Report for 2005NC49B: A Comparison of Drought Tolerance in Common Herbaceous Wetland Macrophytes as Indicated by Plant Growth, Water Status, and Oxidative Stress

Publications

- Articles in Refereed Scientific Journals:
    - Touchette, B.W., In Press, Salt tolerance in a Juncus roemerianus brackish marsh: Spatial variations in plant water relations. Journal of Experimental Marine Biology and Ecology.

Report Follows

Title

A Comparison of Drought Tolerance in Common Herbaceous Wetland Macrophytes as Indicated by Plant Growth, Water Status, and Oxidative Stress (70216)

Problem and Research Objectives

Part 1: Drought Susceptibility in Emergent Wetland Angiosperms: a Comparison of Water Deficit Growth in Five Herbaceous Perennials

Wetland ecosystems by nature are integrally tied to hydrology (Collins and Battaglia 2001; De Steven and Toner 2004). Consequently, mechanisms that alter prevailing hydrologic conditions, including mechanical and climateological, may sharply influence wetland function and value. Whereas water fluctuations involving episodic inundations and desiccation can facilitate increased plant diversity (Bush et al. 1998; Olson 2004; Mulhouse et al. 2005), extended periods of submersion or drought may foster decreased plant diversity, including the possible promotion of monotypic stands of invasive aquatic species (Pezeshki et al. 1998; Galatowitsch et al. 2000; Bonilla-Warford and Zedler 2002; Kercher and Zedler 2004). Williams and Hudak (2005) suggested that drought and low water availability are among the greatest threats to constructed wetlands in north-central Texas, and that herbaceous species (e.g., *Sagittaria latifolia*, and *Eleocharis quadrangulata*) are particularly vulnerable to water deficits. Similarly, Holland et al. (1995) reported the loss of several urban wetlands in Oregon due to drought-associated water deficits, and that drier-end wetlands (e.g., seasonally flooded) were often more susceptible to human disturbances. Moreover, droughts beyond recoverable time periods for established macrophytes, could eliminate valuable habitat necessary for both migratory waterfowl and indigenous wildlife (Sorenson et al. 1998; Williams and Hudak 2005).

Despite selective environmental pressures that would seemingly promote tolerance to both flooding and exposure, many wetland plants are unable to withstand even short periods of water scarcity (Steudler and Touchette 2003; Mulhouse et al. 2005; Williams and Hudak 2005). This is a fundamental concern, as wetlands are considered to be among the most threatened habitats globally (Gopal and Junk 2000). In a paper published in 2002, Jacobs et al. noted our lack of knowledge and the need for further studies on how extreme water table fluctuations influence wetland vegetation. While, there is growing interest in defining drought-associated changes in natural vegetation, driven primarily by climate change models predicting increases in drought severity and duration in the mid-latitudes, much of this work has been focused on grasslands and forests (e.g., Mangan et al. 2004; Breshears et al. 2005), and comparatively fewer studies have exclusively considered wetland systems (Sorenson et al. 1998; Dawson et al. 2003). Therefore, the purpose of this study was to evaluate growth responses of five herbaceous wetland species (monocots *Carex alata*, *Juncus effusus*, and *Peltandra virginica*, and dicots *Saururus cernuus*, and *Justicia americana*) to simulated drought conditions (up to 6 wks with 1-in-25 yr precipitation low and water withdrawal). Emergent herbaceous plants were selected in favor of woody vegetation because of their ease of manipulation under

controlled greenhouse conditions and due to their relative vulnerability to low water supply (Williams and Hudak 2005). For this study, it was anticipated that the herbaceous wetland plants would demonstrate varying degrees of drought tolerance, ranging from rapid vegetative die-off to minimal adverse effects. Thereby, the results of this study could be useful in providing a framework to gauge relative tolerance to drought among different wetland plant species. As a secondary application, this study could also provide valuable insight into proper plant selection for wetland restoration/ creation in areas with sporadic water availability (including stormwater retention wetlands).

Freshwater wetlands often exist as transitional areas between terrestrial uplands and deep open water. Thus they are fundamentally sensitive to changes in hydrology. Some of the more dramatic changes in wetland water supply occur during extensive droughts, where both precipitation and soil water table markedly decline. While it is generally understood that herbaceous wetland macrophytes are more sensitive to decreased water availability than wetland trees, the degree of susceptibility among wetland herbs remains relatively unexplored. Therefore, the purpose of this study was to evaluate plant growth responses of five herbaceous wetland species (monocots *Carex alata*, *Juncus effusus*, and *Peltandra virginica*, and dicots *Saururus cernuus*, and *Justicia americana*) to simulated drought conditions (up to 6 wks in a 1-in-25 yr precipitation low with receding soil water tables).

Part 2: Drought Tolerance Versus Drought Avoidance: A Comparison of Plant-Water Relations in Herbaceous Wetland Plants Subjected to Water Withdrawal and Repletion

Water deficits can result in significant declines in overall plant productivity and with increasing water scarcity can promote high rates of plant mortality. While a number of studies have addressed physiological acclimations to low water availability on agriculturally important species, comparatively fewer studies have considered wetland vegetation. This discrepancy is not surprising when considering aquatic plants, by nature, are constrained to environments characteristically dominated by excessive water. Nevertheless, wetlands represent an intermediate between terrestrial and open-water systems, and are thus fundamentally sensitive to changes in hydrology. Seemingly slight changes in water level may result in substantial adjustments in both species richness and productivity (Mitch and Gosselink 1986; Amlin and Rood 2002). Furthermore, when considering wetland hydroperiods, some systems (e.g., intermittently exposed, and seasonally flooded wetlands) can sustain extended periods of flooding and exposure (Cowardin et al. 1979; Wilcox 2002). In extreme cases, seasonally flooded wetlands will undergo enormous fluctuations in water availability as soil water tables oscillate from 50 cm aboveground to 100 cm belowground over a period of weeks (Mitsch et al. 1979). Furthermore, the degree of water deprivation can worsen during episodes of unseasonably low precipitation or drought; influencing both the degree of water deficit and extending the period of which these aquatic plants must tolerate water stressed conditions.

Drought, as defined as the absence of appreciable precipitation over an extended period of time allowing for the depletion of soil moisture with a concomitant injury to plants

(Kramer 1983), can influence natural plant distributions and productivity. Adjustments by plants to drought may involve avoidance and/or tolerance. Drought avoidance includes responses such as increased stomatal and cuticular resistance, changes in leaf area and anatomy, and changes in leaf orientation (Morgan 1984; Jones and Corlett 1992; Zlatev 2005). Whereas, drought tolerance involves maintaining adequate cell turgor, while preventing disruptions in cellular metabolism (Munns 1988; Savé et al. 1993). Tolerance has been attributed to at least two mechanisms - osmotic adjustment (involving inorganic ions, carbohydrates, and organic acids), and changes in cellular/ tissue elasticity (i.e., bulk elastic modulus; ϵ).

Studies suggest that plant metabolic processes are more responsive to turgor and cell volume conditions rather than fluctuations in water potential (Jones and Corlett 1992; Zlatev 2005). While dehydration of cells during water deficits can result in lower osmotic potential by confining existing solutes into smaller volumes, true osmotic adjustment necessitates the accumulation and buildup of these ions or compounds in excess of pre-stress conditions (Bray 1993). Drought-induced changes in tissue elasticity can also modify the relationship between turgor pressure and cell volume contributing further to drought tolerance (Blake et al. 1991; Saito and Terashima 2004).

Understanding the basis of plant water relations in emergent wetland herbs may provide some insight into the capacity of wetland species to maintain metabolic activity during extended periods of drought. Furthermore, any species that is capable of modifying their water relations during periods of low water availability may have a competitive advantage over plants incapable of altering water status. Therefore, the purpose of this study was to evaluate the effects of water stress on plant water relations in five herbaceous wetland species (monocots *Carex alata* Torr., *Juncus effusus* L., *Peltandra virginica* L., and dicots *Saururus cernuus* L., *Justicia americana* L. Vahl.). The ability of these plants to adjust to simulated drought conditions was evaluated using pressure-volume isotherms, which provided insights into leaf osmotic adjustment, tissue elasticity, plant water potential, and turgor pressure. Furthermore, plant productivity and water use efficiencies (WUE) were also evaluated to gain additional insights into wetland plant responses associated with short periods of water deficit and repletion.

Methodology

Part 1: Drought Susceptibility in Emergent Wetland Angiosperms: a Comparison of Water Deficit Growth in Five Herbaceous Perennials

Growth Conditions
Five herbaceous obligate wetland plants (*Carex alata* Torr., *Juncus effusus* L., *Peltandra virginica* L., *Saururus cernuus* L., and *Justicia americana* L. Vahl.) were grown under controlled greenhouse conditions in 20 L microcosms containing natural lake water (~ 25 cm) and sediments (~20 cm) at plant densities comparable to those observed in natural field populations (60-100 shoots m^{-2}). Prior to the initiation of water deficits, the plants were allowed to acclimate within the microcosms for 4 weeks to ensure plant establishment as indicated by active growth and productivity. Drought conditions were

initiated by removing surface water, over a 1-wk period, until the water level reached the upper portion of the substratum. During this period drought-treated plants (n=5 for each treatment) received watering of foliage and sediment comparable to a 1-in-25 year low precipitation rate and periodicity (1.0 cm water at 7-day intervals; based on summer precipitation data from the central Piedmont region of North Carolina over a 75 yr period). Control microcosms (n=5) were watered at mean summer precipitation rates and periodicity (2.9 cm water at 7-day intervals), while maintaining water levels at 25 cm above the substratum. Drought treated microcosms were exposed to 2-, 4-, or 6-wks of simulated drought, followed by a 2- to 6-wk recovery period consisting of pre-drought conditions (i.e., mean summer precipitation rates and periodicity, and 25 cm of standing water). Throughout the study, temperature (daily maximum and minimum) and relative humidity (RH; daily maximum and minimum) were monitored using a temperature and humidity data logger (Hobo H8 logger, Onset Computer Corporation, Bourne, MA).

Growth and Productivity Measurements
Growth measurements (n = 5) were recorded at weekly intervals and included phytomass (above- and belowground tissue), leaf area (LA), relative growth rate (RGR), and unit leaf rate (ULR; also termed net assimilation rate). Phytomass was determined by carefully removing plants from microcosms, as facilitated by the soft sediments which minimized loss of belowground tissues. The plants were sorted between aboveground- (stems and leaves) and belowground tissues (roots and rhizomes), and dried (70°C) to constant weight. LAs were measured using scanned digital images (7100 USB scanner, Visioneer Inc., Pleasanton, CA) of individual leaves against a white background (as described in Ferris et al. 2001, with modifications described in O'Neal et al. 2002). The images were then imported into an image processing and analysis program, Scion Image (Scion Corporation, Frederick, MD), for leaf area calculations. RGRs were calculated based on the production of dry matter at weekly intervals as defined by the following equation:

$$RGR = \frac{\ln W_{x+1} - \ln W_x}{t_{x+1} - t_x}$$

where W is the weight of dry matter reported for consecutive collection periods (x and x+1), and t represents the time interval (in wks) between collections. While RGRs are considered a fundamental measure of plant productivity and are important in the comparisons of plant performance between species and/or treatment effects, it is limited in its ability to evaluate causal factors that shape plant productivity (Beadle 1985). Differences in productivity are often associated with the plant's assimilation capacity as reflected in leaf area. Therefore, ULR measurements are often considered in growth analyses because they encompass both dry-mass production and assimilation capacity. ULR is defined as the increase in plant dry-mass over time per unit of assimilatory material, and was calculated in this study as follows:

$$(W_{x+1} - W_x) \, (\ln LA_{x+1} - \ln LA_x)$$

$$ULR = \frac{\rule{3cm}{0.4pt}}{(LA_{x+1} - LA_x)\,(t_{x+1} - t_x)}$$

where LA (as described above) and W were measured at consecutive sample periods (Beadle 1985; Hunt 1990).

Data Analysis
Along with other measurements, mean percent differences from controls for growth parameters were presented for comparisons. These values were calculated as follows:

$$\% \text{ Difference} = \left(1 - \frac{\text{treatment}}{\text{control}}\right) * 100$$

and allowed for general evaluations between treatments and their respective controls. These values were not analyzed statistically, and were used to merely represent the magnitude of change when significant differences were observed.

A repeated measure ANOVAs (general linear model [GLM] procedure) were performed using SAS statistical software (SAS Institute Inc., Cary, NC) on RGR, ULR, phytomass, leaf area, and aboveground/belowground tissue ratios. Pre-planned comparisons were performed for each sample collection using LS-means to evaluate treatment responses at each time interval. All comparisons were considered statistically significant when p-values were less than 0.05.

Part 2: Drought Tolerance Versus Drought Avoidance: A Comparison of Plant-Water Relations in Herbaceous Wetland Plants Subjected to Water Withdrawal and Repletion

Growth Conditions
Five herbaceous obligate wetland plants (*Carex alata* Torr., *Juncus effusus* L., *Peltandra virginica* L., *Saururus cernuus* L., and *Justicia americana* L. Vahl.) were grown under controlled greenhouse conditions in 20 L microcosms containing natural lake water (~ 25 cm) and sediments (~20 cm) at plant densities comparable to those observed in natural field populations (60-100 shoots m^{-2}). Prior to the initiation of water deficits, the plants were allowed to acclimate within the microcosms for 4 weeks to ensure plant establishment as indicated by active growth and productivity. Drought conditions were initiated by removing surface water, over a 1-wk period, until the water level reached the upper portion of the substratum. During this period drought-treated plants (n=5 for each treatment) received watering of foliage and sediment comparable to a 1-in-25 year low precipitation rate and periodicity (1.0 cm water at 7-day intervals; based on summer precipitation data from the central Piedmont region of North Carolina over a 75 yr period). Control microcosms (n=5) were watered at mean summer rates and periodicity (2.9 cm water at 7-day intervals), while maintaining water levels at 25 cm above the substratum. Drought treated microcosms were exposed to 2 wks of simulated drought, whereas drought-recovered microcosms consisted of 2 wks of simulated drought

followed by a 2 wks return to pre-drought conditions (i.e., mean summer precipitation rates and periodicity, and 25 cm of standing water).

Plant-Water Status
Leaf relative water content (θ) was evaluated according to Joly (1985) using the following equation:

$$\theta = \frac{(W_f - W_d)}{(W_t - W_d)}$$

where W_f was the fresh weight recorded during collection, W_t was the turgid weight, and W_d was the oven dry weight (70°C, until constant weight). Pre-dawn Ψ_{xylem} were determined by using a Scholander pressure chamber (Model 1000, PMS Instrument Co., Albany, Oregon, USA) on young fully extended leaves enclosed within foil bags for 2 hrs.

A Scholander pressure chamber was used to determine Ψ_{leaf} on leaves from each species to compare water status of control and drought recovered plants. Water deficits were established by exposing leaves to transpirational water loss on a laboratory bench. Turner et al. (1984) favored this approached, over elevated pressurization, because it minimized the possibility of Ψ disequilibria between apoplastic and symplastic tissues. Pressure-volume isotherms were constructed by plotting the reciprocal of Ψ_{leaf} against θ. First order regression analyses were performed on the linear portion of the curve. This line is equivalent to leaf Ψ_π, and can be used to determine θ at turgor loss point (θ^{tlp}), the osmotic potential at full saturation ($\Psi_\pi{}^{sat}$), osmotic potential at turgor loss point ($\Psi\pi^{tlp}$), and symplastic volume of the total water content (θ_{sym}). Bulk elastic modulus (ϵ) was obtained from the initial part of the curve, following Ψ_π correction, as described in the following equation:

$$\epsilon = \frac{d\,\Psi_p}{d\,\theta}\,\theta_{sym}$$

where changes in tugor potential (Ψ_p) were compared against changes in θ, and relative symplastic water content (Koide et al. 1989).

Data collected from pressure-volume isotherms were also used to generate Höfler diagrams for control and drought accumulated plants. The values derived for each point within the diagram represents the mean value among replicates with comparable water content. Because θ for these replicates were within rages, the best polynomial fit represents a population estimate for the mean value within that range of water content. Consequently, data represented by Höfler diagrams may not precisely match the data derived from P-V analysis on each individual plant.

Transpiration and Water Use Efficiency
A gravimetric technique was used to estimate transpiration on whole plants according to Slavík (1974) and Kramer (1983). This involved careful removal of plants from the

microcosm and enclosing the sediment/ root complex in polyethylene bags to prevent water evaporation from the soil. The soft sediment used during this experiment facilitated the plants removal with negligible damage to root structure. The plants were maintained within a greenhouse under environmental conditions comparable to plants within the microcosms (i.e., 10% neutral density shading of ambient light; $26 \pm 2°C$; 45.4 ± 3.2 % RH). Transpiration measurements were integrated over the course of the day with measurements reported at 60 min intervals. Drought treated plants were restricted to sediments collected from the 2-week drought treatment with no additional water added, whereas control and drought-recovered plants were placed in saturated soils with standing water to replicate typical water supply.

Water use efficiency (WUE) was estimated according to Kramer (1983; as modified by Gaiser et al. 2004, and Gao et al. 2004), defined as the amount of water used (via transpiration) per unit dry matter produced.

$$WUE = \frac{\text{Water used in transpiration}}{\text{Dry mater produced}}$$

Dry matter productivities were estimated as the mean increase in total biomass (both aboveground and belowground tissues) reported during the week of transpiration measurements (n = 5 for each microcosm).

Growth and Productivity
Growth measurements included both absolute growth (i.e., the amount of dry matter produced plant^{-1} day^{-1}), and relative growth (i.e., the amount of dry matter produced gram^{-1} [of plant] day^{-1}). In this case plants were collected at weekly intervals (n=5) and the increase in total dry mass (above- and belowground biomass collectively) were used to estimate plant productivity/ growth. Survival measurements were estimated as the percent change in living plants over the two week drought treatment.

Data Analysis
Data for controls and drought treated plants were compared using a non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA), followed by a Tukey multiple comparison test for post-hoc evaluations. All comparisons were considered significant at a p-value of less than 0.05.

Prinicipal Findings

Report 1: Drought Susceptibility in Emergent Wetland Angiosperms: a Comparison of Water Deficit Growth in Five Herbaceous Perennials

Of the five species studied, three (*J. americana*, *S. cernuus*, and *J. effusus*) had no survivors after six weeks of simulated drought. *J. americana*, appeared to be the most sensitive to water deprivation with a 67% decrease in plant phytomass and an 85% decrease in leaf area with only two weeks of drought, and complete mortality after three

weeks. While *P. virginica* also had significant decreases in biomass, leaf area, relative growth rate (RGR) and unit leaf rate (ULR), in as little as two weeks of drought, no noticeable decreases in survival were observed. In contrast, when *J. effusus* experienced between 2- and 4-weeks of water deprivation, there were significant increases in RGR, ULR, phytomass, leaf area, and shoot: root ratios. *S. cernuus* and *C. alata* remained relatively unaffected following four weeks of drought; however by the fifth week, there were significant declines in leaf area for both species. In general, this study provides experimental evidence on how herbaceous macrophytes grow under drought conditions. This basic understanding is fundamental if we are to develop better working models on how wetlands will respond to changing environmental conditions that lead to decreased water supply.

In conclusion, our current understanding on how emergent wetland perennials respond to water deficits is incomplete. This study provides experimental evidence on how plant growth and productivity can be altered during drought events. In general, plants in this study were severely impacted (*J. americana*), moderately impacted (*S. cernuus*, and *P. virginica*), largely unaffected (*C. alata*), or benefited (*J. effusus*) by a combination of decreased precipitation and water table drawdown that simulated a 1-in-25 year drought.

Table 2. Summary of growth responses observed in five species of herbaceous wetland plants to 2-, 4-, and 6-wks of drought. Parameters include relative growth rate (RGR), unit leaf rate (ULR), total plant phytomass (Biomass), leaf area, shoot: root ratio (S:R ratio), and percent survival. Numerical values represent the mean maximum percent difference observed from controlled (emergent) conditions, and the values in parentheses represent the week when the greatest difference was observed. The plus or minus signs indicate an increase/ positive response or a decrease/ negative response. Survival is based on the number of individuals remaining as a percent of the initial (for weeks 4 and 10). NC was used to indicate no significant change from the control (repeated measures ANOVA).

Species	RGR	ULR	Biomass	Leaf Area	S:R Ratio	% Survival Week-4	% Survival Week-10
Justicia americana							
2-wk	NC	NC	$-67^{(7)}$	$-85^{(7)}$	NC	75 ± 15	87 ± 7
4-wk[5]	NC	NC	$-46^{(5)}$	$-19^{(5)}$	$+83^{(5)}$	61 ± 22	0 ± 0
6-wk[5]	NC	NC	$-48^{(5)}$	$-35^{(5)}$	NC	54 ± 8	0 ± 0
Saururus cernuus							
2-wk	NC	NC	NC	NC	$+369^{(7)}$	84 ± 19	80 ± 18
4-wk	NC	NC	NC	NC	$+351^{(5)}$	83 ± 24	86 ± 15
6-wk[7]	NC	NC	$-75^{(7)}$	$-32^{(7)}$	NC	32 ± 8	0 ± 0
Peltandra virginica							
2-wk	$-231^{(4)}$	$-235^{(4)}$	$-53^{(10)}$	$-64^{(5)}$	NC	91 ± 7	103 ± 10
4-wk	$-395^{(6)}$	$-394^{(6)}$	$-64^{(8)}$	$+44^{(3)}/-77^{(8)}$	NC	90 ± 7	98 ± 4
6-wk	$-226^{(6)}$	$-356^{(7)}$	$-84^{(9)}$	$-82^{(9)}$	NC	93 ± 13	94 ± 9
Juncus effusus							
2-wk	$+1062^{(4)}$	$+1579^{(4)}$	$+306^{(10)}$	$+180^{(4)}$	NC	86 ± 18	92 ± 9
4-wk	$+692^{(4)}$	$+842^{(4)}$	$+198^{(10)}$	$+136^{(10)}$	NC	115 ± 30	96 ± 24
6-wk[8]	$+655^{(4)}$	$+925^{(4)}$	NC	$+175^{(4)}$	$+209^{(8)}$	49 ± 4	0 ± 0
Carex alata							
2-wk	NC	NC	NC	NC	NC	113 ± 9	108 ± 13
4-wk	NC	NC	NC	NC	NC	126 ± 22	122 ± 25
6-wk	NC	NC	NC	$-47^{(10)}$	NC	98 ± 3	79 ± 4

Part 2: Drought Tolerance Versus Drought Avoidance: A Comparison of Plant-Water Relations in Herbaceous Wetland Plants Subjected to Water Withdrawal and Repletion

In this study, simulated drought resulted in significant decreases in xylem water potential (Ψ_{xylem}) for all five species, suggesting that these plants were physiologically affected by water deficit. Four of the five species showed outward signs of drought avoidance, including significant reductions in transpiration (*C. alata*, *P. virginica*, *J. americana*, and *S. cernuus*) and modifications of leaf area (*P. virginica* and *J. americana*). Interestingly, while adjustments in transpiration were observed for most plants during the dry period, no significant changes in water use efficiencies (WUE) were detected until after water repletion. That is, only two species (*C. alata* and *P. virginica*) had enhanced WUE as water availability returned to normal. Drought conditions also promoted drought tolerance responses in all five species, as indicated by a change in bulk modulus of elasticity (ϵ; all species) and decreased osmotic potential (Ψ_{π}; *P. virginica*). Taken as a whole, this study reveals two contrasting drought tolerance strategies in wetland herbs. While four of the species alter ϵ to generate declines in Ψ, *P. virginica* favored decreases in osmotic potentials (as indicated by decreases in Ψ_{π} at full saturation and at turger loss point).

Table 1. Plant and soil parameters collected following two weeks of simulated drought. Data includes relative water content (θ), xylem water potential (Ψ_{xylem}; MPa), aboveground biomass, belowground biomass, and percent survival. Letters represent the statistical relationship between each treatment when differences were detected (the same letter on different values are considered statistically similar). Data is presented as means ± 1 S.E. (n = 5).

Species (treatment)	θ (%)	-Ψ_{xylem}	Aboveground (g)	Belowground (g)	Survival (%)
Monocots					
Carex alata					
Control	91.7 ± 3.7	0.24 ± 0.07	0.03 ± 0.003	0.007 ± 0.001	108.3 ± 8.3
Drought	84.5 ± 7.3	0.76 ± 0.18*	0.04 ± 0.009	0.004 ± 0.004	125.5 ± 21.7
Recovered	91.1 ± 2.4	0.51 ± 0.07*	0.03 ± 0.004	0.004 ± 0.003	113.3 ± 9.4
Juncus effusus					
Control	91.2 ± 3.3	0.66 ± 0.08	0.14 ± 0.01	0.10 ± 0.02	119.4 ± 19.0
Drought	70.6 ± 3.5*	0.94 ± 0.14*	0.19 ± 0.05	0.09 ± 0.01	114.6 ± 29.9
Recovered	89.9 ± 4.8	0.51 ± 0.12	0.21 ± 0.07	0.09 ± 0.02	86.1 ± 17.8
Peltandra virginica					
Control	87.9 ± 1.0	0.03 ± 0.01	0.91 ± 0.21	1.05 ± 0.30	87.3 ± 3.6
Drought	84.3 ± 3.4	0.12 ± 0.03*	0.37 ± 0.07*	1.81 ± 0.32	90.0 ± 7.1
Recovered	84.1 ± 3.1	0.59 ± 0.04*	0.62 ± 0.12	1.04 ± 0.23	90.7 ± 7.1
Dicots					
Justicia americana					
Control	95.9 ± 0.5	0.32 ± 0.04	0.66 ± 0.06	1.17 ± 0.21	92.6 ± 7.28
Drought	74.8 ± 1.9*	0.87 ± 0.25*	0.34 ± 0.05*	1.01 ± 0.19	61.3 ± 22.0
Recovered	90.1 ± 5.1	1.12 ± 0.11*	0.16 ± 0.06*	0.32 ± 0.11*	74.9 ± 15.0
Saururus cernuus					
Control	96.9 ± 2.4	0.34 ± 0.05	0.24 ± 0.05	0.37 ± 0.12	102.6 ± 9.8
Drought	88.2 ± 1.1*	0.96 ± 0.16*	0.20 ± 0.03	0.14 ± 0.05	82.9 ± 23.5
Recovered	92.9 ± 2.0	0.89 ± 0.16*	0.21 ± 0.03	0.17 ± 0.04	83.9 ± 19.2

Table 2. Plant water status parameters derived from pressure-volume isotherms on control and drought-recovered plants. Parameters include water fraction at turgor loss point (θ_{tlp}; %), symplastic water fraction (θ_{sym}; %), osmotic potential at full saturation (-Ψ_π^{sat}; MPa), osmotic potential at the turgor loss point (-Ψ_π^{tlp}; MPa), and bulk modulus of elasticity (ε; MPa). Statistical differences from the control are indicated by asterisks ($p < 0.05$; one-way ANOVA). Data is presented as means ± 1 S.E. (n = 8).

Species (treatment)	θ_{tlp}	θ_{sym}	- Ψ_π^{sat}	- Ψ_π^{tlp}	ε
Monocots					
Carex alata					
Control	0.79 ± 0.01	0.54 ± 0.03	1.11 ± 0.06	1.26 ± 0.09	1.69 ± 0.36
Recovered	0.77 ± 0.04	0.50 ± 0.04	0.37 ± 0.03*	0.67 ± 0.09*	0.56 ± 0.06*
Juncus effusus					
Control	0.84 ± 0.03	0.52 ± 0.05	0.33 ± 0.03	0.52 ± 0.04	0.71 ± 0.10
Recovered	0.86 ± 0.03	0.61 ± 0.05	0.36 ± 0.05	0.54 ± 0.08	1.64 ± 0.26*
Peltandra virginica					
Control	0.92 ± 0.01	0.82 ± 0.01	0.52 ± 0.02	0.84 ± 0.02	4.26 ± 0.88
Recovered	0.85 ± 0.03*	0.61 ± 0.05*	0.86 ± 0.08*	1.38 ± 0.11*	1.95 ± 0.47*
Dicots					
Justicia americana					
Control	0.85 ± 0.01	0.32 ± 0.06	1.15 ± 0.08	1.43 ± 0.10	1.91 ± 0.24
Recovered	0.92 ± 0.02*	0.77 ± 0.04*	0.69 ± 0.03*	1.11 ± 0.06*	4.18 ± 0.62*
Saururus cernuus					
Control	0.90 ± 0.01	0.38 ± 0.05	1.38 ± 0.15	1.58 ± 0.17	3.60 ± 0.45
Recovered	0.93 ± 0.01*	0.71 ± 0.01*	0.76 ± 0.01*	1.03 ± 0.06*	8.49 ± 0.99*

<u>**Significance**</u>

Part 1: Drought Susceptibility in Emergent Wetland Angiosperms: a Comparison of Water Deficit Growth in Five Herbaceous Perennials

As our basic understanding of how different wetland macrophytes respond to changing soil water tables increases with future studies (including both controlled greenhouse experiments and field investigations) we should be able to develop more generalized patterns necessary for predicting plant-drought interactions. This basic understanding is fundamental if we are to develop better working models on how wetlands will respond to changing environmental conditions that lead to decreased water supply - including mechanical disturbances associated with human activities and projected decreases in water availability due to climate change.

Part 2: Drought Tolerance Versus Drought Avoidance: A Comparison of Plant-Water Relations in Herbaceous Wetland Plants Subjected to Water Withdrawal and Repletion

In contrast, the former case of increased cell wall rigidity in drought stressed plants would allow for decreases in both turgor and water potential with only a small decrease in plant water content. Furthermore, a change in cell wall elasticity requires far less energy than the metabolically driven alternative of increasing organic compatible solutes (Lo Gullo et al. 1986). Consequently, Corcuera et al. (2002) suggested that plants growing in soils low in both water and nutrient content would favor the lower energy process of cell wall modification. While all species studied in this investigation can be found in organically rich soils typical of many freshwater wetland habitats, *J. americana*, *J. effusus*, and *S. cernuus* are also commonly found in nutrient poor clay soils typical of central Piedmont reservoirs of North Carolina (Touchette et al. 2000).

<u>**References**</u>

Part 1: Drought Susceptibility in Emergent Wetland Angiosperms: a Comparison of Water Deficit Growth in Five Herbaceous Perennials

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