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[Article]

The Response of Water Willow *Justicia americana* to Different Water Inundation and Desiccation Regimes

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Abstract.—American water willow *Justicia americana* has been planted in reservoirs to provide important littoral habitat for fish because of its ability to form dense stands, spread along shorelines, grow in water up to 1.2 m deep, and withstand harsh conditions. The response of water willow to periods of inundation or desiccation has not previously been quantified and is critical for evaluating its potential success in reservoirs. We tested the inundation response of plants at depths of 0.75, 1.50, and 2.25 m for 2, 4, 6, and 8 weeks. Response to desiccation was investigated using drying durations of 2, 4, 6, and 8 weeks. In addition, 2- and 4-week drying periods were tested separately in June, July, and August. Number of leaves, total height, and total dry weight were measured as indicators of plant condition. Condition rapidly declined after inundation for 4 weeks at all experimental depths and plants did not recover by the end of the experiment. A significant decrease in height and increase in leaf number was observed after 8 weeks of desiccation. Condition also declined from June to August during the second desiccation experiment. Overall, water willow appeared to be more resistant to desiccation than to inundation. A 5% overall mortality was observed for the desiccation trials versus a 69% overall mortality from the inundation trials. Even the shortest inundation duration in this study (2 weeks) resulted in mortality of 40% or more across all depth treatments and was probably due to light limitation. Our findings provide information that can be used to select candidate reservoirs for water willow establishment based on expected water-level fluctuations. Additionally, this information could be used to manage water levels in reservoirs where water willow currently provides important habitat for fish.

The ecological processes that occur as reservoirs age are relatively well documented. In particular, reservoirs typically go through a trophic upsurge, which is stimulated by nutrients released from newly inundated organic matter in the watershed, followed by trophic depression, which occurs as that nutrient pool is processed through the system (Kimmel and Groeger 1986). During the upsurge, increased aquatic productivity and inundated vegetation provide abundant food and habitat for sport and bait fish and other aquatic organisms (Kimmel and Groeger 1986; Ploskey 1986). As the system stabilizes during the trophic depression, the littoral habitat complexity declines and the fish assemblage is typically dominated by less desirable species, such as common carp *Cyprinus carpio*, bigmouth buffalo *Ictiobus cyprinellus*, and freshwater drum *Aplodinotus grunniens* (Kimmel and Groeger 1986; Ploskey 1986). Thus, a negative relation between reservoir age and sport fish abundance is

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common throughout North America (Kimmel and Groeger 1986; Miranda and Durocher 1986; Ploskey 1986).

Since the 1950s, several biomanipulation techniques have been investigated and implemented to prolong the initial high-quality sport fisheries in U.S. reservoirs (Miranda 1996). Reservoir water-level manipulations can be used to increase or sustain sport fish populations by inundating terrestrial vegetation to increase nutrients, food resources, and habitat and to concentrate prey for predators (Ploskey 1986; Willis 1986). However, this technique is limited to reservoirs with predictable inflows and regulations that support water-level fluctuations (Ploskey 1986; Willis 1986). Habitat enhancement is another technique used to mitigate the effects of trophic depression. Artificial and natural structures such as brush piles, tire structures, stake beds, standing timber, and rock reefs are placed in specific areas of reservoirs to benefit targeted fish (Brown 1986). These structures can be cost and labor prohibitive, and are usually short-term solutions. Another option that is often more feasible and long term is the planting of native aquatic macrophytes (Durocher et al. 1984; Smart et al. 1996; Dick et al. 2004).

Native aquatic macrophyte establishment can benefit fish and a variety of other aquatic organisms (Brown 1986; Kahl 1993; Dibble et al. 1996; Smart et al. 1996). Macrophytes provide refugia from predation and abundant food resources for many fish species (Wiley et al. 1984; Killgore et al. 1989). For example, large-bodied cladocerans, an important food source for age-0 fish, use macrophytes for shelter from predation, leading to an increase in their overall abundance (Quade 1969; Timms and Moss 1984; Moss et al. 1996). Stems and leaves provide surfaces for colonizing by epiphytic bacteria and algae (Dodds 2002) that are the principal food source of many invertebrates (Baker and Orr 1986). Macrophyte decomposition releases nutrients that were taken from the sediments, which stimulates pelagic production (Carpenter 1980) and increases organic substrates used by benthic organisms (Beckett et al. 1992). Additionally, native aquatic macrophytes contribute to increased water quality and clarity by reducing shoreline erosion (Kahl 1993; Summerfelt 1999) and turbidity (Kahl 1993; Vestergaard and Sand-Jensen 2000).

Many reservoirs remain unvegetated because of insufficient native plant propagules and harsh conditions for seedling establishment (Smart et al. 1996). In an effort to increase sport fish production and control shoreline erosion, native aquatic macrophytes are being intensively planted in reservoir littoral areas (Marteney 1993; Dick et al. 2004). Unfortunately, success has been limited by high abundances of herbivores and benthic feeding organisms (e.g., common carp) that uproot macrophytes (Cox 1999; Dick et al. 2004; Smart et al. 2005). American water willow *Justicia americana* L. (Vahl.)(hereafter water willow) is resistant to these biotic disturbances and is now being extensively planted in reservoirs (Dick et al. 2004).

Water willow is an emergent species with a native range from Quebec to Texas and from Kansas to the Atlantic coast (Gleason and Cronquist 1993; Niering and Olmstead 1997). It typically grows on the margins and shallow areas of lotic and lentic systems (Penfound 1940; Niering and Olmstead 1997) in areas exposed to ample sunlight (Fritz and Feminella 2003; Smart et al. 2005). As a colonial plant it forms dense stands by rhizomatous growth and can quickly spread along shorelines through fragmentation, growing in water up to 1.2 m (Penfound 1940). In some areas of the USA, water willow is considered a pest species because of its dense vegetative patches and rapid spread (Penfound 1940; Couch 1976). A semirigid, but flexible fibrous stem enables it to withstand scouring floods in lotic systems (Fritz and Feminella 2003) and strong wave action in lentic systems (Penfound 1940). Water willow is also tolerant of moderate water-level fluctuations (including drought) and high turbidity (Niering and Olmstead 1997; Dick et al. 2004; Smart et al. 2005).

Water levels in many reservoirs can widely fluctuate within and among years. However, the amount of time that water willow could be either inundated or desiccated has not been quantified. This information is critical, particularly for newly established macrophytes (Dick et al. 2004), to evaluate the potential success of water willow for sport fish management in reservoirs that vary in magnitude and timing of water level fluctuations. Thus, the objectives of our study were to (1) investigate the response of water willow to different inundation periods and depths, and (2) examine the desiccation tolerance of water willow.

Methods

Plant collection and establishment.—Water willow was harvested from Lake Wabaunsee, Kansas. Plants collected were 0.25 m or more in height, exhibited no visible signs of stress (i.e., yellowing leaves, broken stalks, insect infestations), and had the majority of their root system intact. Immedi-

TABLE 1.—Mean ± SE duration of increased or decreased water levels in respect to the conservation pool level from April to September for 1995 through 2002; maximum duration is reported in parentheses. Durations were calculated by counting the number of consecutive days the water level was a certain elevation above or below that of the conservation pool.

Reservoir	Duration of water level (d)				
	≥0.75 m	≥1.50 m	≥2.25 m	≤0.60 m	≤1.20 m
Big Hill	2 ± 0.7 (3)	2	0	6 ± 3.3 (30)	0
Council Grove	14 ± 6.1 (48)	13 ± 5.6 (37)	13 ± 7.1 (34)	65 ± 26.8 (183)	39 ± 13.3 (74)
El Dorado	9 ± 5.1 (28)	9 ± 5.0 (14)	5	65 ± 26.8 (183)	89
Elk City	16 ± 4.2 (55)	17 ± 4.3 (45)	16 ± 4.4 (41)	11 ± 6.3 (28)	0
Fall River	15 ± 4.4 (78)	20 ± 6.4 (76)	17 ± 5.6 (66)	0	0
John Redmond	15 ± 4.7 (74)	23 ± 8.7 (68)	36 ± 12.8 (62)	21 ± 7.7 (77)	0
Marion	29	5 ± 3.5 (9)	0	24 ± 15.8 (71)	0
Toronto	17 ± 5.1 (75)	14 ± 4.9 (70)	12 ± 3.4 (36)	0	0
Overall	14 ± 2.7 (78)	13 ± 2.6 (76)	12 ± 4.1 (66)	30 ± 13.9 (183)	16 ± 11.5 (89)

ately after removal, individuals were placed upright in containers with water covering the entire root system. Plants were transported to a water supply pond of Milford Hatchery, Geary County, Kansas, and individually planted in 19-L experimental plastic containers (cylindrical, 36.2 cm high, 29.2 cm in diameter) that were filled with 15–16 L of soil (silt loam) taken from nearby riparian areas. Containers were numbered, and 1.3-cm holes were drilled around the bottom and sides to allow an exchange of water and organisms. All experimental plants were placed in the pond at a depth of 0.10 m (Penfound 1940) and allowed to acclimate 3 weeks before the start of experiments; this depth served as the control for all experiments. Plants grew 3–4 cm during the acclimation period, and all individuals were approximately the same height at the beginning of the experiments. Depth was defined as the distance from the top of the substrate in the experimental container to the water's surface, allowing for direct comparison to reservoir water level data.

Inundation tolerance.—We tested the response of water willow to inundation at three treatment depths and four durations. The number of leaves, total height (mm; distance from container substrate to end of longest stem), and total dry weight (g) were used as indicators of plant health (Kramer and Boyer 1995; Crawley 1997a; Stern et al. 2003). Twenty containers were randomly selected and placed at each of the three treatment depths: 0.75, 1.50, and 2.25 m. Ten randomly selected controls were retained at 0.10 m. Four simulated inundation durations were tested: 2, 4, 6, and 8 weeks. We derived experimental inundation depths and durations using water level data from U.S. Army Corp of Engineers, Tulsa District, for eight Kansas reservoirs (Table 1) that have or are under consideration for water willow plantings. Water levels from April through September (1995–2002) were used to correspond with the primary growing season of water willow (Penfound 1940), during which it would be most susceptible to inundation or desiccation (Smart and Dick 1999). Treatment depths were based on the overall mean of water level above conservation pool for the eight reservoirs, which was 0.76 m (SE = 0.02). The mean inundation duration was calculated for each reservoir by counting the number of consecutive days the water level equaled or exceeded 0.75, 1.50, and 2.25 m above conservation pool (Table 1).

At the end of each inundation period, five containers were randomly selected from each depth treatment and moved to the control depth, and the height and number of leaves were recorded. After 11 weeks, water willow survival was recorded. Plants were removed from containers, thoroughly rinsed, and dried at 60°C for a minimum of 4 d. Dry weight of the whole plant was recorded and used as an index of final biomass. A multivariate analysis of variance (MANOVA) was used to investigate whether number of leaves and total height (dependent variables) differed among inundation depths and durations (fixed effects). An analysis of variance (ANOVA) was used to test whether the final dry weight differed among the plants after the recovery period.

Desiccation tolerance.—The desiccation tolerance of water willow was tested with two experiments. The first experiment investigated the effects of drying periods of 2, 4, 6, and 8 weeks, which represented typical periods of low water levels in Kansas reservoirs (Table 1). The mean duration (number of consecutive days) of water levels were 30 d (SE = 13.9) for 0.6 m below conservation pool and 16 d (11.5) for 1.2 m below conservation pool. Water levels were based on the maximum depth (1.2 m) at which water willow was reported to colonize (Penfound 1940). Two-week intervals were used for experimental durations. Drought and drawdown conditions were simulated by placing experimental containers on a dry, well-drained area on a shore of the pond having sparse to no vegetation. Both the drying and control areas received direct sunlight for at least 85% of the day. Containers in the desiccation area were arranged in a square pattern approximately 5 cm apart. At the beginning of the experiment, five containers were randomly assigned to each drying duration (2, 4, 6, and 8 weeks; $N = 20$ total) and moved from the control depth (0.10 m deep) to the drying area. Total height and number of leaves were recorded at the beginning of the experiment and when plants were returned to the control depth. Mortality was recorded at the end of 19 weeks. Plants were removed from containers, thoroughly rinsed, and dried at 60°C for a minimum of 4 d; dry weight of the whole plant was then recorded. The percent change in plant height and leaf number that occurred over the drying duration was calculated for each plant. A MANOVA was used to test whether percentage changes in plant height and leaf number and actual change in dry weight differed among drought durations (2, 4, 6, and 8 weeks).

In a second experiment, we followed the same procedures as in the first experiment to test whether desiccation response differed across months. Using MANOVA, we tested drying durations of 2 and 4 weeks in the months of June, July, and August by examining percentage changes in plant height and leaf number and actual dry weight change among months, drying durations, and the interaction between month and drying duration.

For all MANOVAs, Wilk's lambda was used to calculate the multivariate *F*-statistic (SPSS 2001). If an overall MANOVA was significant ($\alpha = 0.05$), separate ANOVAs were conducted to investigate each variable separately. Type III sums of square were used in all ANOVAs. For multiple tests, post hoc comparisons were conducted, via the Bonferroni correction, to the control type I error rate.

Results

The results from the inundation experiment revealed that water willow condition rapidly declined after 4 weeks for all experimental depths (Figure 1) and did not recover by the end of the experiment (Table 2). A significant depth–week interaction was found for both leaf number and plant height (MANOVA, $P < 0.001$; subsequent ANOVAs, $P < 0.001$). The post hoc comparisons for leaf number indicated that plants at the control depth had significantly ($P < 0.001$) more leaves than all the treatment depths after 4 weeks, and the number of leaves had significantly ($P < 0.001$) increased by week 8. In contrast, no significant increase in height occurred for the control plants over the duration of the experiment. The ANOVA testing for differences in final dry weight revealed a significant week effect ($P = 0.002$). In general, control plants had significantly greater dry weights ($P < 0.01$; Table 2) than those from the 2.25-m treatment and all plants inundated for more than 4 weeks regardless of depth.

TABLE 2.—Final mean water willow survival and dry weights for water inundation trials at four depths: 0.10 (control), 0.75, 1.50, and 2.25 m. Values sharing the same letter were not significantly different ($P \geq 0.05$).

Inundation duration (d)	Experimental depth (m)	Mortality (%)	Dry weight (g)
0	0.10	0	48.9 (10.1) z
2	0.75	40	48.6 (32.0) zy
	1.50	60	5.8 (3.6) y
	2.25	80	7.7 (7.7) y
4	0.75	40	20.8 (10.3) zy
	1.50	60	10.3 (8.3) zy
	2.25	100	0 y
6	0.75	100	0 y
	1.50	80	0.26 (0.26) y
	2.25	100	0 y
8	0.75	100	0 y
	1.50	100	0 y
	2.25	100	0 y

The overall mortality rate for the desiccation experiments was low (5%). The MANOVA for duration of drying indicated a significant week effect ($P = 0.003$) for the dependent variables: dry weight and percentage changes in height and leaf number. Separate ANOVAs for these dependant variables all showed a significant effect for drying duration ($P < 0.032$). The post hoc tests indicated a significant decrease ($P = 0.035$) in height between weeks 2 and 4 (Figure 2) and a significant increase ($P = 0.025$) in leaf number between week 2 and week 8.

A significant month–week interaction effect ($P = 0.009$) was found when testing the effects of desiccation across different months. Individual ANOVAs revealed that dry weight significantly differed ($P < 0.001$) among months, plants in the June trials being significantly heavier ($P < 0.046$) than those tested in August (Figure 3). Total height significantly decreased in the 4-week versus 2-

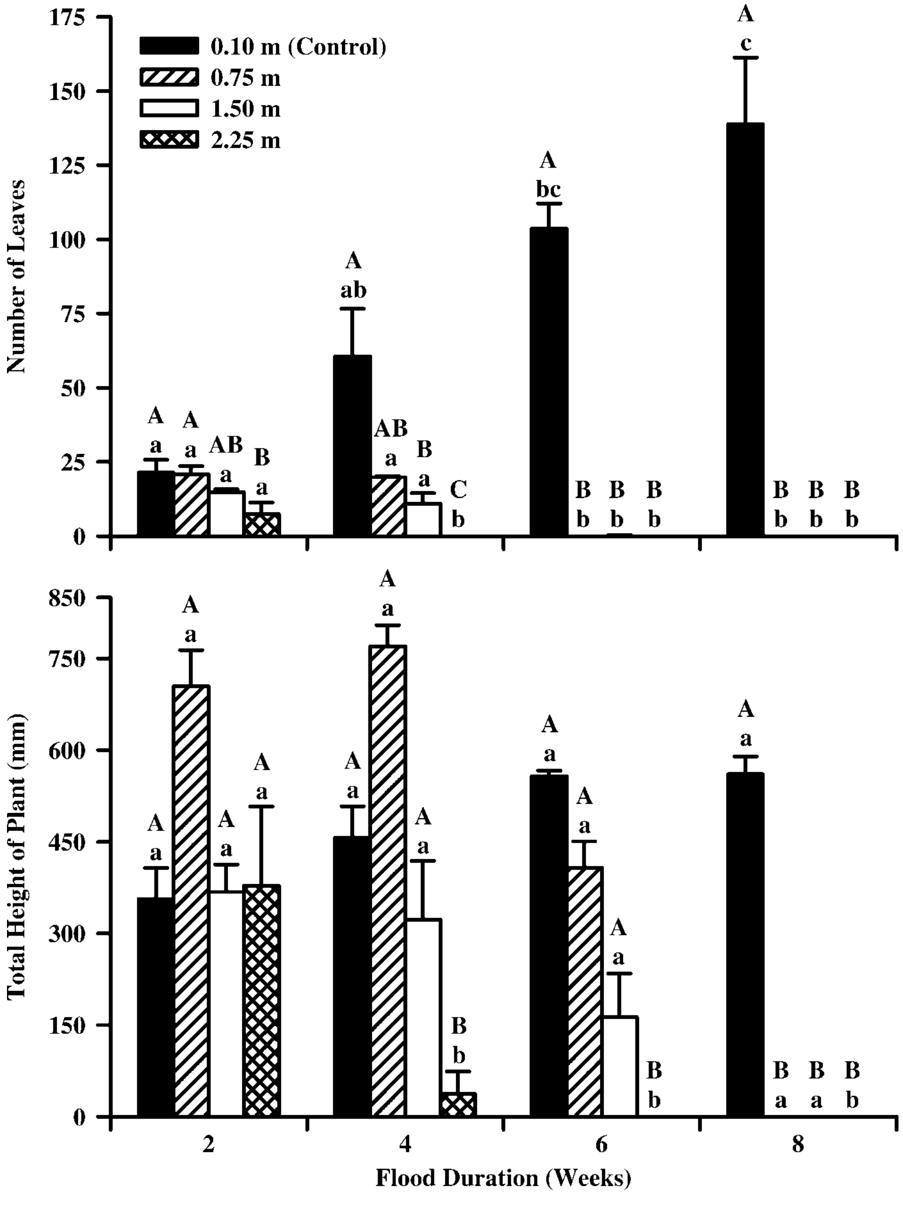

FIGURE 1.—Mean (error bars = 1 SE) number of leaves and plant height in an experiment testing the tolerance of water willow to water inundation durations of 2, 4, 6, and 8 weeks at depths of 0.10 (control), 0.75, 1.50, and 2.25. Bars with same capital letter are not significantly different ($P > 0.05$) for that week. Within each depth, the bars with the same lowercase letter are not significantly different ($P > 0.05$) across inundation durations.

week duration ($P = 0.005$) and during August compared with June or July ($P = 0.007$). The ANOVA testing the percentage change in leaf number indicated a significant interaction ($P = 0.008$) between week and month. In June and July there was a greater number of leaves in the 4-week trial than in the 2-week trial. In contrast, the number of leaves in August declined from 2 to 4 weeks. Mean temperatures were similar but precipitation totals differed across the months of June (21.7°C, 15.0 cm), July (23.8°C, 14.0 cm), and August (22.4°C, 2.8 cm; National Weather Service data).

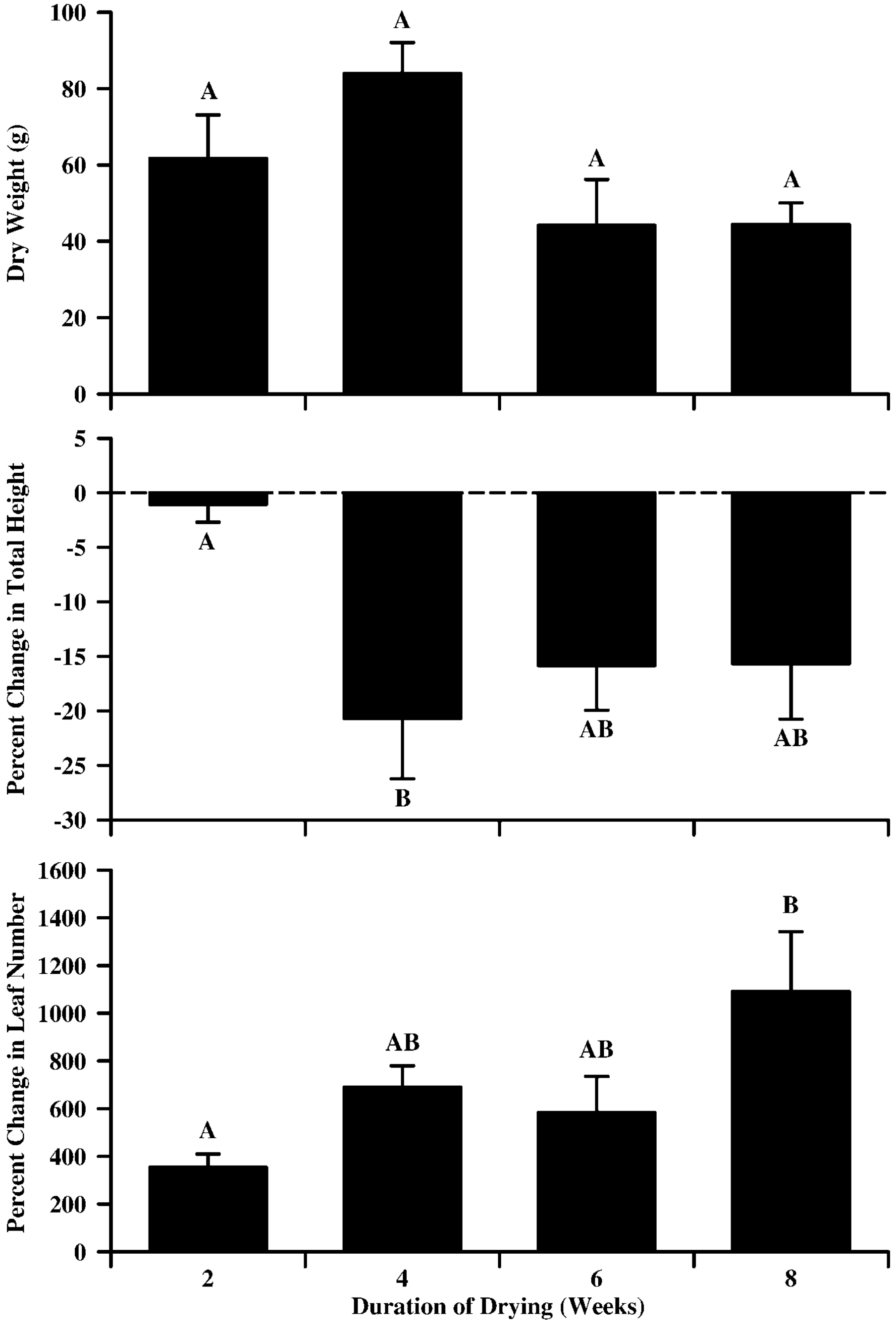

FIGURE 2.—Mean (error bars = 1 SE) dry weights and percentage changes in plant height and leaf number after exposure to drying durations of 2, 4, 6, and 8 weeks. Bars with same letter are not significantly different ($P > 0.05$).

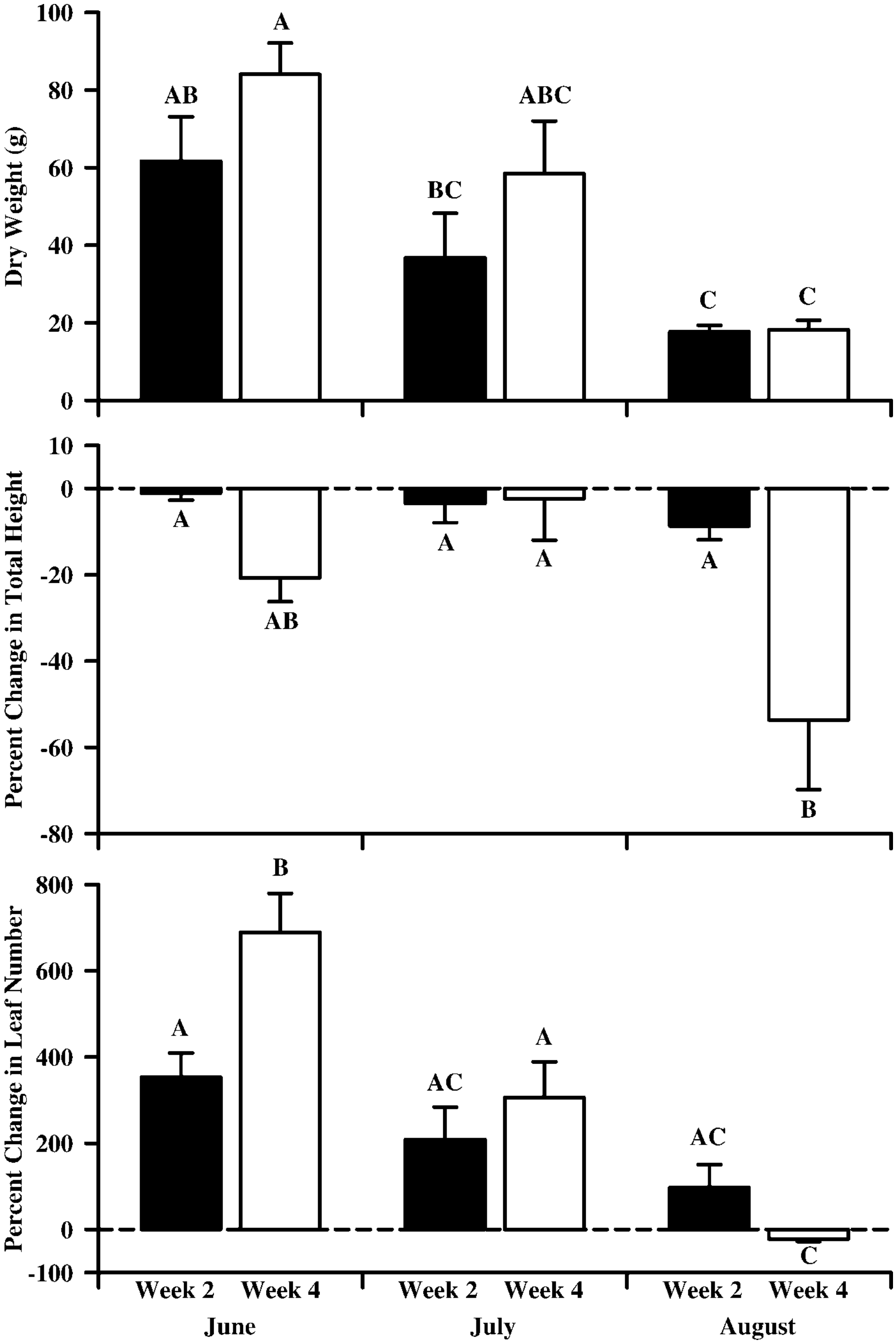

FIGURE 3.—Mean (error bars = 1 SE) dry weights and percentage changes in plant height and leaf number in an experiment investigating whether water willow response to drying differed among summer months (June–August). Drying occurred for 2- and 4-week periods within each month. Bars with same letter are not significantly different ($P > 0.05$).

Discussion

In general, water willow appears to be more resistant to desiccation than to inundation. A 5% overall mortality was observed in the desiccation trials versus a 69% overall mortality during the inundation trials. Even the shortest inundation duration in this study (2 weeks) resulted in a 40% or greater mortality across all depth treatments. Our results concur with Dick et al. (2004) who also found that water willow was resistant to drought but perished when depths exceeded 1.2 m over an extended period. The probable cause of the susceptibility to inundation could be light limitation. In an inundation study conducted on three species of the riparian plant *Rumex*, Nabben et al. (1999) reported that mortality rates of juvenile plants were greater when flooded with all light blocked (70%) than for plants in conditions where light was provided (0%). They also found a decrease in dry weight for plants exposed to longer inundation durations. The average turbidity in the pond used in our study was 19 nephelometric turbidity units, and several cyanobacteria blooms were observed during the trial period; thus, light was limiting to inundated plants. An additional indication of light limitation was the longer stems of the plants at 0.75 m during the 2-week and 4-week trials (Figure 3). These plants were most likely receiving small but inadequate amounts of sunlight triggering a stem elongation response (Stern et al. 2003). The susceptibility to light limitation is consistent with Fritz and Feminella (2003), who noted water willow was confined to areas exposed to direct sunlight. Additionally, it commonly inhabits areas in and around lotic systems that typically are prone to flooding in late winter and spring when most river macrophytes are still dormant (Haslam 1978).

Water willow in the desiccation experiments lost height and increased the total number of leaves. This response also was observed in the seaside alder *Alnus maritima*, which responded to drought by maintaining a high rate of photosynthesis and increasing leaf specific weight and root: shoot ratio (Schrader et al. in press). The large root and rhizomes of water willow (Penfound 1940) probably facilitate its ability to extract water from the soil and store ample amounts of food, thereby increasing resistance to drying conditions (Stern et al. 2003; Schrader et al. in press). The decrease in height that occurred in both desiccation trials could be a response of the plant to reallocate energy to leaves to produce more food, rather than upward growth. However, the increase in lateral growth also occurs when the apical meristem is removed, which could be the result of herbivory (Crawley 1997b) or the death of the upper stem. Plants in the monthly desiccation trial also showed a decrease in dry weight throughout the experiment. Typically, decreases in precipitation are coupled with increases in temperature from June through August in the midwestern USA, which could result in both water and heat stress for plants (Crawley 1997a). Despite the similar temperatures for June, July, and August during our desiccation experiment, we still detected differences between treatments, which could indicate that warmer and dryer conditions could have more of an effect on water willow.

Our findings provide information that can be used to select candidate reservoirs for water willow establishment based on historical water level fluctuations. For example, based on our results we recommend a 4-week inundation limit for water-level increases of 0.75 m to 1.5 m, and a 2-week limit for 2.25-m increases (longer durations result in about 100% mortality). Applying these limits to the reservoirs listed in Table 1, Big Hill, El Dorado, and Marion reservoirs would be the most likely to successfully support water willow populations. This assessment is further supported by the fact that large populations of water willow successfully established in El Dorado and Big Hill reservoirs (D. D. Nygren, Kansas Department of Wildlife and Parks, personal communication). Additionally, this information could be used to mitigate the magnitude and timing of water levels in reservoirs where water willow is established.

For future research we recommend quantification of the minimum light and moisture requirements for growth and survival, specifically investigation of the range of suitable water clarities and depths and the effects of inundation and light limitation, in combination and independently. Future desiccation experiments should investigate how soil type and plant interactions (e.g., shading, competition, etc.) may affect growth and survival during periods of drought.

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