Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Taming the Beast: Managing Hydrology to Control Carolina Willow (*Salix caroliniana*) Seedlings and Cuttings

Pedro F. Quintana-Ascencio,[1,2] John E. Fauth,[1] Luz M. Castro Morales,[1] Kimberli J. Ponzio,[3] Dianne Hall,[3] and Ken Snyder[3]

Abstract

Historically, wetlands along the St. Johns River, Florida, were dominated by herbaceous marshes. However, in the last 50 years many areas transformed to shrub-dominated wetlands, at the same time a system of levees and canals was constructed to control flooding. We tested the role of water management in controlling Carolina willow (*Salix caroliniana*), a native shrub that accounts for most of this shift. We assessed survival and growth of seedlings and cuttings on four artificial islands. We planted willow seedlings and cuttings at the spring waterline and at three higher levels (+17.5, +35, and +50 cm) and evaluated their responses to natural hydrologic fluctuations. Overall, seedlings had lower survival than cuttings. Highest mortality occurred during summer floods and willows greater than 50 cm above marsh surface had the highest survivorship. Surviving seedlings attained similar height and biomass among elevations, but the cuttings had greater stem diameter, stem height, and biomass at higher elevations. In the second experiment, we planted seedlings and short (25 cm) and tall (50 cm) cuttings at the waterline and at three higher levels (+25, +35, and +50 cm) in artificial ponds with controlled water levels. Before flooding, seedlings at the highest elevation suffered some mortality due to desiccation, but after flooding, they had the highest survival. Elevation did not affect cutting survival, but those at the lowest elevation had the greatest height and biomass. Hydrologic manipulation can be a powerful tool to control willow establishment. However, its success depends on timely and prolonged inundation or water drawdown.

Key words: **artificial island, artificial pond, hydrology, river, wetland restoration, woody shrubs.**

Introduction

Hydrology is a major factor determining the composition of wetland plant assemblages (Mitsch & Gosselink 1993; Busch et al. 1998). Long-term changes in wetland inundation can dramatically change community structure and composition (Thibodeau 1985; van der Valk et al. 1994; Fisher et al. 1996). Prolonged flooding favors submerged and floating vegetation (Thibodeau 1985; van der Valk et al. 1994), while shorter inundation periods favor woody species (Thibodeau 1985; Fisher et al. 1996; Wheeler et al. 1999; Timoney & Argus 2006). Consequently, shortened inundation can promote the conversion of herbaceous wetlands into shrub-dominated wetlands (shrub swamps). Complete replacement of herbaceous wetlands by shrub communities decreases landscape heterogeneity (Kinser et al. 1997), biodiversity (Miller et al. 1998), and ecological (Southall et al. 2003) and economic values.

Management of streams and other freshwater bodies has had unintentional negative consequences for native ecosystems. In some instances, there is a demise of native species, as in the Mary River, Alberta, Canada, where river impoundment and over-allocation has reduced the abundance of *Populus* spp. (Rood et al. 1995). In other systems, human-induced alterations of the hydrology have increased the distribution of nonnative species, as in the case of Russian olive (*Elaeagnus angustifolia*) in western North America (Katz & Shafroth 2003). In Australia and South Africa, exotic willows (*Salix* spp.) were introduced to stabilize soil around water courses, but their spread has resulted in obstructed streams, displaced native vegetation, and reduced water quality and availability (Hendersona 1991; Cremera 2003; Stokes 2008; Giljohann et al. 2011).

The headwater region of the Upper St. Johns River (USJR) in east-central Florida, U.S.A., contains 120,000 ha of herbaceous wetlands, shrub swamps, and forested wetlands. Beginning in the early 1900s, a network of levees and canals was established to facilitate agricultural production and control flooding (St. Johns River Water Management

---

[1] Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816-2368, U.S.A.
[2] Address correspondence to P. F. Quintana-Ascencio, email pedro.quintana-ascencio@ucf.edu
[3] Division of Environmental Sciences, St. Johns River Water Management District, PO Box 1429, Palatka, FL 32178-1429, U.S.A.

doi: 10.1111/j.1526-100X.2012.00940.x

District [SJRWMD] 2007). Thirteen of these canals diverted water from the USJR to the Intracoastal Waterway (Clapp & Wilkening 1984). By 1980, approximately 38% of the annual floodplain wetlands were converted for agricultural uses (Tai & Rao 1982). Concomitantly, in the upper reaches of the USJR, flood elevations increased by 0.60 m, average flow rates fell to 55%, and average 30-day low-flow rates dropped to 15% of predevelopment rates (Tai & Rao 1982). During the same time, woody shrubs, primarily Carolina willow (*Salix caroliniana* Michx.), invaded areas that historically were herbaceous marsh (Hall 1987; Kinser et al. 1997; Miller et al. 1998).

Considerable resources are being expended by the SJRWMD to manage and restore herbaceous wetlands, both in natural and former agricultural lands. It is imperative to manage these areas to prevent expansion of shrub swamps. Effective management requires a better understanding of how changes in hydrology affect expansion by woody species and exacerbate loss of herbaceous wetlands. We experimentally investigated the potential role of water management in controlling the expansion of Carolina willow in the St. Johns River marshes. First, we evaluated the effect of in situ water level variation on willows transplanted onto artificial islands in the headwaters of the St. Johns River. Second, we assessed how constant inundation affected vital rates of willows transplanted into artificial ponds. We evaluated the tolerance of transplanted willow seedlings and cuttings (as surrogates of juvenile plants) to inundation. We identified hydrologic conditions useful for reducing willow establishment and maintaining herbaceous wetlands within the USJR.

Methods

Study Sites

The St. Johns River is the longest river in Florida. It is shallow (during normal conditions, <3–4 m deep in the USJR), traverses the central and northeastern portions of the peninsula, and only drops 8 m along its 440 km length (DeMort 1991). Its headwaters are dominated by vast marshes and swamps with a defined river channel forming approximately 45 km from the most upstream boundary of the USJR Basin. We conducted Experiment 1 in the headwater region on the eastern margin of Blue Cypress Water Management Area—West (BCWMA-W), Indian River County, Florida. We conducted Experiment 2 within the St. Johns River watershed, in 40-year-old artificial ponds on the University of Central Florida (UCF) campus.

Experiment 1. Flooding on Artificial Islands

We created artificial islands in BCWMA-W to evaluate the effect of water depth, plant stage (seedling vs. cutting), and cardinal orientation on survival and growth of Carolina willow. We constructed four islands 100 m apart and 10 m from the eastern levee. Heavy machinery was used to pile submerged, peaty soil into mounds that we shaped using a polyvinyl chloride (PVC) frame constructed of 1/2 inch Schedule 40 PVC (Charlotte Pipe and Foundry Company® (Charlotte Pipe®, Charlotte, NC, U.S.A.) pipe and fittings. The resulting islands were shaped as truncated pyramids rising 0.5 m above the waterline, with a 1.5 × 1.5 m base at the waterline and 0.75 × 0.75 m tops (volume = 0.66 m^3).

In January 2009, before leaf out, we obtained willow cuttings by harvesting branches and pruning them to a length of 25 cm (mean stem diameter = 0.56 cm, SD = 0.14 cm, $n = 600$). We maintained cuttings for 3 weeks in buckets with water, where they grew roots and shoots, and then were transferred into 420 mL pots with approximately 90 g of commercial potting soil until transplanting. We collected seeds in March 2009 and planted 30 seeds into similar pots within 24 hours. We collected both plant stages (cuttings and seeds) from four different locations or provenances along the southern half of the St. Johns River: at the intersections of the river with Florida State Road (SR) 46, SR 520, US Highway 192, and SR 60. By including plants from different locations we incorporated potential regional genetic variation in traits into our experiments. On 7 April 2009, we transplanted seedlings ($n = 270$) and cuttings ($n = 60$) onto the artificial islands at all cardinal directions (north, south, east, and west) and at four different heights: marsh soil level and +17.5, +35, and +50 cm above it. Because of variable germination and seedling survival among pots, final number of seedlings transplanted varied by location (mean = 4 + 3.1 SD, minimum 1, maximum 10 seedlings). We maximized distance (>20 cm) and interspersion among transplants across eight possible locations at each height and randomly distributed plants from the different provenances. On each island, one random location remained empty because we did not have enough cuttings from Hwy 192. We only tested provenance and island as main effects because of the unbalanced design. We used colored flags and tags to mark the positions of seedlings and cuttings, and monitored them monthly until February 2010. At this time, cuttings started losing leaves and flowering, so we removed willows to avoid spreading seeds. We estimated daily marsh water levels by averaging hourly values obtained from a radio-telemetered staff gauge at this site.

Experiment 2. Flooding in Artificial Ponds

We used three experimental ponds (~15 m wide × 60 m long × 2.5 m deep) at UCF to manipulate flooding directly. We transplanted three stages of willow (seedlings and short [25 cm] or tall [50 cm] cuttings: each $n = 48$, 144 total) at each of four positions above the initial pond waterline: 0, +25, +35, and +50 cm. Each treatment was replicated twice within each of six experimental blocks, which were located on the east and west sides of three separate ponds. We obtained willow cuttings and seeds from the intersection of the St. Johns River and SR 520. We collected cuttings in January 2010 and pruned branches to either 25 or 50 cm. We maintained cuttings for 3 weeks in buckets with water and then transferred them to 420 mL pots of potting soil until transplanting. We obtained seeds in March 2010 and sowed 30 per pot within 24 hours. One day before transplanting, we thinned seedlings to one per pot. In April 2010, we planted willow seedlings and cuttings at least 1 m apart. We maintained ponds without standing water and watered plants for a month-long acclimation phase while they became established. In May 2010, we gradually raised the water level until the root collar of the plants at the highest level (50 cm) was at the waterline. At this point, the root collars of the other plants were 0.25, 0.35, or 0.5 m under water. We maintained this flooded condition and monitored plants monthly until November 2010 when the experiment was terminated, recording survival and growth. Then we drained the ponds and removed the willows.

Analysis

We used analysis of variance (ANOVA) in both experiments to test for differences in mean stem diameter, height, and biomass among treatments and locations. Differences among treatments were evaluated using regression models with dummy variables. We compared parametric regressions with the function *survreg* in *R* to evaluate survival trajectories among plants in different treatments and locations. We assessed final number of survivors with linear models with Poisson errors. We checked compliance of model assumptions by inspecting plots of standardized residuals against fitted values of independent variables.

Results

Experiment I. Artificial Islands

In April 2009, at the beginning of Experiment 1, cuttings from different provenances, and located on different islands, elevations, or orientations, did not differ significantly in initial stem diameter (overall mean 0.62 cm, SD = 0.12 cm, $n = 60$, all $p > 0.19$). However, cuttings from the northernmost and southernmost provenances had significantly fewer leaves (24 ± 15 and 22 ± 6 leaves; mean and SD, respectively, hereinafter) than those from central populations (36 ± 13 and 41 ± 18 leaves; by provenance starting at the northernmost). In contrast, the initial number of leaves on cuttings did not differ significantly among different islands, elevations, or orientations (all $p > 0.22$, data logarithmic transformed). Seedlings were too small for measurement.

Seedlings. Only 48 seedlings (17%) survived until the end of the experiment. Survival was heterogeneous across time and most mortality was associated with inundation, when marsh water levels increased circa 0.5 m (Fig. 1). Survival was intermediate for seedlings at +35 cm (45%) and +50 cm (41%) elevation, low at +17.5 cm (6%), and zero at the initial waterline ($p < 0.001$ for all comparisons except 35 cm vs. 50 cm, with $p = 0.126$; Fig. 1). Final number of survivors was affected by initial seedling density, orientation, and island. The number of survivors was positively related to the number of initial seedlings transplanted (coefficient 0.44 ± 0.09, $p < 0.001$). Survivorship was significantly greater on the northern side of islands than on eastern sides ($p = 0.03$), and more seedlings survived on the northernmost island than on the next island to the south ($p = 0.02$). Final seedling height (51.8 ± 7.6, 38.9 ± 25.3, and 36.3 + 24.4 cm, respectively for seedlings at increasing elevation) and biomass (1.60 ± 0.85, 1.17 + 1.24, and 1.09 + 1.25 g) did not differ significantly among elevations. At the end of the experiment, only eight (16%) seedlings had leaves and none flowered.

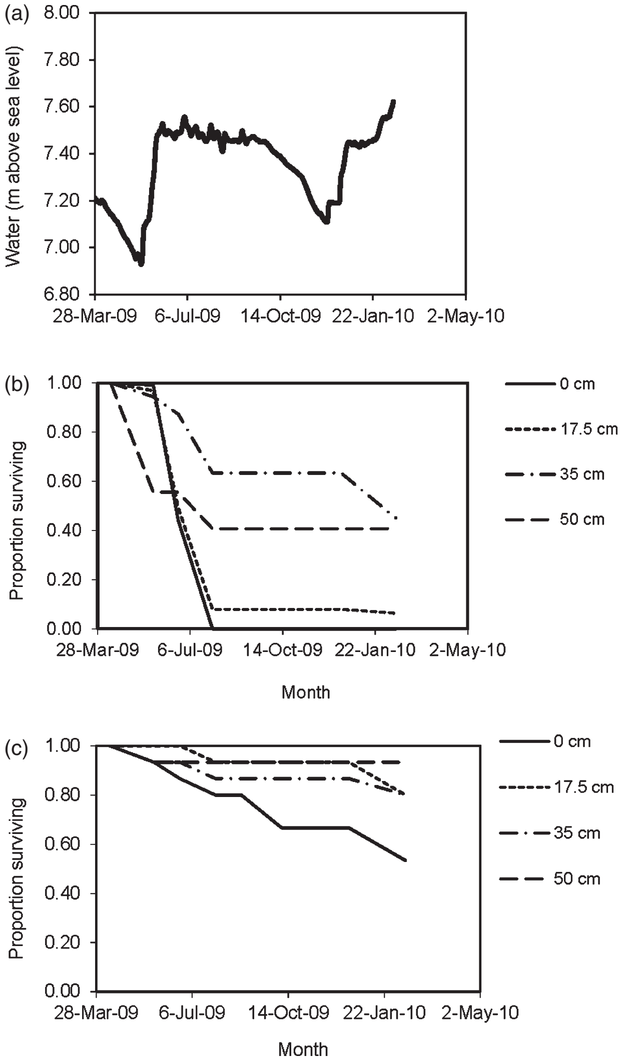

Figure 1. Water level (m) in Blue Cypress Water Management Area-West (BCWMA-W) (a), and proportion of seedlings (b) and cuttings (c) surviving on artificial islands by elevation and date.

Cuttings. Forty-six cuttings (77%) survived until the end of the experiment, 10 months after transplanting, and most mortality occurred during the highest inundation (Fig. 1). Although our data showed no significant differences in survival trajectories among elevations ($p > 0.37$), there was a general trend of increased survivorship at higher elevations. Most cuttings (93%) survived at the +50 cm elevation, slightly fewer (80%) at intermediate elevations (+35 and +17.5 cm), but only half (53%) at the initial marsh waterline. Many cuttings at the lowest elevation were smothered by algae

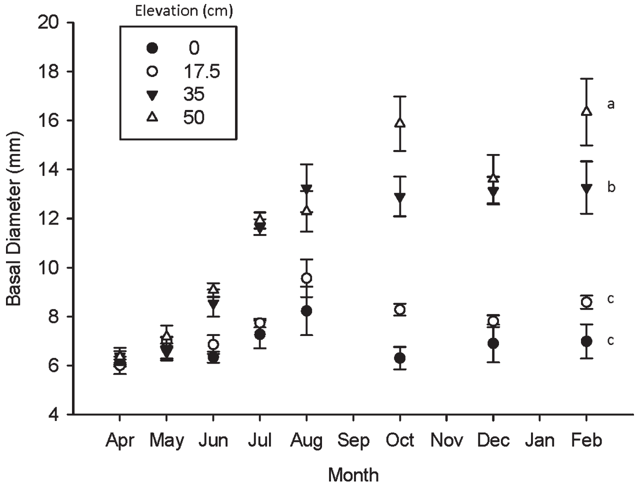

Figure 2. Mean (± SE) basal stem diameter (mm) of Carolina willow cuttings by elevation and month on artificial islands. Different letters indicate significantly different final diameters at $\alpha < 0.05$ level.

and floating plants, and were unable to keep their leaves and stems above water. Consistent with the phenology of native Carolina willows, 35% of survivors were defoliated and 30% flowered (10 males and 4 females). Percentage of flowering individuals was 0, 42, 50, and 21% for increasing elevation, respectively.

Stem diameter increased during the first 4 months after transplanting and then leveled off (Fig. 2), coinciding with the highest inundation level, which flooded plants below +35 cm elevation. Mean stem diameter at the end of the experiment differed statistically among all elevations except 0 and +17.5 cm and was greater at higher elevations (Table 1; Fig. 2). Elevation had a weak effect on mean stem height (70.3 ± 18.8, 70.4 ± 15.6, 92.5 ± 27.1, and 93.7 ± 31.9 cm, respectively with increasing elevation, Table 1) but substantially affected aboveground biomass (8.9 ± 4.8, 12.6 ± 5.7, 28.4 ± 17.7, and 41.5 ± 39.7 g, Table 1). Stem diameter was significantly correlated with height and aboveground biomass ($r^2 = 0.50$ and 0.61 respectively, $p < 0.001$, $n = 46$). Stem diameter, height, and biomass of willow cuttings at the end of the experiment did not differ significantly among islands, provenances, or cardinal orientation (Table 1).

Experiment 2. Flooding in Artificial Ponds

In April 2010, at the beginning of Experiment 2, stem diameter did not differ significantly among cuttings of different lengths, or those planted at different elevations (overall mean = 0.97 cm, SD = 0.24 cm, $n = 144$, all $p > 0.3$). Seedlings were too small (<1 cm high) and delicate to be measured at transplant.

Seedlings. At the end of the acclimation phase (May 2010) and before flooding the ponds, willow growth already differed significantly among ponds, plant stages, and elevations, and with the interactions of plant stage with elevation and pond (Table 2). At this time, seedlings were still smaller but grew faster than cuttings, which had negligible growth in height and diameter (Table 2; Fig. 3). Seedling growth was negatively associated with elevation and related to a gradient in shade and soil among the ponds. While not tested specifically, we noted that seedlings in the easternmost pond grew more under prolonged morning shade and fertile soils (based on soil color and texture), whereas those at the westernmost pond had the least growth under more sun exposure and the driest, sandy soil. These initial differences in early growth were maintained until the end of the experiment (Fig. 3).

Survival was heterogeneous across time with highest mortality associated with inundation, except for seedlings at the highest elevation, which had higher initial mortality due to desiccation prior to inundation. Despite this, overall survival at the end of the experiment was highest for seedlings at the highest elevation (Fig. 4; $p < 0.001$ for all comparisons among elevations and between cuttings and seedlings).

Cuttings. Survival of cuttings did not differ significantly between the two sizes or among elevations ($p > 0.93$). Cuttings maintained leaves above the waterline throughout the experiment and were never completely covered by floating vegetation. At the end of the experiment in November 2010, biomass was correlated with stem diameter ($y = 2.05 \times \ln(x) + 4.95$, $r^2 = 0.62$) and height ($y = 20.03 \times \ln(x) + 23.81$, $r^2 = 0.59$). These final measurements confirmed the differences between

Table 1. Results of ANOVA on final stem diameter, height, and biomass for cuttings as a function of island, provenance, elevation and orientation, and the interaction between elevation and orientation. Bold values indicate factors significant at alpha < 0.05.

		Basal Stem Diameter			*Height*			*Biomass*		
Source of Variation	*df*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*
Island	3	0.267	1.55	0.226	1151.4	2.04	0.135	992.6	2.14	0.121
Provenance	3	0.091	0.53	0.665	795.3	1.41	0.264	487.7	1.05	0.387
Elevation	3	1.950	11.36	**<0.001**	1669.2	2.96	**0.053**	2142.1	4.63	**0.011**
Orientation	3	0.208	1.21	0.327	1100.8	1.95	0.148	1221.7	2.64	0.073
Elev × Orient	9	0.112	0.65	0.741	508.4	0.90	0.539	740.6	1.60	0.172
Residuals	23	0.172			564.1			463.2		

Model $r^2 = 0.67$, 0.58, and 0.66, respectively. Values in boldface are smaller than 0.001.

Table 2. Results of ANOVA on height growth, height, and basal diameter at the end of acclimation period during the first month after transplanting as a function of pond, stage (seedling, small cutting, and large cutting), and elevation (0, 0.25, 0.35, 0.5 m from the bottom of the pond) of Carolina willows on artificial islands. Bold values indicate factors significant at alpha < 0.05.

		Change in Height			*Height*			*Basal Stem Diameter*		
Source of Variation	*df*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*
Pond	5	0.31	3.7	**0.005**	79	1.0	0.40	3.7	0.87	0.50
Elevation	3	2.82	33.1	**<0.001**	1118	14.7	**<0.001**	6.4	1.53	0.21
Stage	2	54.03	635.2	**<0.001**	38941	511.7	**<0.001**	952.6	226.7	**<0.001**
P × E	15	0.09	1.0	0.45	76	1.00	0.46	4.5	1.07	0.40
P × S	10	0.66	7.8	**<0.001**	100	1.32	0.24	5.1	1.21	0.30
E × S	6	0.83	9.8	**<0.001**	165	2.16	0.06	7.8	1.86	0.10
P × E × S	28	0.08	0.9	0.60	134	1.76	**0.03**	4.3	0.99	0.49
Residuals	68	0.08			76			4.2		

Model $r^2 = 0.92$, 0.94, and 0.89, respectively.

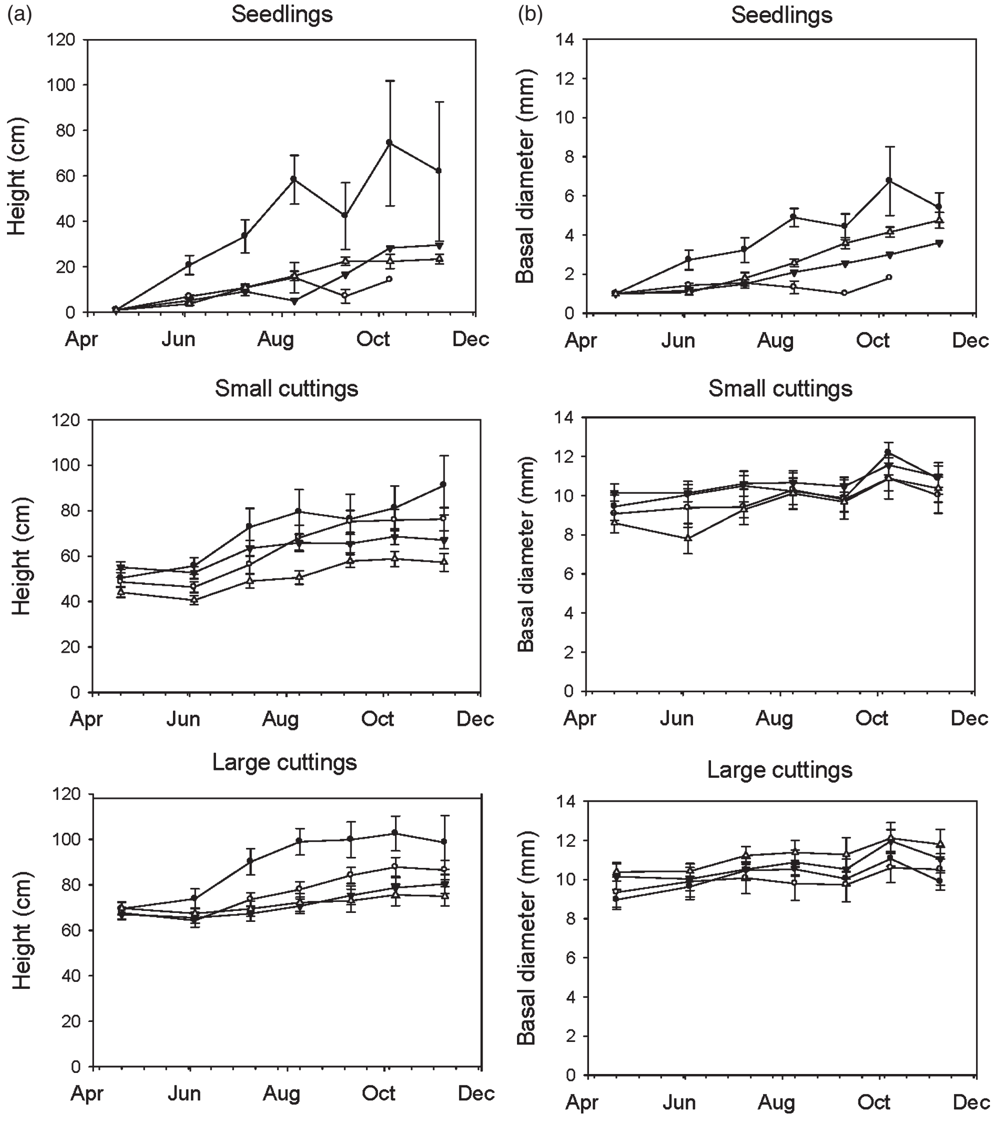

Figure 3. Growth of Carolina willow by plant stage, elevation and month: (a) mean stem height ± SE (cm) and (b) mean stem diameter ± SE (mm). Arrows indicate the start of flooding.

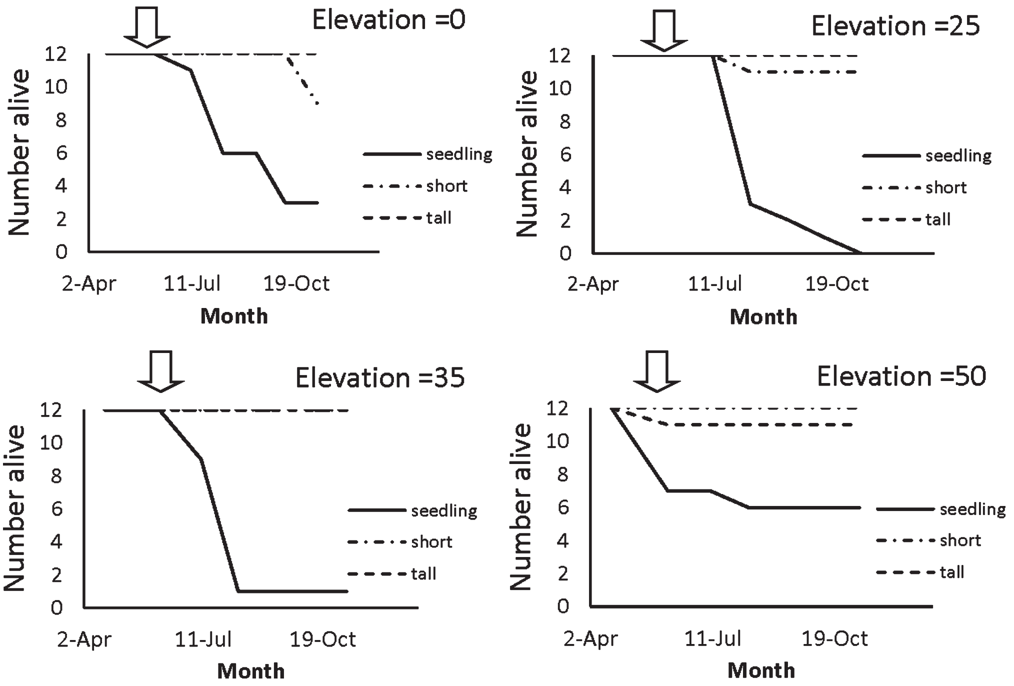

Figure 4. Numbers of seedlings and short and tall cuttings of Carolina willow surviving in artificial ponds by elevation and date. Arrows indicate the start of flooding.

blocks also found among the seedlings. We attributed these differences to the effect of shade and soil type on plant height and biomass initially detected at the end of the acclimation phase (Table 3; Fig. 4). Survivors at the lowest elevation were taller and had more biomass than plants at higher elevations (Table 3; Fig. 4). Plant stage was the only variable that significantly affected final stem diameter (Table 3), with cuttings attaining larger diameters than seedlings.

Discussion

Desiccation and flooding are major factors determining the persistence of wetland and riparian tree species (Mitsch & Rust 1984; Scott et al. 1997; Michener & Haeuber 1998; Wetzel et al. 2005; Hofmockel et al. 2008). Our experiments showed that hydrological manipulations can be a powerful tool in controlling the establishment and early growth of Carolina willow. Timely desiccation and flooding can control willow by killing seedlings and reducing growth of cuttings.

The success of water level manipulations depends on timely application of drawdown or flooding. As in many other willow species (Niiyama 1990; Siegel & Brock 1990; Karrenberg et al. 2002; Gage & Cooper 2005), Carolina willow seeds have short viability and germination is very sensitive to drought and flooding (Ponzio et al. unpublished data). Our hydrologic experiments indicate that mortality was high for seedlings on dry soils or for seedlings overtopped by water. Dry conditions are usually present in the USJR during the January to June dry season, which overlaps Carolina willow's January to April seed set. However, moist soils may be exposed during construction and restoration projects, and along roads, levees, and airboat trails. Peat soils are better than sandy soils for willow survival because of their ability to hold moisture (Fauth et al. unpublished data). Minimizing wet conditions during the dry season will limit seedling germination and establishment. Our experiments showed that once seedlings persist into the wet season, most mortality occurs during flooding events. Maintaining relatively high water levels (+50 cm above soil level) during the wet period (June to September) can reduce establishment of willow seedlings. Supporting evidence comes from District management of one area near US 192, where mature Carolina willows were uprooted entirely by roller-chopping, and then suffered drought and subsequent inundation; Carolina willow remained absent from the site for three years (Ponzio et al. 2006) and reverted back to a herbaceous marsh.

Once established as a large sapling or tree, Carolina willow can persist under both hydrologic extremes (prolonged drought and high water conditions: >1 m water depth). Neither soil compaction nor flooding significantly reduced growth of cuttings of several species of willow, including Carolina willow, under greenhouse conditions (Kuzovkina et al. 2004; Fauth et al. unpublished data). Most willow (*Salix*) species have physiological adaptations that improve persistence in areas subjected to water level variation. Carolina willows established from cuttings tolerate hypoxic conditions and grow in compacted soils, allowing them to tolerate prolonged flooding (Kuzovkina et al. 2004). Most plant species cannot persist under extended inundation because water limits diffusion of CO_2 and O_2 (Armstrong et al. 1994).

Table 3. Results of ANOVA on final height, basal diameter, and biomass as a function of pond, stage (seedling, small, and large cutting), and elevation (0, 0.25, 0.35, 0.5 m from the bottom of the pond) for Carolina willow plants in artificial ponds. Interaction degrees of freedom are reduced due to plant mortality. Bold values indicate factors significant at alpha < 0.05.

		Height			*Basal Stem Diameter*			*Biomass*		
Source of Variation	*df*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*	*Mean Sq*	*F*	*p*
Pond	5	1462	5.0	**<0.001**	7.04	1.40	0.24	181.6	1.45	0.22
Elevation	3	4162	14.2	**<0.001**	3.30	0.66	0.58	517.1	4.13	**0.01**
Stage	2	10503	35.96	**<0.001**	154.72	30.96	**<0.001**	1954.6	15.63	**<0.001**
P × E	15	528.3	1.81	0.06	2.70	0.54	0.90	110.5	0.88	0.59
P × S	8	758.6	2.60	**0.02**	3.17	0.63	0.74	147.8	1.18	0.33
E × S	5	206	0.71	0.62	5.14	1.02	0.41	69.6	0.56	0.73
P × E × S	15	968	3.31	**<0.001**	8.97	1.79	0.06	263.0	2.10	**0.03**
Residuals	47	292			5.00			125.1		

Model $r^2 = 0.84$, 0.71, and 0.70, respectively.

However, several species of willow produce aerenchymatous, adventitious roots that mitigate anoxia which allows them to survive under these harsh conditions (Krasny et al. 1988; Jackson & Attwood 1996; Kuzovkina et al. 2004). Nine species of willow exhibit other rapid morphological changes that occur in response to flooding, including floating roots, negative gravitropism, and lenticel hypertrophy (Kuzovkina et al. 2004). Along the St. Johns River, we observed mature Carolina willow growing extensive adventitious roots during prolonged floods. Trees and plants established from cuttings of Carolina willow also tolerate some drought, reducing leaf number and size in response to water availability (Fauth et al. unpublished data and personal observation). Similarly, survival and growth of other tree seedlings (*Annona glabra*, *Acer rubrum*, *Bursera simaruba*, *Chrysobalanus icaco*, *Ficus aurea*, *Ilex cassine*, *Morella cerifera*, and *Persea palustris*) improved with increasing elevation on artificial islands in the Everglades (van der Valk et al. 2007; Stoffella et al. 2010).

If control at the seedling or sapling stage is not achieved, managers will have to control the establishment of willow by other means. Other methods that have been shown to decrease the abundance of other woody plants (Craighead 1971; Wade et al. 1980; Kushlan 1990; Nyman & Chabreck 1995) can be unreliable in controlling Carolina willow or can negatively affect recovery of some wetland herbaceous species. Fire can reduce the basal area and canopy cover of Carolina willow and restrain encroachment in areas with sufficient herbaceous fuel loads (Miller et al. 1998), but it resprouts profusely and can recover stem density to prefire levels just 2 years later (Lee et al. 2005). In herbaceous marshes with lower fuel loads, Carolina willow forms pockets of reduced plant cover where fire does not propagate (Fauth et al. personal observation). Roller-chopping can effectively control Carolina willow, but may result in ancillary negative effects including topographic alteration, soil compaction, and altered drainage patterns (Ponzio et al. 2006). Cattle grazing in the river floodplain can kill Carolina willow seedlings and damage or destroy cuttings (Fauth et al. unpublished data). However, cattle only create a browse line on mature Carolina willows and trampling/soil erosion and manure loads can be problematic in the floodplain.

Native willow species are used for wetland restoration, erosion control, and sustainable harvesting throughout the world (Densmore et al. 1987; Dulohery et al. 2000; Pezeshki et al. 2007). Clonal reproduction, rapid growth, and the ability to survive on marginal soils and under fluctuating hydrologic conditions make willow highly favored in these environments (Cremera 2003). However, in the USJR system, these life history traits allow Carolina willow to rapidly invade herbaceous marshes and convert them into willow swamps. Historical management in the USJR emphasized drainage and compartmentalization, which decreased water fluctuations and reduced water levels, favoring establishment and persistence of Carolina willow. Future management to reduce encroachment of Carolina willow should consider a variety of control methods. These must be applied to take advantage of ecosystem conditions (e.g. seasonal drought and flooding, fuel loads, grazing intensity) and to target sensitive Carolina willow seedlings and small saplings.

Implications for Practice

- Desiccation and flooding are powerful tools to control establishment and growth of young Carolina willow and potentially other woody species.
- However, their success depends on timely application of water management. Floodwaters should inundate willows entirely, and remain high for several months to ensure complete mortality. Drawdowns must last for weeks to months, with longer times needed for organic soils that retain water.
- Hydrologic manipulation may be applied to take advantage of ecosystem conditions (e.g. seasonal drought and flooding) and target sensitive life stages of these species.

Acknowledgments

This study was supported by the St. Johns River Water Management District. Personnel from the St. Johns River Water

Management District helped to construct the islands, provided feedback on experiments, and shared many ideas about Carolina willow expansion. E. Boughton, M. Ferrer, L. McCauley, J. Navarra, L. Sánchez Clavijo, and B. Stephens helped during many stages of the project. The suggestions of two anonymous reviewers improved the manuscript. We particularly thank graduate students of Restoration Ecology and Conservation Biology Practice and the Biology Graduate Student Association at UCF for their efforts. A complete list of people that helped in this project is at: http://pascencio.cos.ucf.edu/.

LITERATURE CITED

Armstrong, W., R. Brandle, and M. B. Jackson. 1994. Mechanisms of flood tolerance in plants. Acta Botanica Neerlandica **43:**307–358.

Busch, D. E., W. F. Loftus, and O. L. Bass Jr. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades. Wetlands **18:**230–241.

Clapp, D. A., and H. A. Wilkening III. 1984. Interbasin diversion in the Upper St. Johns River Basin. Technical Publication SJ 84–10. St. Johns River Water Management District, Palatka, Florida.

Craighead, F. C. 1971. The trees of South Florida. Vol **1**. The natural environments and their succession. University of Miami Press, Coral Gables, Florida.

Cremera, K. W. 2003. Introduced willows can become invasive pests in Australia. Biodiversity **4:**17–24.

DeMort, C. L. 1991. The St. Johns river system. Pages 97–120 in R. J. Livingston, editor. The rivers of Florida. Ecological Series No 83. Springer-Verlag, New York.

Densmore, R. V., B. J. Neiland, J. C. Zasada, and M. A. Masters. 1987. Planting willow for moose habitat restoration on the north slope Alaska, U.S.A. Arctic and Alpine Research **19:**537–543.

Dulohery, C. J., R. K. Kolka, and M. R. McKevlin. 2000. Effects of a willow overstory on planted seedlings in a bottomland restoration. Ecological Engineering **15:**57–66.

Fisher, A. S., G. S. Podniesinski, and D. J. Leopold. 1996. Effects of drainage ditches on vegetation in abandoned agricultural peatlands in central New York. Wetlands **16:**397–409.

Gage, E., and D. J. Cooper. 2005. Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. Canadian Journal of Botany **83:**678–687.

Giljohann, K. M., C. E. Hauser, N. S. G. Williams, and J. L. Moore. 2011. Optimizing invasive species control across space: willow invasion management in the Australian Alps. Journal of Applied Ecology **48:**1286–1294.

Hall, G. B. 1987. Establishment of minimum surface water requirements for the greater Lake Washington Basin. Technical Publication SJ87-3, St. Johns River Water Management District, Palatka, Florida. 85 pp.

Henderson, L. 1991. Alien invasive *Salix* spp. (Willows) in the grassland biome of South Africa. South African Forestry Journal **157:**91–95.

Hofmockel, K., C. J. Richardson, and P. N. Halpin. 2008. Effects of hydrologic management decisions on Everglades tree islands. Pages 191–214 in C. J. Richardson, editor. The Everglades experiments: lessons for ecosystem restoration. Springer, New York.

Jackson, M. B., and P. Attwood. 1996. Roots of Carolina willow (*Salix viminalis* L.) show marked tolerance to oxygen shortage in flooded soils and in solution culture. Plant Soil **187:**37–45.

Karrenberg, S., P. J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biology **47:**733–748.

Katz, G. L., and P. B. Shafroth. 2003. Biology, ecology and management of *Elaeagnus angustifolia* L. (Russian olive) in western North America. Wetlands **23:**763–777.

Kinser, P., M. A. Lee, G. Dambek, M. Williams, K. J. Ponzio, and C. Adamus. 1997. Expansion of Carolina willow in the Blue Cypress Marsh Conservation Area, Upper St. Johns River Basin. Professional Paper SJ97-PP1, St. Johns River Water Management District, Palatka, Florida, 13.

Krasny, M. E., J. C. Zasada, and K. A. Vogt. 1988. Adventitous rooting of four Salicaceae species in response to a flooding event. Canadian Journal of Botany **66:**2597–2598.

Kushlan, J. A. 1990. Freshwater marshes. Pages 324–362 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando.

Kuzovkina, Y. A., M. Knee, and M. F. Quigley. 2004. Effects of soil compaction and flooding on the growth of 12 Carolina willow (*Salix* L.) species. Journal of Environmental Horticulture **22:**155–160.

Lee, M. A., K. J. Ponzio, and S. J. Miller. 2005. Response of Carolina willow (*Salix caroliniana* Michx.) in a floodplain marsh to growing season prescribed fire. Natural Areas Journal **25:**239–245.

Michener, W. K., and R. A. Haeuber. 1998. Flooding: natural and managed disturbances. BioScience **48:**677–680.

Miller, S. J., K. J. Ponzio, M. A. Lee, L. W. Keenan, and S. R. Miller. 1998. The use of fire in wetland preservation/restoration: are there risks? Pages 127–139 in T. L. Pruden and L. A. Brennen, editors. Fire in ecosystem management: shifting the paradigm from suppression to prescription, Proceedings of the Tall Timbers Fire Ecology Conference, No. 20, May 22–25, 1996, Boise, Idaho.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. 2nd edition. Van Nostrand Reinhold, New York.

Mitsch, W. J., and W. G. Rust. 1984. Tree growth responses to flooding in a bottomland forest in northeastern Illinois. Forest Science **30:**499–510.

Niiyama, K. 1990. The role of seed dispersal and seedling traits in colonization and coexistence of *Salix* species in a seasonally flooded habitat. Ecological Research **5:**317–331.

Nyman, J. A., and R. H. Chabreck. 1995. Fire in coastal marshes: history and recent concerns. Proceedings of the Tall Timbers Fire Ecology Conference **19:**134–141.

Pezeshki, S. R., L. Shuwen, F. D. Shields, and L. T. Martin. 2007. Factors governing survival of black willow (*Salix nigra*) cuttings in a streambank restoration project. Ecological Engineering **29:**56–65.

Ponzio, K. J., S. J. Miller, E. Underwood, S. P. Rowe, D. J. Voltolina, and T. D. Miller. 2006. Responses of a Carolina willow (*Salix caroliniana* Michx.) community to roller-chopping. Natural Areas Journal **26:**53–60.

Rood, S. B., J. M. Mahoney, D. E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. Canadian Journal of Botany **73:**1250–1260.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, U.S.A. Ecological Applications **7:**677–690.

Siegel, R. S., and J. H. Brock. 1990. Germination requirements of key southwestern woody riparian species. Desert Plants **10:**3–8.

Southall, E. J., M. P. Dale, and M. Kent. 2003. Floristic variation and Carolina willow carr development within a southwest England wetland. Applied Vegetation Science **6:**63–72.

St. Johns River Water Management District (SJRWMD). 2007. Upper St. Johns River Basin, Surface Water Improvement and Management Plan. St. Johns River Water Management District, Palatka, Florida, 39.

Stoffella, S., M. S. Ross, J. P. Sah, R. M. Price, P. L. Sullivan, E. A. Cline, and L. J. Scinto. 2010. Survival and growth responses of eight Everglades tree species along an experimental hydrological gradient on two tree island types. Applied Vegetation Science **13:**439–449.

Stokes, K. E. 2008. Exotic invasive black willow (*Salix nigra*) in Australia: influence of hydrological regimes on population dynamics. Plant Ecology **197:**91–105.

Tai, C. C., and D. V. Rao. 1982. Hydrologic change due to floodplain impoundment and encroachment by agricultural activities. Pages 193–200 in E. G. Kruse, C. R. Burdick, and Y. A. Yousef, editors. Environmentally sound water and soil management. American Society of Civil Engineers, New York.

Thibodeau, F. R. 1985. Changes in a wetland plant association induced by impoundment and drainage. Biological Conservation **33:**269–280.

Timoney, K. P., and G. Argus. 2006. Carolina willows, water regime, and recent cover change in the Peace-Athabasca Delta. Ecoscience **13:**308–317.

van der Valk, A. G., L. Squires, and C. H. Welling. 1994. Assessing the impacts of an increase in water level on wetland vegetation. Ecological Applications **4:**525–534.

van der Valk, A. G., P. Wetzel, E. Cline, and F. H. Sklar. 2007. Restoring tree islands in the Everglades: experimental studies of tree seedling survival and growth. Restoration Ecology **16:**281–289.

Wade, D., J. Ewel, and R. Hofstetter. 1980. Fire in South Florida ecosystems. General Technical Report SE-17, U.S. Department of Agriculture, Forest Service, Washington, DC.

Wetzel, P. R., A. G. van der Valk, S. Newman, D. E. Gawlik, T. Gann, C. A. Coronado-Molina, D. L. Childers, and F. H. Sklar. 2005. Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key. Frontiers in Ecology and Environment **3:**370–376.

Wheeler, B. D., S. C. Shaw, and P. A. Eades. 1999. The biodiversity value of wet woodlands in comparison to open herbaceous wetlands. Countryside Council for Wales. Report No. 336.