny days. Posts were maintained under well-watered and well-drained conditions for 7 days before treatments were begun. Posts were fertilized weekly with 200 ml of 20-20-20 Peters Fertilizer mixed with tap water at 1.25 g per liter.

Five treatments were used to examine responses of willow posts to soil moisture regimes. The treatments represented a range of soil moisture regimes and soil Eh conditions that could be expected in the field during the growing season. The treatments were (1) control (C), (2) intermittent-flooding (IF), (3) partial-flooding (PF), (4) continuous-flooding (CF), and (5) drought (D). In the control treatment, soil water content was maintained close to field capacity so that plants were subjected to well-watered yet well-drained conditions. Each pot was watered daily with at least 500 ml water, and the water was allowed to flow from the bottom of the pot. The intermittent treatment represented a fluctuating water table. The plants were flooded to 5 cm above the soil surface for two weeks then drained to 60 cm below the soil surface for two weeks. This treatment regime cycled through the study period for a total of 4 flooded periods and 3 drained periods. In the partially-flooded treatment, the water level was maintained at 45 cm below the soil surface for the duration of the study. In the continuous-flooding treatment, pots were flooded to 5 cm above the soil surface throughout the experiment. In the mild drought treatment, representing field drought conditions, drought was imposed by periodically withholding water. The drought treatment was not initiated until day 20 of the study to allow for the initial development of roots and leaves. Droughted posts were watered with 1000 ml (applied as one dose) on every fourth day of the study. Each treatment consisted of eight replicate posts for a total of 40 posts. The study was conducted for a total of 92 days.

Soil Measurements

Measurements of Eh, taken at 15, 30, 60, and 90 cm below the soil surface were conducted daily using platinum-tipped electrodes, a millivoltmeter, and a calomel reference electrode as described in detail elsewhere (Patrick and DeLaune 1977). Measurements were replicated twice at each depth per treatment per measurement day. Soil pH was recorded weekly at 15-cm depth using a pH meter and a pH electrode in all treatments except the mild drought treatment.

Morphological and Anatomical Responses

The general health of all study posts was assessed weekly, carefully noting any changes in leaf and branch color, leaf or branch death. Root porosity, a measure of the percent air space within a root, was measured on posts at the conclusion of the study. Root samples weighing between 0.6336 and 0.8802 g were collected by clipping roots throughout the profile (to provide a sample representative of the whole root system). Root porosity was measured using 50 mL pycnometers as described by Jensen et al. (1969). The pycnometer was first filled with water and weighed. The root was weighed and placed in the water-filled pycnometer and re-weighed. The root was then extracted and ground to a paste with mortar and pestle. The ground root was returned to the pycnometer and weighed.

Gas Exchange and Water Relations

Stomatal conductance (gw) and net photosynthesis (Pn) were measured using a portable photosynthetic system (CIRAS1, PP Systems, England). The gas exchange measurements were conducted periodically on sunny days between 10:00 and 13:00 hours when PAR was close to daily maximum. PAR and air temperature were also measured during each sampling period. Gas exchange was measured on five posts (one fully expanded leaf per post) per treatment on days 16, 18, 27, 35, 37, 49, 60, 68, and 85. Pre-dawn water potential was quantified using a portable pressure chamber. Measurements of pre-dawn water potential provide an estimate of plant water status and soil moisture availability (Kozlowski et al. 1991). Pre-dawn water potential was measured on leaf samples from five posts (one sample leaf from each post) per treatment (excluding intermittently flooded posts) on days 67, 74, and 91. Measurements of pre-dawn water potential were conducted in the latter part of the study because of the schedule followed for the drought treatment.

Leaf Area and Chlorophyll Concentration

Leaf area was measured on ten sample leaves of different sizes from each plant using a leaf area analysis system (AgVision, Decagon Devices, Pullman, WA). Leaf area was then regressed by dry weight. The model used to calculate leaf area was $LA=0.983+(137.24)\ LDW$ ($r^2=0.98$) where LA=leaf area (cm^2), and LDW=leaf dry weight (g).

Chlorophyll concentrations of eight randomly chosen sample leaves from each treatment (one sample per post) were measured at the conclusion of the study. Leaf samples weighing between 0.0272 and 0.0465 g were cut using a hole punch, placed in 10 ml of DMSO and incubated at 70 °C for 2 hours. A spectrophotometer was then used to record absorbance at 645 and 663 nm. Chlorophyll concentration was calculated according to Hiscox and Israelstam (1979).

Biomass

Posts were weighed to obtain initial biomass before planting. Since posts were collected during dormancy, the initial biomass for leaf, branches and root components was zero. At the beginning of the study, no plants had established leaves, although 78% were breaking bud. At the conclusion of the study, posts were carefully removed from the pots and soil was washed from the roots. Posts were divided into above- and below-ground biomass components. The above-ground biomass was further divided into live and dead leaves, live and dead branches, and the above-ground post. The numbers of live and dead branches were also recorded for each post. Below-ground biomass was separated into live and dead root biomass between 0–15, 15–30, 30–60, 60–90, and 90–117 cm below the soil surface. At each depth interval, the number of lateral roots originated from the post was also counted. Roots originated from the post at the depths of between 90–117 cm were not counted due to the difficulty of obtaining accurate data. Roots at that depth had grown into fine mesh placed in the pots to keep the soil from washing through the side holes during watering. No dead roots were found on the study posts at the conclusion of the study. The above- and below-ground portions of each post (without leaves, branches, and roots) were air-dried for three weeks in a greenhouse. All other biomass components were oven-dried at 70°C until reaching a constant weight. To examine the root biomass relationship with soil Eh, root biomass at each depth class was recalculated to correspond with the depth that Eh measurements were conducted. For example, root biomass at 15 cm depth = (root biomass 0–15 cm + root biomass 15–30 cm)/2.

Data Analysis

The general linear models (GLM) and T-test procedures of the Statistical Analysis System (SAS) was used to test differences in measured variables' means. Repeated measures analysis was used to test differences in means of gas exchange data (SAS 1990). SigmaPlot software (version 2.03, Jandel Scientific, Inc.) was used for computing the regression models for the relationship between Eh and gas exchange measurements.

RESULTS

Soil Measurements

Mean soil pH ranged between 7.16 and 7.22 and was not significantly different among treatments. The entire soil profile in control and in the drained zone of the PF pots (0–45 cm depth) remained well-aerated throughout the study as shown by Eh data (Figure 1A). In contrast, soil Eh at all depth classes in the CF treatment, in the continuously-flooded portion of the IF treatment (60–120 cm), and in the flooded portion (45–120 cm) of the PF treatments remained reduced throughout the study (Figures 1B-D). In the IF pots, soil Eh conditions in the upper soil portion (0–60 cm)

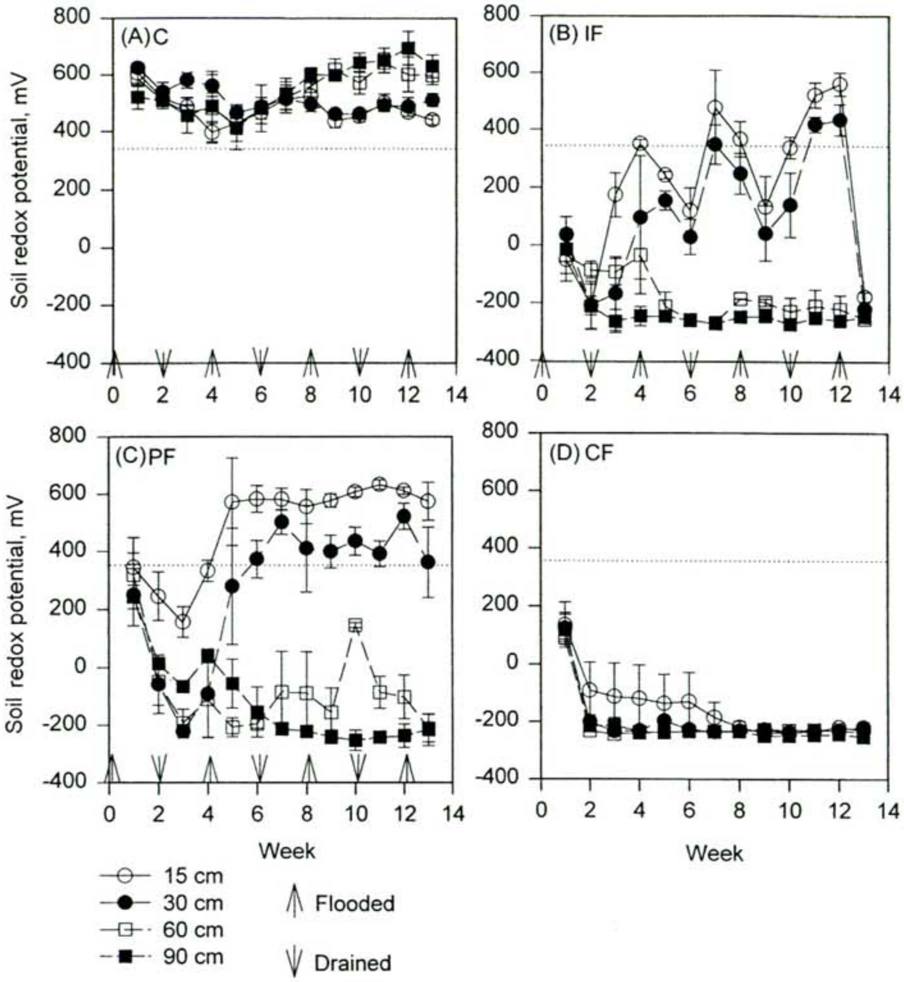

Figure 1. Weekly mean soil redox potential (Eh) at various levels below the soil surface (cm) for control (A), intermittently flooded (B), partially flooded (C), and continuously flooded (D) treatments. Each point is the mean for 14 measurements. Bars represent standard error. Dashed line represents +350 mV Eh, the approximate Eh where oxygen disappears from the soil system. Abbreviations: Control (C), intermittently flooded (IF), partially flooded (PF), continuously flooded (CF), drought (D).

fluctuated from reduced to aerated conditions as water level was raised or lowered, respectively (Figure 1B). Comparison of soil Eh averages over the study period among treatments for each measurement depth showed significant differences among treatments (Table 1).

Plant Responses

Flooded posts developed hypertrophied lenticels, water roots (roots initiated and developed from the portion of each post located under water), and displayed enhanced root porosity. However, root porosity was significantly greater only in CF posts (Figure 2) indicating that development of substantial root porosity in willow posts required continuously-flooded treatment over an extended period of time.

On day 45 of the study, 63% of the posts in the drought treatment appeared stressed as evaluated by the presence of yellowish or brownish leaves, death of branch tips, and leaf senescence. None of the posts in any other treatments displayed any stress symptoms at day 45. At the conclusion of the study 100% of the droughted and 50% of the CF posts displayed stress symptoms. Posts in other treatments displayed no stress symptoms. Mortality of posts in the drought treatment was 25%. Mortality was not observed in the other treatments.

Gas Exchange and Water Relations. Stomatal conductance (gw) of posts in all treatments remained lower than that of control posts throughout the study with the exception of IF posts (Figure 3A). In IF posts, gw fluctuated substantially, from high gw during the first drained period to lower than controls (70% of control) during the second flooding episode (Figure 3A). During the second drained period, gw of IF posts recovered to levels comparable to those of control; however, gw had not recovered in the third drained period (Fig-

Table 1. Soil redox potential (Eh, mV) at 15, 30, 60, and 90 cm below the soil surface, predawn water potential (ψ, MPa) on day 67, 74, and 91 of the study, and mean predawn water potential (ψ, MPa) of willow posts under various treatments. Standard error is shown following mean in ( ). Means followed by the same letter in rows are not significantly different across treatments at the $p < 0.05$ level.

	Treatment				
Dependent Variable	Control (C)	Intermittently Flooded (IF)	Partially flooded (PF)	Continuously Flooded (CF)	Drought (D)
Eh 15 cm	486.3 (10.4) a	149.0 (46.0) b	477.0 (26.0) a	−130.6 (21.8) c	—
Eh 30 cm	524.6 (9.0) a	57.0 (40.0) c	252.0 (42.0) b	−174.4 (22.4) d	—
Eh 60 cm	545.3 (11.0) a	−162.0 (17.0) c	−59.0 (31.0) b	−187.0 (23.4) c	—
Eh 90 cm	550.1 (13.8) a	−215.0 (18.0) c	−86.0 (28.0) b	−184.4 (22.0) c	—
ψ day 67	−0.463 (0.04)	—	—	−0.600 (0.10)	−0.930 (0.09)
ψ day 74	−0.224 (0.03)	—	−0.162 (0.03)	−0.452 (0.08)	−1.220 (0.09)
ψ day 91	−0.300 (0.04)	—	−0.284 (0.01)	−0.452 (0.04)	−0.700 (0.03)
ψ mean	−0.34 (0.03) a	—	−0.22 (0.02) a	−0.51 (0.05) b	−0.95 (0.07) c

ure 3A), showing continued stomatal closure and delayed recovery. The response was in accord with changes in water level imposed on the root system by draining the pots to 60 cm below soil surface during the drained periods and flooding the soil to 5 cm above the soil surface during flood periods. Such shifts in water table resulted in major shifts in soil Eh conditions (Figure 1B). In the PF, CF, and D treatments, gw remained lower than control posts throughout the study (Figure 3A). Over the course of our study, the soil moisture regime apparently had a significant effect on mean gw rate. For instance, mean gw was significantly lower in posts under PF and CF treatments as compared to control (Figure 4A). However, mean gw of posts under IF treatment remained comparable to mean gw of controls. Posts in the drought treatment showed the most sensitivity to the treatment and had the lowest gw, significantly lower than all other treatments (Figure 4A).

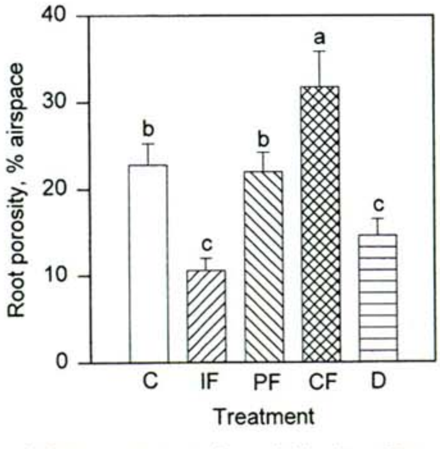

Figure 2. Mean root porosity of black willow posts by treatments. Values represent average over the experimental period. Bars above means represent standard error. Different letters represent significant differences among treatments at the $p<0.05$ level. Abbreviations: Control (C), intermittently flooded (IF), partially flooded (PF), continuously flooded (CF), drought (D).

Net Pn of flooded and droughted posts was lower than that of controls during the entire experiment (Figure 3 B). Minimum values of 10, 21, 23, and 29% of control Pn were observed in the PF, CF, IF, and D treatments, respectively (Figure 3B). Early during the study, Pn in PF posts showed the most sensitivity (Figure 3B) among various flooding regimes. The response may be attributed to less development of hypertrophied lenticels and water roots under this treatment as compared to other flooded treatments. Posts subjected to IF, PF, and CF treatments all had significantly lower mean Pn than control (Figure 4B). In addition, the posts in the drought treatment had significantly lower mean Pn compared to all other treatments (Figure 4B). Repeated measures analysis for gw showed that both the Time (d.f.=8, F=29.68) and the Time × Treatment interactions (d.f.=32, F=3.0) were significant (p=0.0001). Repeated measures analysis for Pn also showed that the Time (d.f.=8, F=25.53) and the Time × Treatment interactions (d.f.=32, F=3.19) were significant (p=0.0001). The "Time × Treatment" interaction indicated that the patterns of changes in gw and Pn over time were different among treatments.

Plant water relations were significantly affected by the soil watering regimes. Pre-dawn water potentials of droughted plants, measured during the last phase of study, were lower (more negative) than those of posts in C, CF, and PF treatments on each measurement date (Table 1). Limited soil watering under drought treatment resulted in development of soil water deficits that in turn induced water stress in posts. The CF posts also showed significantly lower (more negative) pre-dawn water potential than controls, while posts in the C and PF treatments showed similar pre-dawn water

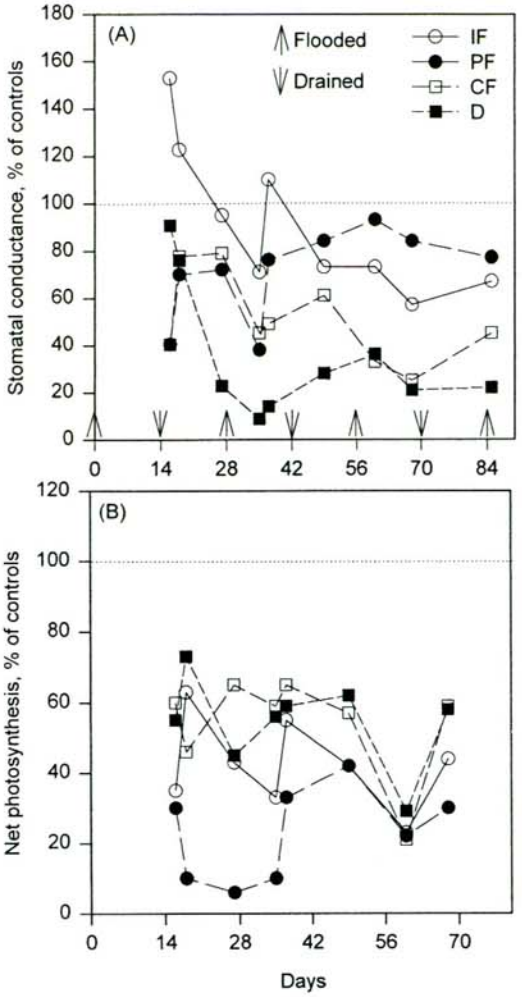

Figure 3. Responses of stomatal conductance (A) and net photosynthesis (B) of black willow posts on each measurement day presented as % of controls. Values represent average of 5 measurements per treatment on each measurement day. Arrows indicate beginning and end of flood periods. Abbreviations: Control (C), intermittently flooded (IF), partially flooded (PF), continuously flooded (CF), drought (D).

potential values (Table 1). The pre-dawn water potential data showed that D and CF treatments resulted in more negative pre-dawn leaf water potential, and thus, the posts under these treatments experienced greater internal water deficits than controls. Such internal water deficits may partially explain the observed reductions in gw and Pn in willows.

Leaf chlorophyll concentration at the end of the experiment did not show any clear pattern of response to the treatments. Posts under IF and PF treatments had significantly lower chlorophyll concentration than the controls, while the concentration was high in CF posts (Table 2). This finding indicated that, while there was some chlorophyll degeneration in willow leaves in IF and PF posts, none was detected in the more severe CF treatment. The high chlorophyll concentrations in leaves of posts subjected to drought treatment (Table 2) resulted from sampling newly developed leaves for chlorophyll determination due to the death of mature leaves.

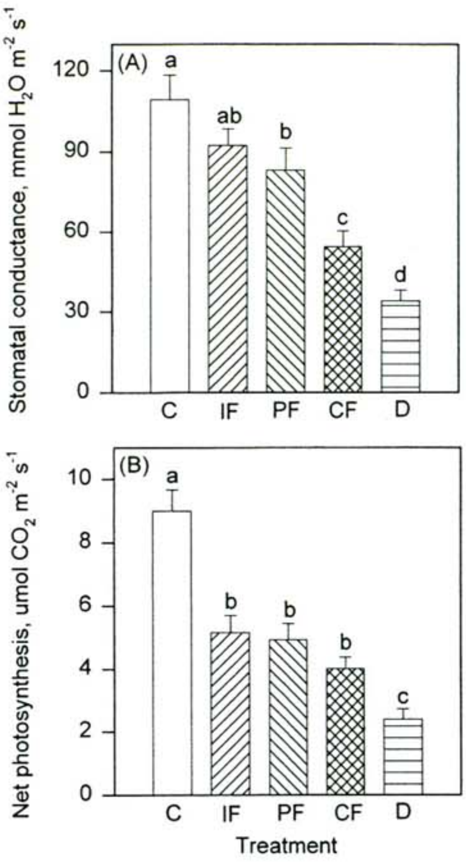

Figure 4. Mean stomatal conductance (A) and net photosynthesis (B) for black willow posts under various treatments. Values represent average over the experimental period. Bars above means represent standard error. Different letters represent significant differences among treatments at the $p<0.05$ level. Abbreviations: Control (C), intermittently flooded (IF), partially flooded (PF), continuously flooded (CF), drought (D).

Growth and Biomass Production. The development of branches and roots on the posts varied depending on the soil watering regime. For instance, the number of live branches on posts in the drought treatment was significantly lower and number of dead branches was significantly greater than in other treatments (Table 3). The number of live branches on CF posts was also significantly lower compared to those in the control and IF treatments. Biomass in willow posts was also negatively affected by soil watering regimes, particularly in the posts subjected to CF and D treatments (Table 2).

The depth at which roots were present varied with

Table 2. Leaf area (cm^2), leaf chlorophyll concentration (mg g^{-1} FW), leaf (g), branch (g), shoot (leaf plus branch, g), root biomass at various soil depths (g), total biomass (g), root/shoot ratio, and root/weight ratio of willow posts under various treatments. Standard error is shown following mean in ( ). Means in each row followed by the same letter are not significantly different across treatments at the $p < 0.05$ level.

	Treatment				
Variable	Control (C)	Intermittently Flooded (IF)	Partially Flooded (PF)	Continuously Flooded (CF)	Drought (D)
Leaf area	62.7 (4.6) a	61.9 (7.7) a	65.6 (5.0) a	23.4 (6.2) b	11.5 (0.6) b
Leaf biomass	45.7 (3.4) a	45.1 (5.6) a	47.8 (3.6) a	17.0 (4.5) b	8.4 (0.5) b
Chlorophyll	3.66 (0.3) a	2.88 (0.2) c	2.94 (0.2) bc	3.57 (0.1) ab	4.18 (0.3) a
Branch biomass	30.6 (4.1) a	36.5 (5.4) a	37.4 (2.5) a	11.4 (3.8) b	4.6 (0.7) b
Shoot biomass	76.3 (6.6) a	81.6 (10.8) a	85.2 (5.0) a	28.4 (8.1) b	13.0 (2.2) b
Root 0–15 cm	3.8 (1.7) b	10.4 (3.6) a	4.1 (0.8) b	4.1 (2.1) b	0.4 (0.1) b
Root 15–30	4.9 (1.5) a	7.4 (1.3) a	6.0 (0.7) b	0.6 (0.2) b	0.5 (0.2) b
Root 30–60	5.8 (1.4) bc	10.0 (3.6) ab	15.5 (2.7) a	0.5 (0.3) c	1.6 (0.5) c
Root 60–90	5.0 (1.3) a	6.5 (3.2) a	1.0 (0.4) b	0.0	1.0 (0.2) b
Root 90–117	14.4 (3.3) a	0.4 (0) b	0.0	0.0	3.0 (0.8) ab
Root 0–117	33.9 (5.0) a	34.7 (5.7) a	26.6 (3.3) a	5.2 (2.5) b	6.5 (0.9) b
Total biomass	110.3 (7.7) a	110.7 (15.6) a	111.8 (7.1) a	33.4 (10.3) b	16.3 (1.7) b
Root/shoot ratio	0.47 (0.08) a	0.35 (0.05) ab	0.31 (0.03) ab	0.19 (0.05) b	0.46 (0.09) a
Root/weight ratio	0.31 (0.04) ab	0.26 (0.03) b	0.23 (0.02) b	0.15 (0.03) b	0.48 (0.12) a

the treatments. The posts in control and drought treatments had roots present along the entire portion of the post under the soil surface. In contrast, the average depths beyond which no rooting occurred under flooded conditions were 58.8, 70.4, and 45.8 cm for posts in IF, PF, and CF treatments, respectively. The number of roots from 0–15 cm was significantly greater in the IF and CF posts compared to control and drought treatments (Table 3). Although posts in the IF and CF treatments produced more roots at 0–15 cm than control posts, the roots did not elongate as much under flooded conditions. Partially flooded posts had a significantly lower number of roots at this depth class compared to the posts in CF treatment (Table 3). No significant difference was found among treatments for the number of roots in the 15–30 cm depth class. The number of roots growing between 30 and 60 cm in CF posts was significantly lower than in all other treatments. All flooded treatments had significantly lower roots at 60–90 cm depth compared to the controls. Total number of roots was significantly lower on the CF posts compared to the IF and D posts. However, drought did not significantly affect the total number of roots.

Biomass of roots growing between 0 and 15 cm below the soil surface was significantly greater on the IF posts compared to all other treatments (Table 2). Root biomass between 15 and 30 cm was significantly lower on CF and D posts compared to posts in the other treatments. Posts subjected to the CF and D treatments also had significantly lower root biomass between 30 and 60 cm compared to the IF and PF posts (Table 2). However, root production was enhanced in posts under PF treatment at the depth that corresponded to the water-table level (i.e., 45 cm below the soil

Table 3. Number of live and dead branches and number of roots originated from 0–15, 30–60, 60–90 cm, and total number of roots from 0–90 cm of willow posts under various moisture regimes. Standard error is shown following mean in ( ). Means in each row followed by the same letter are not significantly different across treatments at the $p < 0.05$ level.

	Treatment				
Variable	Control (C)	Intermittently Flooded (IF)	Partially Flooded (PF)	Continuous Flooded (CF)	Drought (D)
No. of live branches	26.4 (2.7) a	25.5 (2.4) a	23.4 (3.0) ab	16.8 (3.5) b	7.8 (2.2) c
No. of dead branches	1.3 (1.3) b	0.0	1.6 (1.6) b	1.8 (1.4) b	16.3 (3.4) a
No. of root 0–15 cm	15.6 (4.3) c	38.0 (5.4) ab	25.8 (3.1) bc	41.3 (7.0) a	18.3 (4.1) c
No. of root 15–30 cm	26.3 (6.8) a	40.0 (6.2) a	36.0 (6.5) a	25.5 (6.5) a	27.3 (3.4) a
No. of root 30–60 cm	47.9 (9.7) a	53.1 (9.8) a	65.1 (10.3) a	17.9 (8.3) b	53.3 (6.1) a
No. of root 60–90 cm	60.4 (12.5) a	23.6 (14.3) b	22.0 (7.0) b	0.0 c	60.0 (12.5) a
No. of root, total	150.1 (30.6) ab	154.8 (22.4) a	148.9 (18.9) ab	84.6 (16.6) b	158.8 (19.1) a

surface). At 60–90 cm depth, no root growth occurred for the CF posts, and root biomass was significantly lower for posts in the control and IF treatments. Between 90 and 117 cm, both the PF and CF posts had no root production, and root biomass of IF posts was significantly lower than in control posts (Table 2). Overall, the total root biomass (0–117 cm) was significantly lower in posts subjected to the CF and D treatments as compared to other treatments. In contrast, total root biomass was not affected significantly under IF and PF treatments.

The pattern of root development along the posts appeared to be associated with the watering regime. For instance, posts in the control treatment had a fairly uniform pattern of root production between 0 and 90 cm, with substantially more root production found at the deepest portion of the post (90–117 cm depth, Table 2). In contrast, in IF posts where the water level was maintained at 60 cm depth throughout the experiment, the posts developed most roots (80%) in the zone above the water level (i.e., between 0 and 60 cm depth). In PF posts, where water level was maintained at 45 cm depth, little root biomass (only 3.8%), was found below 45 cm depth. Posts under the CF treatment developed most roots in the 0–15 cm depth class (78.8%). Except for portions of posts located in continuously flooded conditions, roots originated fairly uniformly along the posts; however, roots became stunted in the lower zones if standing water and low Eh conditions were present, thus resulting in low root biomass accumulation for that depth class.

Root-Shoot Ratios. Root-shoot ratios of posts in the CF treatment were significantly lower than in controls (Table 2). Further, total root biomass in the CF treatment was 84.7% lower and branch biomass was 62.8% lower than posts under the control treatment. In the IF and PF treatments, roots were more sensitive to low soil Eh than shoots. In posts under droughted conditions, root and shoot biomass were 80.8 and 83.0% lower than controls, respectively. However, in this treatment, root and shoot were affected similarly, and the root-shoot ratio remained comparable to that of control plants (Table 2).

The Relationship Between Soil Eh and Gas Exchange

Plant gas exchange variables were closely correlated with soil Eh conditions. For instance, leaf gw and soil Eh were highly correlated ($r=0.65$, d.f.$=18$, $p<0.01$), with low leaf gw values associated with reducing Eh conditions (Figure 5A). Similarly, low Pn was associated with reducing Eh conditions ($r=0.78$, d.f.$=18$, $p<0.01$; Figure 5B).

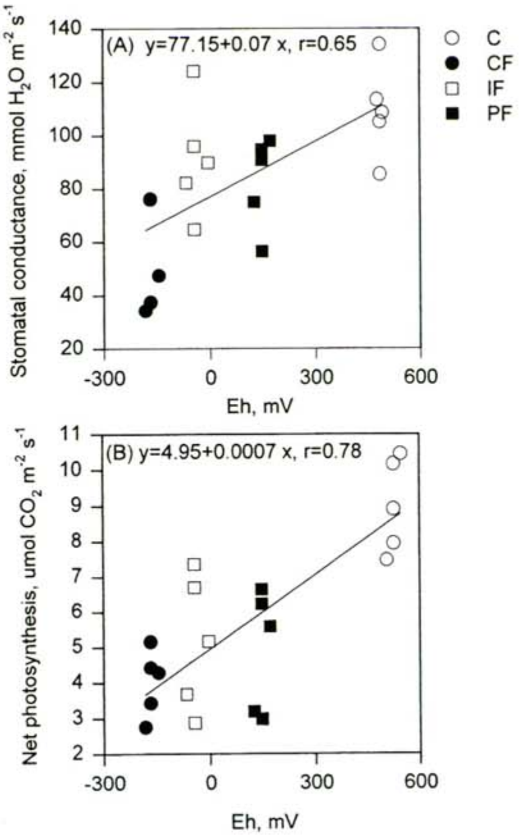

Figure 5. The relationship between (A) mean stomatal conductance and (B) mean net photosynthesis and mean soil redox potential (Eh) over the entire study period for black willow (*Salix nigra*) posts. Abbreviations: Control (C), intermittently flooded (IF), partially flooded (PF), continuously flooded (CF), drought (D).

DISCUSSION

As expected, willow posts displayed many of the characteristics of flood-tolerant plants, including development of specialized morphological and anatomical features. Flooded posts developed hypertrophied lenticels and water roots. Similarly, Donovan et al. (1988) reported massive adventitious root production and hypertrophied lenticel development in black willows under flooded condition. The significance of such morphological adaptations to flood-tolerance has been reported for many woody species (Kozlowski 1984). Willow posts also had high root porosity typical of wetland species even under non-flooded conditions. Posts subjected to flooding had enhanced aerenchyma tissue formation as root porosity in CF posts was significantly higher than the control plants.

Gas exchange data from the present study demonstrated the sensitivity of stomata and net photosynthetic carbon fixation in willow posts to low soil Eh conditions and drought. In PF and CF posts, stomatal conductance and net photosynthesis were significantly lower than in controls (Figure 4A), indicating substantial stomatal closure. Similar results were found in the drought treatment. Stomatal closure in response to both excess soil moisture and moisture deficit has been reported for willows (Dawson 1990, Shields et al. 1998). Decreases in leaf photosynthetic capacity in flooded plants have been attributed to diffusional limitations imposed by stomatal closure and to metabolic (non-diffusional) effects of flooding and drought on photosynthetic processes (Kozlowski 1982). Net photosynthesis of flooded *Salix caprea* L. was reduced while stomata remained open, indicating metabolic effects on the photosynthetic pathway (Talbot et al. 1987). Talbot et al. (1987) reported that the extent of photosynthetic decline in response to flooding in *Salix* spp. was species-specific. Photosynthesis in continuously flooded *S. caprea* seedlings decreased to 25% of control plants. Flooding and low soil Eh conditions can adversely affect photosynthetic activity in woody species considered to be moderately or highly flood-tolerant (Pezeshki 1994). For instance, a decrease in soil Eh from +540 mV to −225 mV reduced net photosynthesis in nuttall oak (*Quercus nuttallii* Palmer) and baldcypress (*Taxodium distichum* (L.) Rich.) by 76 and 19%, respectively (Pezeshki and Anderson 1997).

Net carbon fixation was highest in posts that were subjected to well-watered but drained conditions (Control) or posts subjected to water levels that fluctuated periodically (IF treatment). However, continuous flooding with water levels standing above soil surface (CF treatment) and droughty soil conditions (D treatment) creates stressful situations for willow posts. Abt et al. (1996) noted that willow posts planted along an elevational gradient from a creek differed in survival rates. The posts closest to the creek that were exposed to prolonged, frequent flooding had mortality rates of 80%. The posts at the highest elevations and greatest distance from the creek, which were likely to have experienced droughty conditions, had mortality rates of about 91%. They noted that higher survival rates were associated with the posts located in the area in-between these zones where soil moisture condition was likely to be more favorable to plants.

Root numbers and biomass data indicated the influence of soil moisture regime, water level, and Eh conditions on root initiation and development along the posts. Soil drought and flooding had adverse effects on both root initiation and subsequent root elongation in willow posts (Tables 2, 3). Total root biomass in most depth classes decreased significantly under low soil Eh, suggesting sensitivity of willow roots to reduced soil Eh conditions. The response was similar to the reported patterns of root development and growth in other woody species in response to low soil Eh condition. For instance, in baldcypress seedlings, Eh below +200 mV resulted in significant inhibition of root growth (Pezeshki 1991). In less flood-tolerant woody species such as oaks, Eh below +350 mV resulted in complete cessation of root growth in laboratory rhizotrons (Pezeshki 1991). Root biomass of black willow cuttings decreased significantly in response to flooding (McLeod et al. 1986, Donovan et al. 1988).

Black willow is a flood-tolerant species that possesses the ability to develop morphological and anatomical adaptations to flooding, allowing oxygen transport from aerial parts to the roots. However, as soil Eh decreases, the chemical and biological demand for soil oxygen increases (DeLaune and Pezeshki 1991). Thus, the oxygen delivery system may be overwhelmed by the increasing demand that is concomitant with increased internal demand for oxygen (Armstrong et al. 1994, Pezeshki 1994). In the present study, little or no root growth was found for willow posts at locations that remained subjected to continuous flooding and soil Eh around −200 mV (Table 2). Such a lack of root presence indicated that willow posts either failed to initiate roots or that such roots, if initiated, died after emergence in response to the continued intense soil reducing conditions. The cessation of root elongation in reduced soils may occur for a number of reasons. The increased demand for oxygen within the soil leads to radial loss of oxygen from the root to the surrounding soil (DeLaune and Pezeshki 1991). Oxygen is essential for root growth in both flood-tolerant and intolerant species (Yamasaki 1952). Also, as Eh drops in the soil, anaerobic microbial respiration and chemical reactions may result in the transformation of nutrients to forms that are not available or such that levels become excessive (toxic) to plants. The intensity of the reduction also affects the availability of other macro- and micro-nutrients (Gambrell et al. 1991, Mitsch and Gosselink, 1993).

In CF posts, 78.8% of live root biomass was in the 0–15 cm depth class. Under flooded conditions, this is the zone of greatest potential for root production and activity due to the proximity to soil surface and the water-air interface. This is also the zone close to the portion of the posts where hypertrophied lenticels and water roots developed. Many flood-tolerant woody species develop an extensive shallow rooting system under continuous waterlogging (Kozlowski 1984). Posts growing in IF and PF treatments had a uniform root distribution in different depth classes down to the depth where the permanent water table was present. Below the permanent water table, little root growth was found. Significant reductions in root biomass of black willow cuttings in response to soil flooding has been reported, while wet but well-drained soil appeared to provide the optimum environment for root growth (Donovan et al. 1988). The influence of soil watering regime, water level and Eh condition on above-ground biomass production in willow posts was also observed. Flooding had a significant negative impact on above-ground biomass production (leaf, branches) when flooding was continuous and the standing water remained above the soil surface (Table 2). The sensitivity of willow cuttings to flooding as evidenced by biomass decreases has been reported previously by McLeod et al. (1986). In the present study, similar sensitivity was also found for posts subjected to drought. This response was attributed to several effects of drought on willow posts. For instance, posts under drought treatment had lower predawn leaf water potentials compared to control plants, signifying leaf and root water deficits. A water potential decrease from an average of −0.3 MPa (in control posts) to −0.9 MPa (in posts under drought treatment) was correlated with a 75% decrease in photosynthetic rates. Plant water stress can disrupt many metabolic activities and thus interfere with normal plant growth and development (Kozlowski et al. 1991). It was also evident that leaf stomatal conductance and photosynthetic activities were reduced in response to both continuous flooding and drought.

Greatest gas exchange rates and growth in black willow posts required ample soil moisture but non-waterlogging condition in the upper soil layers. Low soil Eh conditions adversely affected root production, root elongation, and branch growth in willow posts, although roots showed more sensitivity than branches. Black willow posts also showed high levels of sensitivity to droughty conditions. In stream corridor restoration projects, willow posts are planted to stabilize eroding banks in order to facilitate development of a diverse native riparian community through succession. Posts are used to provide physical stability required by pioneer and early succession species. Presumably, survival of a fraction of the willow posts, perhaps as low as 50 percent, for only a few years, may be adequate if survivors are well-distributed in space. The questions of minimum survival rates and time were beyond the scope of this study and need additional research.

The use of willow posts for streambank restoration remains a viable strategy; however, sites should be evaluated prior to planting. As the data of the present study demonstrated, many factors must be considered in future streambank restoration using black willow posts. Pre-planting characterization of such factors as water table, soil texture, soil moisture regime, and soil Eh conditions could improve the prospect for successful results. For instance, areas that are continuously flooded and impose continuous low Eh conditions or upper slopes prone to severe drought could be avoided. Additional work is needed to develop a pre-planting site evaluation protocol.

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