EVALUATION AND PROPAGATION OF *CAREX* SPECIES FOR USE IN RAIN GARDENS

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

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In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Department:
Plant Sciences

July 2017

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

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ABSTRACT

A study was conducted to evaluate cyclical flood and drought on the growth of seven sedge species. A second study was conducted to determine if perigynia removal would accelerate germination for four sedge species. Results suggested plains oval sedge (*Carex brevior* Dewey), yellow fox sedge (*C. annectens* E.P. Bicknell), and Gray's sedge (*C. grayi* Carey) may be planted at any elevation in the rain garden. Sprengel's sedge (*C. sprengelii* Dewey ex Spreng) should be planted at higher elevations. Pennsylvania sedge (*C. pensylvanica* Lam.) should be planted on the highest elevation of the rain garden. Porcupine sedge (*C. hystericina* Muhl. Ex Willd) and palm sedge (*C. muskingumensis* Schwein) should be planted in the deepest part of the rain garden. Perigynia removal increased percent germination of yellow fox sedge and reduced time needed to reach 50% germination of yellow fox sedge and porcupine sedge but not palm sedge or plains oval sedge.

ACKNOWLEDGEMENTS

I would like to thank my advisors, Dr. Esther McGinnis and Dr. Aaron Daigh for all of their guidance and support throughout my entire research project. I would also like to thank Dr. Larry Cihacek, Dr. Harlene Hatterman-Valenti, and Dr. Todd West for serving on my graduate committee. The expert technical assistance with laboratory equipment provided by Radu Carcoana was greatly appreciated as was the kindness of Rodney Utter and Joseph Thompson for allowing me to borrow equipment.

A special thank you goes to my wife Anne, and children; Grace, Ian, Celia, and Flora. Without your love and support this project would not have been possible. Please know this thesis is as much yours as it is mine.

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CHAPTER I. LITERATURE REVIEW

Storm water

Over 80% of the United States population lives in urban areas (U.S. Census Bureau, 2010). Within an urban area, residential and commercial districts may have 20% and 85% of the land covered with impervious surfaces, respectively (Dietz and Clausen, 2005). As urban areas develop, permeable surfaces are replaced with impervious surfaces that do not allow water to infiltrate into the ground which leads to increased runoff. Urban runoff contains contaminants such as sediment, nitrogen, phosphorus, pathogens, road salts, petroleum hydrocarbons, and heavy metals that adversely impact downstream waters (Dietz and Clausen, 2005); [U.S. Environmental Protection Agency (USEPA)], 2005). Urban stormwater runoff is responsible for 36,305 impaired river km (9%), 283,689 impaired lake ha (7%), and 2,246 km^2 (11%) of impaired estuary area in the United States (USEPA, 2009).

Rain gardens

Commercial and residential rain gardens are frequently constructed to increase water infiltration, reduce stormwater runoff, and improve water quality (Asleson et al., 2009; Hunt et al., 2008). A rain garden is a shallow depression in the landscape planted with herbaceous perennials, shrubs, or small trees with the soil surface covered with shredded hardwood mulch, that collects stormwater from impervious surfaces such as roofs, driveways or parking lots (Dietz, 2007). Rain gardens allow stormwater to infiltrate into the ground and recharge groundwater supplies (Dietz and Clausen, 2006; Shuster et al., 2007) while removing stormwater pollutants (USEPA, 1999). Rain gardens are usually designed to hold 2.5 cm of water from a specified impervious surface. Ponding depth may vary from 15 to 46 cm depending on the water volume and the soil’s hydraulic conductivity (Davis et al. 2009; [Minnesota Pollution Control

Agency (MPCA), 2015]. Ponded water should not persist longer than 24 h and the soil pore space should drain excess waters within 48 to 96 h (Davis et al, 2009; MPCA, 2015). Rain garden soil should have a hydraulic conductivity of 2.5 $cm \cdot h^{-1}$ and contain up to 8 – 12% fines (silt and clay) by volume (Davis et al., 2009; Hunt and Lord 2006). Soils with greater amounts of fines can lead to reduced water infiltration and ultimately, failure of the rain garden. Several engineered soil/media mixes with high infiltration rates have been developed for use in rain gardens. Prince George's County, MD (2007) recommends a mix of 50% sand, 20-30% topsoil, and 20-30% leaf compost by volume. The MPCA (2015) recommends mixes containing 60 – 85% sand, 15 – 25% top soil (less than 5% clay), and 15 – 25% organic matter (by volume) depending on what type of pollutant removal is targeted.

Rain garden plants depend on seasonal precipitation and are subjected to drought and flooding cycles. Plants may remain dry for several days or weeks between rain events and remain flooded for extended periods of time following multiple rain falls. Although ponded water should not persist longer than 24 h and the soil pore space in the rain garden planting media should drain excess waters within 48 – 96 h, it is possible that during times of frequent rainfall both parameters may extend beyond what is recommended. Therefore, rain garden plants need to be tolerant of periodic soil flooding and drought conditions to sustain long-term functions and desired benefits to urban landscapes. The USEPA (1999) recommends using native plants tolerant of pollutants and varying wet and dry conditions.

Sedges

Sedges belong to the genus *Carex* L. which is composed of approximately 2,000 species of herbaceous perennials and is the largest genus in the Cyperaceae family (Bernard, 1990; Reznicek, 1990). The genus is distributed worldwide (Ball, 1990) and found in a wide range of habitats. This is especially true for sedges growing in the north temperate and Arctic regions (Bernard, 1990). Temperate sedge species can be found in wet meadows, pond and lake edges, dry grasslands, and mesic and dry forests (Schütz, 2000). It is estimated that 500 species occur in North America (Catling et al., 1990). Sedges are commonly used in wetland restoration projects (Kettenring and Galatowitsch, 2007b).

Cyclic flooding and drought

Rain garden plants depend on seasonal precipitation and are subjected to periods of flooding and drought. Soil may remain dry for several days or weeks between rain events and remain flooded for several days when rain events occur frequently (e.g., less than 48 h apart). Both flooding and drought cause plant stress. Flooded soils subject plants to oxygen deficiency causing an accumulation of toxic compounds and multiple physiological dysfunctions in plants that result in plant injury and growth inhibition (Jackson and Colmer, 2005; Kozlowski, 1997; Vartapetian, 2006). Oxygen deficiency occurs in waterlogged soils because oxygen diffusion is 10,000 times slower through water than in air (Jackson and Colmer, 2005). Plant response to flooding varies by plant species, floodwater properties, and duration of flooding (Kozlowski, 1997). Some plants have the ability to survive in water-logged soils due to adaptions such as oxygen transport and rhizopheric oxidation, hypertrophied lenticels, aerenchyma, root regeneration, and metabolic adaptions (Kozlowski, 1997). Drought stress affects plants by reducing cell division and expansion, root proliferation, and water use efficiency. Plants have the ability to survive drought by morphological, physiological, and molecular adaptions such as drought escape, drought avoidance, osmotic adjustment, plant growth hormones, and an antioxidant defense system (Farooq et al., 2012).

Available literature evaluating the flood tolerance of sedges is limited. Moog and Janiesch (1990) evaluated root growth and morphology of longbract sedge (*C. extensa* Goodenough), remote sedge (*C. remota* L.) and cypress-like sedge (*C. pseudocyperus* L.) with soil moisture preferences of dry, moist, and saturated, respectively. Sedges were grown in water culture with oxygen (aerobic) or nitrogen (anaerobic) bubbled through the solution for 40 d. All sedges survived both aerobic and anaerobic treatments and all sedges had an increase in aerenchyma tissue under anaerobic conditions. Total biomass increased under oxygen deficiency for remote sedge and cypress-like sedge but not longbract sedge.

A similar study by Visser et al. (2000) evaluated flood tolerance and aerenchyma formation of six alpine meadow sedges. Sedges were clearly distributed in the meadow based on soil water content with evergreen sedge (*C. sempervirens* Vill.) and rust-colored sedge (*C. ferruginea* Scop.) growing in non-flooded soil, Davall's sedge (*C. davalliana* Sm.) and smooth black sedge [*C. nigra* (L.) Reichard] in water logged soil, and mud sedge (*C. limosa* L.) and beaked sedge (*C. rostrata* Stokes) were partially submerged in water. Field collected sedges were placed in flooded (water level at soil surface), submerged (water level 5 cm above soil surface), and drained (watered as needed) conditions for 150 d. All species survived flooding, while partial submergence killed evergreen sedge and Davall's sedge. Although evergreen sedge and rust-colored sedge grew in non-flooded soil, both tolerated flooded conditions for 150 d with similar shoot and root dry weights when compared to the drained treatment. The authors evaluated aerenchyma formation of the sedges by growing them in stagnant or aerated nutrient solutions. Aerenchyma increased in all species grown in oxygen-deficient compared to the aerated nutrient solution. Aerenchyma tissue improves internal root aeration and may help explain the survival of evergreen sedge and rust-colored sedge in flooded soil.

Luo et al. (2008) evaluated flooding and drought tolerance of three Chinese wetland plants: woollyfruit sedge (*C. lasiocarpa* Ehrh.), mud sedge (*C. limosa* L.), and narrow-leaf small reed (*Deyeuxia angustifolia* (Komarov) Y.L. Chang). In Sanjiang Plain, woollyfruit sedge, mud sedge, and narrow-leaf small reed typically occur in water depths of 10-50, 10-30, and 0-10 cm, respectively. Flooding tolerance was assessed over a 25 d period and water depth in each tub was maintained at 50 cm above the soil surface. At the end of the study, survival of woollyfruit sedge, mud sedge, and narrow-leaf small reed were 100, 44, and 11%, respectively. Luo et al (2008) also assessed the drought tolerance of these plants in a second study. Soil water was measured daily over the 25 d study and decreased from 37.3 to 2.4% in the first 15 d and then slowly decreased to 0.1% by the end of the experiment. The only plants surviving at the end of the study were narrow-leaf small reed. This study illustrates that species able to survive flooding may not be able to survive drought.

There are two research studies evaluating landscape shrubs for rain garden use by mimicking a rain garden environment in a greenhouse (Dylewski et al., 2011; Jernigan and Wright 2011). Dylewski et al (2011) evaluated three shrubs native to the southeastern United States: inkberry holly (*Ilex glabra* (L.) A. Gray 'Shamrock'), Virginia sweetspire (*Itea virginica* L. 'Henry's Garnet'), and possumhaw (*Viburnum nudum* L. 'Winterthur'); all are considered wetland plants in Alabama (Lichvar et al., 2014). Flooding treatments of 0, 3, or 7 d were followed by a 7 d draining period. Substrate volumetric water content after a draining period ranged from 19% to 35% depending on species, flooding treatment, and substrate. All plants except 'Winterhur' possumhaw showed decreased root dry weight, shoot dry weight, and final growth index when compared to non-flooded plants. A similar study looked at repeated flooding of dwarf witchalder (*Fothergilla* x*intermedia* 'Mount Airy'), winterberry (*Ilex verticillata* L.

‘Winter Red’), coastal sweetpepperbush (*Clethra alnifolia* L. ‘Ruby Spice’) and Bandywine™ possumhaw for 6 weeks for 0, 3, or 6 d with a draining period of 6 d between each flood event (Jernigan and Wright, 2011). All shrubs except ‘Mt. Airy’ dwarf witchalder are considered wetland plants in Alabama (Lichvar et al., 2014). Substrate water content was measured daily using an ECH_2O soil moisture sensor. Volumetric soil water content generally ranged from 53% at the end of a flood treatment to 15% at the end of a draining period. It is unknown how the reduction in soil water content affected total soil water potential energy. All taxa appeared tolerant of flooding conditions except for ‘Mt. Airy’ dwarf witchalder.

Few published studies exist that look at combined flood and drought of sedges. Beaked sedge and awlfruit sedge (*C. stipata* Muhl. Ex Willd.), both obligate wetland plants, were subjected to cyclical flood and drought periods for 36 d in a greenhouse environment (Ewing, 1996). Sedges were flooded with 10 cm of water above the soil, soil dried down to 5% gravimetric water content, or no drought stress. Sedges went through three flooding and two drying cycles. During the drying cycles, mean net CO_2 uptake, stomatal conductance, and leaf elongation were reduced. After flooding, these values increased to pretreatment levels suggesting beaked sedge and awlfruit sedge are tolerant of repeated cycles of flood and drought.

Currently, there is no research available to determine drought or flood tolerance for the sedges used in this study. Previous research indicates sedges can develop aerenchyma tissue which increases tolerance to flooding. It is possible sedges selected for this study could tolerate extended periods of soil flooding regardless of wetland indicator category. Based on wetland indicator category, it is likely that some of the sedges from drier categories will be able to tolerate drought. However, it is unknown how the interaction of flooding and drought over time will impact survival.

Seed dormancy

Carex spp. frequently exhibit physiological dormancy (Baskin and Baskin, 2014) which prevents germination. Cold, moist stratification has proven to be effective at alleviating physiological dormancy in sedges. In a study of 32 temperate sedge species, Schutz and Rave (1999) found that cold, moist stratification at 4 ^{o}C for 6 months improved germination of 28 species compared to achenes receiving no stratification. Kettenring and Galatowitsch (2007b) found that cold, moist stratification at alternating day and night temperatures of 5/1 ^{o}C increased germination percentages, broadened the germination temperature range, and increased germination rate in most of the 12 sedge species tested. Length of cold stratification ranged from 0 (control) to 6 months. Optimum length of cold stratification varied by species and germination temperature, for example porcupine sedge (*C. hystericina* Muhl. ex Willd) and plains oval sedge (*C. brevior* (Dewey) Mack) did not germinate at 14/1 ^{o}C without cold stratification but germinated to 80% after 2 or 3 months of cold stratification. Both species were able to achieve over 80% germination with no cold stratification within 4 weeks when the germination temperature was 27/15 ^{o}C. McGinnis and Meyer (2011) found that 8 weeks of cold stratification at 4 ^{o}C in conjunction with after-ripening resulted in more consistent germination of Pennsylvania sedge (*C. pensylvanica* Lam.).

Other factors may also affect achene germination such as fluctuating temperatures, light, and perigynium removal. Schutz and Rave (1999) suggest sedges are strict spring germinators. Therefore, a diurnally fluctuating temperature regime may be optimal since it mimics temperature changes in the spring. Some studies have shown an increase in percent germination when subjecting seed to fluctuating day and night temperatures compared to constant temperatures. Schütz and Rave (1999) found that a fluctuating germination temperature of 20/10

^{o}C increased achene germination compared to constant germination temperatures when averaged across 32 temperate European sedge species. Kettenring and Galatowitsch (2007a) evaluated the temperature requirements for dormancy break and achene germination in 14 wetland sedge species from North America and found the optimal germination temperature for most species was 27/15 ^{o}C.

It has been well established that light increases achene germination of many sedge species. Schütz and Rave (1999) found 31 of 32 European sedges had a higher percent germination in the light compared to the dark. Kettenring et al (2006) found that eight wetland sedge species had higher percent germination when achenes were exposed to varying lengths of white light compared to achenes germinated in the dark. All species with viable achenes germinated to 100% when given 3 weeks of 14-h daily exposure to white light after being exposed to 4 months cold-moist stratification at 5/1 ^{o}C. McGinnis and Meyer (2011) found higher percent germination in Pennsylvania sedge when achenes were exposed to white fluorescent light compared to achenes kept in the dark.

Sedges have a bladder-like sac called a perigynium that adheres to the pericarp of the achene. Perigynium removal has been shown to increase percent germination of several sedge species such as Nebraska sedge (*C. nebrascensis* Dewey), awlfruit sedge, and Pennsylvania sedge (Hoag et al., 2001; Hough-Snee and Cooper, 2011; McGinnis and Meyer, 2011).

Although physiological dormancy breaking techniques have been established for several sedge species, germination is not uniform and may occur over the course of 8 weeks. It would be beneficial to sedge producers if germination time could be shortened after dormancy requirements have been satisfied.

Research objectives

1) Evaluate plant growth and survival of four sedge species when subjected to continuous flood or drought conditions. During drought conditions, determine the volumetric water content needed to impose visual drought stress on sedges.
2) Evaluate plant growth and survival of seven sedge species subjected to cyclical flood and drought conditions.
3) Determine if perigynia removal would increase percent germination and decrease time needed to reach 50% germination of four sedge species native to the north central U.S.

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CHAPTER II. EVALUATION OF RAIN GARDEN SEDGES TO CYCLICAL FLOOD AND DROUGHT

Introduction

Over 80% of the United States population lives in urban areas (U.S. Census Bureau, 2010). Within an urban area, residential and commercial districts may cover 20% and 85% of the land with impervious surfaces, respectively (Dietz and Clausen, 2005). Increasing the area covered by impervious surfaces decreases water infiltration and increases the amount of stormwater runoff [U.S. Environmental Protection Agency (USEPA), 1993]. Urban runoff contains sediment, soil nutrients, road salts, petroleum hydrocarbons, and heavy metals (Dietz and Clausen, 2005; USEPA, 2005). Urban stormwater runoff is responsible for 36,305 (9%) impaired river km; 283,689 (7%) impaired lake ha; and 2,246 (11%) impaired estuary km^2 in the United States (USEPA, 2009). The quality of urban stormwater runoff can be improved and the quantity greatly reduced by using a rain garden.

A rain garden is a shallow depression in the landscape, typically planted with herbaceous perennials, shrubs, or small trees that collects stormwater from impervious surfaces such as roofs, driveways or parking lots (Dietz, 2007; Dietz and Clausen, 2006). Rain gardens allow stormwater to infiltrate into the ground and recharge groundwater supplies (Dietz and Clausen, 2006; Shuster et al., 2007) while removing stormwater pollutants (USEPA, 1999). Ponded water in a rain garden should not remain longer than 24 h and the soil pore space should drain within 48 to 96 h (Davis et al, 2009; Minnesota Pollution Control Agency, 2015). During periods of frequent rainfall events or in situations where the rain garden does not drain as designed, ponded water may remain for several days.

Rain garden plants depend on seasonal precipitation and will be subjected to cyclical episodes of soil flooding and drought. The USEPA (1999) recommends using native plants tolerant of pollutants and varying amounts of soil moisture. Sedges belong to the genus *Carex* L. and are commonly recommended for rain gardens (Bannerman et al., 2003; Shaw and Schmidt, 2003). Sedges are herbaceous perennials with approximately 2,000 species distributed worldwide and found in a wide range of habitats (Bernard, 1990; Reznicek, 1990; Ball 1990) such as wet meadows, pond and lake edges, dry grasslands, and mesic and dry forests (Schütz, 2000). It is estimated that 500 species occur in North America (Catling et al., 1990).

Few studies are available that evaluate the flood tolerance of sedges. Moog and Janiesch (1990) evaluated root growth and morphology of longbract sedge (*C. extensa* Goodenough), remote sedge (*C. remota* L.) and cypress-like sedge (*C. pseudocyperus* L.) with soil moisture preferences of dry, moist, and saturated, respectively. Under flooded and anaerobic conditions, they found an increase in total biomass for remote sedge and cypress-like sedge, the two sedges that preferred moist and saturated soils, but not longbract sedge. A similar study by Visser et al. (2000) evaluated flood tolerance and aerenchyma formation of six alpine meadow sedges clearly distributed in the meadow based on soil water content with evergreen sedge (*C. sempervirens* Vill.) and rust-colored sedge (*C. ferruginea* Scop.) growing in non-flooded soil, Davall's sedge (*C. davalliana* Sm.) and smooth black sedge (*C. nigra* (L.) Reichard) in water-logged soil, and mud sedge (*C. limosa* L.) and beaked sedge (*C. rostrate* Stokes) were partially submerged in water. Field collected sedges were placed in flooded (water level at soil surface), submerged (water level 5 cm above soil surface), and drained (watered as needed) conditions for 150 d. All species survived flooding, while partial submergence killed evergreen sedge and Davall's sedge. Although evergreen sedge and rust-colored sedge grew in non-flooded soil, both tolerated flooded conditions for 150 d with similar shoot and root dry weights when compared to the drained treatment. The authors evaluated aerenchyma formation of the sedges by growing them in stagnant or aerated nutrient solutions. Aerenchyma increased in all species grown in oxygen deficient conditions compared to the aerated nutrient solution (Visser et al., 2000). Aerenchyma tissue improves internal root aeration (Kozlowski, 1997) and may help explain the survival of evergreen sedge and rust-colored sedge in flooded soil.

Luo et al. (2008) evaluated flooding and drought tolerance of three Chinese wetland plants: woollyfruit sedge (*C. lasiocarpa* Ehrh.), mud sedge (*C. limosa* L.), and narrow-leaf small reed (*Deyeuxia angustifolia* (Komarov) Y. L. Chang), typically occur in water depths of 10-50, 10-30, and 0-10 cm, respectively. Flooding tolerance was assessed over a 25-d period and water depth was maintained at 50 cm above the soil surface. At the end of the study, survival of woollyfruit sedge, mud sedge, and narrow-leaf small reed were 100, 44, and 11%, respectively. Drought tolerance of these three species was also assessed. Soil water was measured daily over the 25-d study and decreased from 37.3 to 2.4% in the first 15 d. Soil water content slowly decreased to 0.1% by the end of the experiment. The only plants surviving at the end of the study were narrow-leaf small reed suggesting that plants able to survive flooding may not be able to survive drought.

Sedge species such as Gray's sedge (*C. grayi* Carey), palm sedge (*C. muskingumensis* Schwein), Pennsylvania sedge (*C. pensylvanica* Lam.), plains oval sedge (*C. brevior* (Dewey) Mack), porcupine sedge (*C. hystericina* Muhl. Ex Willd), Sprengel's sedge (*C. sprengelii* Dewey ex Spreng) and yellow fox sedge (*C. annectens* E.P. Bicknell) have been recommended for rain garden use (Bannerman and Considine, 2003; Hausken and Thompson, 2015; HHRCDC, 2017; Rodie et al., 2010; Schmidt et al., 2007; Shaw and Schmidt, 2003), but no scientific studies have been conducted to support these recommendations. Our objective was to determine the effect of cyclical flood and drought on the growth of these seven sedge species from vastly different soil moisture regimes to determine their fitness for rain garden use.

Materials and methods

Plant material. The seven sedge species selected for this research project were purchased from retail plant nurseries (Table 2-1) and are native to the north central United States (USDA-NRCS, 2015). The sedges represent all five wetland indicator categories (Table 2-1) in the National Wetland Plant List (NWPL) for the Midwest region (Lichvar et al., 2014). Four plants of each sedge species were planted into a 1.07 L (10.7 cm wide x 8.7 cm tall) square vacuum deep pot (T.O. Plastic, Clearwater, MN) filled with Metro Mix 902 (Sungro Horticulture, Agawam, MA) containing Canadian sphagnum peat moss, composted bark, perlite, vermiculite, dolomite lime, and blue chip. Potting medium was amended with 5.0 $kg \cdot m^{-3}$ of controlled release fertilizer (Osmocote® 14-14-14, 3-4 month release; The Scotts Company, Marysville, OH). Plants were grown in a greenhouse maintained at a minimum of 21 ^{o}C day and night with a 16-h photoperiod located on the North Dakota State University (NDSU) campus, Fargo, ND, U.S.A. (latitude 46^{o} 52’ 38” N). After 4 w of growth, one plant of each species exhibiting the most vigorous growth was selected as the stock plant for all experiments and the remaining plants were discarded. Stock plants were propagated by crown division as needed to increase plant numbers.

Substrate. The substrate used for this study was composed of Metro Mix 902 mixed 1:1 (by volume) with all-purpose sand (TCC Materials, Mendota Heights, MN) ranging in particle size from 0.015 to 0.050 mm. The substrate was selected because a uniform supply of both

Table 2-1. *Carex* species, origin of plant material, wetland description and designation, and wetland indicator status. Wetland indicator status, description, and designation are from Lichvar et al., 2014.

Scientific name	Common name	Origin of plant material	Wetland indicator status (Great Plains)	Wetland indicator description and designation
C. hystericina Muhl. ex Willd	Porcupine sedge	Morning Sky Greenery, Morris, MN	Obligate (OBL)	Almost always occur in wetlands (hydrophyte)
C. muskingumensis Schwein.	Palm sedge	Sheyenne Gardens, Harwood, ND	Obligate (OBL)	Almost always occur in wetlands (hydrophyte)
C. annectens E.P. Bicknell	Yellow fox sedge	Morning Sky Greenery, Morris, MN	Facultative Wetland (FACW)	Usually occur in wetlands, but may occur in non-wetlands (hydrophyte)
C. grayi Carey	Gray's sedge	Prairie Nursery Inc., Westfield, WI	Facultative Wetland (FACW)	Usually occur in wetlands, but may occur in non-wetlands (hydrophyte)
C. brevior (Dewey) Mack	Plains oval sedge	Morning Sky Greenery, Morris, MN	Facultative (FAC)	Occur in wetlands and non-wetlands (hydrophyte)
C. sprengelii Dewey ex Spreng.	Sprengel's sedge	Prairie Nursery Inc., Westfield, WI	Facultative Upland (FACU)	Usually occur in non-wetlands, but may occur in wetlands (non-hydrophyte)
C. pensylvanica Lam.	Pennsylvania sedge	Prairie Restorations, Princeton, MN	Upland (UPL)	Almost never occur in wetlands (non-hydrophyte)

components were available from local vendors and the substrate was easy to wash free from plant roots. A water retention curve (Fig. 2-1) was developed for the substrate using pressure cookers and pressure plates between -10 to -200 and -500 to -1,500 kPa, respectively (model 16001F and 1000, Soilmoisture Equipment Corp., Santa Barbara, CA, U.S.A.). Substrate was screened through a 3.35 mm sieve to remove large pieces of bark. Screened substrate was placed into 5 cm diameter plastic rings on the pressure cookers and plates, saturated with deionized water, and allowed to equilibrate until a uniform sheen was noticed on the substrate surface. After drainage from pressure cookers and plates ceased, the wet samples were weighed, dried at 105 ^{o}C for 48 h, and reweighed at oven-dry conditions to determine gravimetric water content. Water retention from -2,190 to -19,700 kPa were determined indirectly with a WP4 dew point potentiometer (Decagon Devices, Pullman, WA) in a 20 ^{o}C constant temperature room. Gravimetric water contents were converted to volumetric water contents (VWC) by multiplying by 0.96 $g \cdot cm^{-3}$, the bulk density of the substrate. Bulk density was calculated by filling a container with a known volume with substrate and watering daily for 7 d. The substrate was then removed and oven dried at 105 ^{o}C for 48 h. Substrate was weighed at oven-dry conditions and bulk density was determined by dividing the weight of the dry substrate by the volume of substrate. The measured VWC data were fitted to the van Genuchten (1980) model. The van Genuchten modeld is described as:

$$\Theta = \Theta_{r} + (\Theta_{s} - \Theta_{r}) / [1 + (\alpha \text{ x } h)^{n}]^{m} \quad (1)$$

$$m = 1 - 1/n \quad (2)$$

where Θ is the volumetric water content (at a given moisture tension in kPa), Θ_s is the volumetric water content at saturation in kPa, Θ_r is the residual volumetric water content in kPa, h is the moisture tension in kPa, α is the inverse of the substrate air entry point, n and m are curve fitting

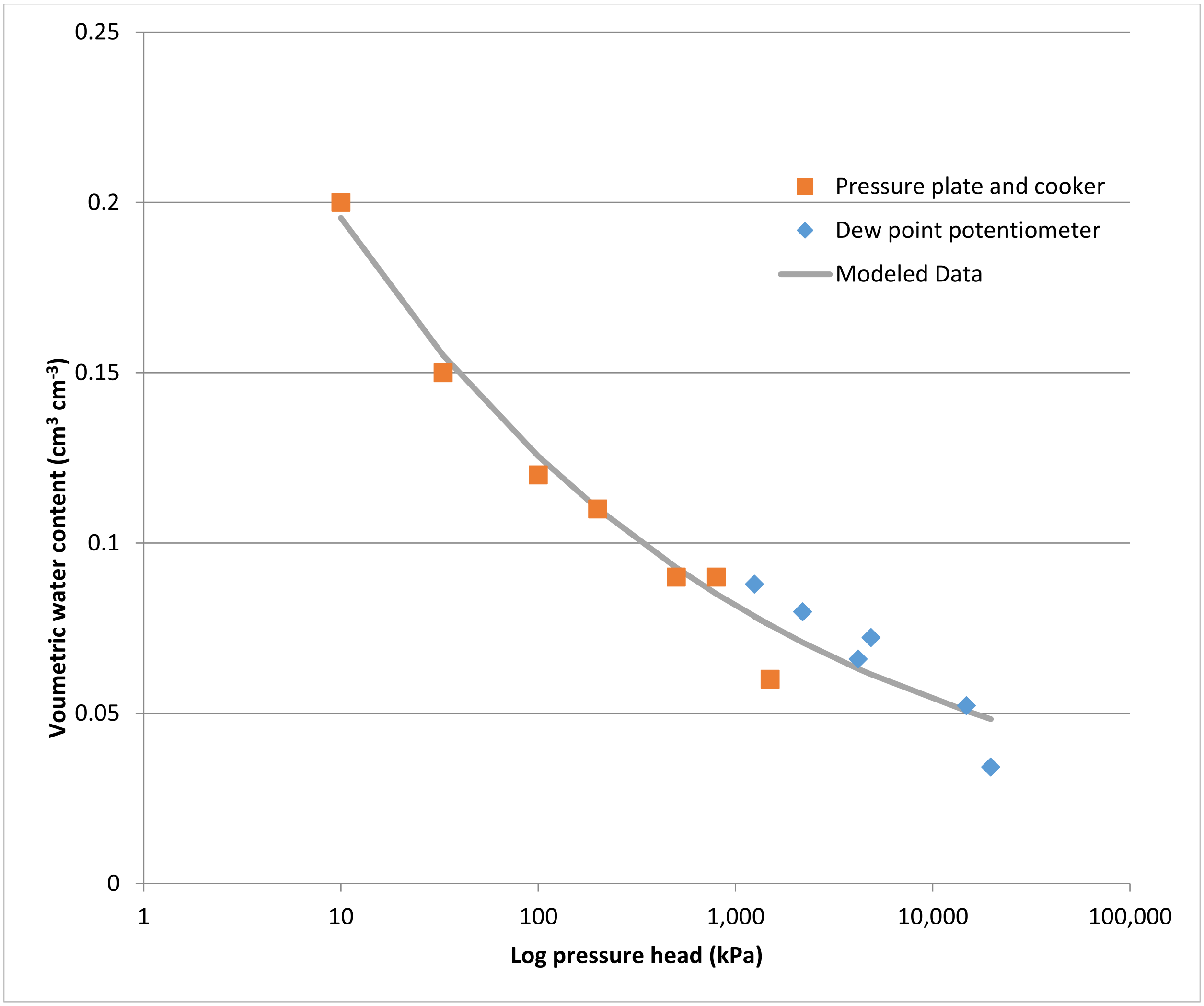

Figure 2-1. Water retention curve of a 1:1 (by volume) mixture of Metro Mix 902 with all-purpose sand.

parameters (van Genuchten, 1980). The VWC of the substrate at saturation was determined by the following equation:

$$f = 1 - (\rho_b / \rho_s) \quad (3)$$

where f is porosity, ρ_b is bulk density, and ρ_s is particle density. Particle density for the substrate (Metro Mix 902 + sand), Metro Mix 902, and sand were 2.65 $g \cdot cm^{-3}$, 1.69 $g \cdot cm^{-3}$, and 2.72 $g \cdot cm^{-3}$, respectively. Particle density was calculated using the pycnometer method as described by Blake and Hartge (1986).

Sensor calibration**.** A range of water contents was established by adding 0 – 200 ml water, in 50 ml increments to metal containers holding 600 g of air dried soil. After adding water, substrate and water were mixed, containers covered with Parafilm M® (Bemis Company Inc., Neenah, WI), and allowed to equilibrate for 2 h. Substrate from each container was transferred into 1.07 L plastic pots and the GS3 sensor, connected to a ProCheck sensor readout storage system (Decagon Devices, Pullman, WA), was inserted into the middle of the container to obtain a reading. Immediately after the reading, three sub-samples from each pot were weighed, oven dried at 105 ^{o}C for 48 h, and reweighed at oven dry conditions to determine gravimetric water content. VWC was determined by multiplying gravimetric water content by bulk density and assuming that 1.0 g of water is equal to 1 mL. The accuracy of the GS3 sensor was evaluated by plotting the VWC measured by the sensor versus the VWC determined by gravimetric water content and bulk density (Fig. 2-2). Because of the variation in VWC between the GS3 sensor and that determined by gravimetric water content and bulk density, a substrate specific equation was developed and used to calculate real time VWC of the substrate during the study (Fig. 2-3).

Preliminary study**.** A preliminary study was conducted with yellow fox sedge, plains oval sedge, porcupine sedge, palm sedge, and Pennsylvania sedge to determine the VWC needed to cause visual drought damage and assess shoot and root growth of sedges. Sedges were divided into equal-sized divisions, within species, based on shoot counts. Yellow fox, plains oval, and Pennsylvania sedge divisions contained 30 shoots and 15 shoots for porcupine and palm sedge divisions. After dividing, shoots were cut to a height of 5.0 cm, soil was removed from roots, and sedges were planted into 2.8 L (16.5 cm wide x 17.8 cm tall) nursery containers (Meyers Industries, Akron, Ohio) filled with Metro Mix 902 mixed 1:1 (by volume) with all-purpose sand

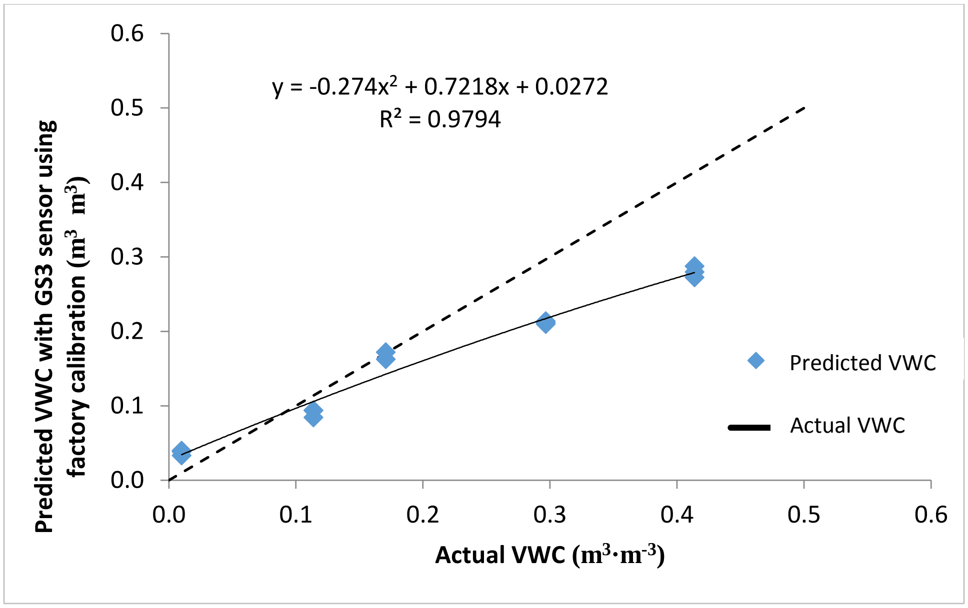

Figure 2-2. The relationship between substrate volumetric water content (VWC) as measured by the GS3 sensor using the factory calibration for mineral soil and the VWC determined by gravimetric water content and bulk density using a 1:1 (by volume) mixture of Metro Mix 902 with all-purpose sand.

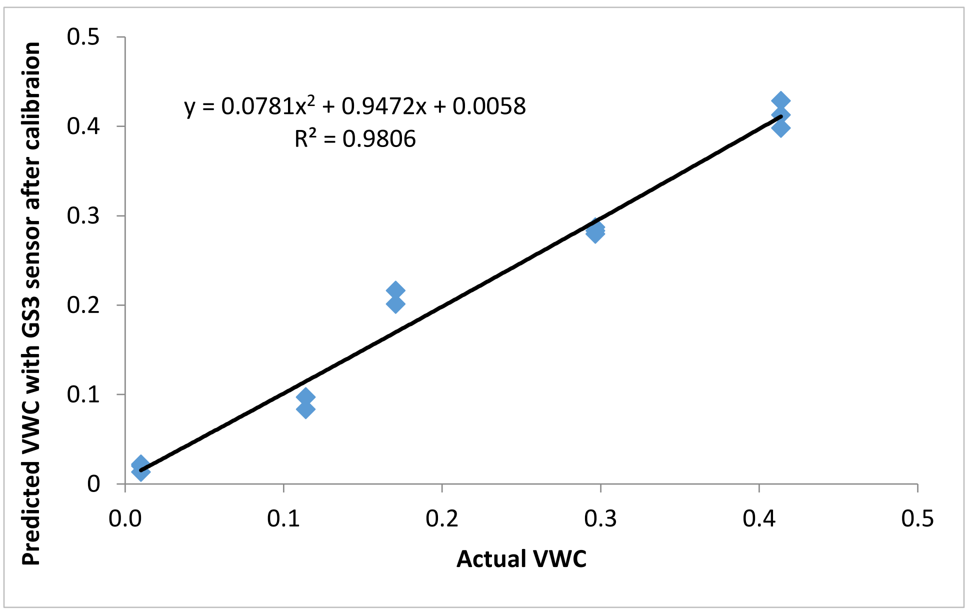

Figure 2-3. The relationship between substrate volumetric water content (VWC) as measured by the GS3 sensor after substrate specific calibration and the VWC determined by gravimetric water content and bulk density using a 1:1 (by volume) mixture of Metro Mix 902 with all-purpose sand.

as described above. Plants were watered as needed to prevent wilting and fertilized weekly, until initiation of treatments on 3 July 2015 with an all-purpose water soluble fertilizer (20N-8.7P-16.6K; JR Peters Inc., Allentown, PA) with each pot receiving 0.2 g N, 0.1 g P, and 0.2 g K. Sedges were grown under a 16-h photoperiod with supplemental lighting provided from 0600 HR to 2200 HR using 400-watt high pressure sodium lights (P.L. Light Systems, Beamsville, ON, Canada) with an output of 139 $\mu mol \cdot m^{-2} \cdot s^{-1}$ irradiance (measured at plant height ~51 cm above bench on a cloudy day with the LI-250 quantum sensor, LI-COR, Inc., Lincoln, NE). Sedges were arranged in a randomized complete block design with 12 single pot replicates for each of three treatments. Sedges were subjected to continual flood or drought for 32 d. A well-watered control was also maintained for treatment comparison. Sedges were flooded by placing the 2.9 L container with sedge into another 2.9 L container lined with a 26.8 cm x 27.3 cm plastic bag (SC Johnson, Racine, WI). Tap water was added until a 2 cm layer was above the substrate surface. Water was added daily to maintain this depth. Substrate VWC readings were taken every other day using a hand held GS3 volumetric water content sensor connected to a ProCheck sensor readout and storage system. Sedges were rated every other day for visual plant damage using a 1-5 scale (1= no plant damage; 2= start of leaf wilt; 3= greater than 50% of plant wilting; 4= leaf dieback; 5= plant dead).

The results of the preliminary study suggested visual plant damage (i.e. leaf wilt) was not occurring until the VWC was reduced to 0.10 m^3 m^{-3} (Fig. 2-4). There was no visual plant damage at 0.15 $m^3 \cdot m^{-3}$ and severe visual plant damage at 0.05 $m^3 \cdot m^{-3}$. Based on this data, the drought setpoints 0.05, 0.10, and 0.15 $m^3 \cdot m^{-3}$, representing severe, moderate, or no visual plant damage, were selected for the main experiment. Shoot count, plant height, shoot dry weight, and root dry weight data can be found in the Appendix (Table A1 and A2).

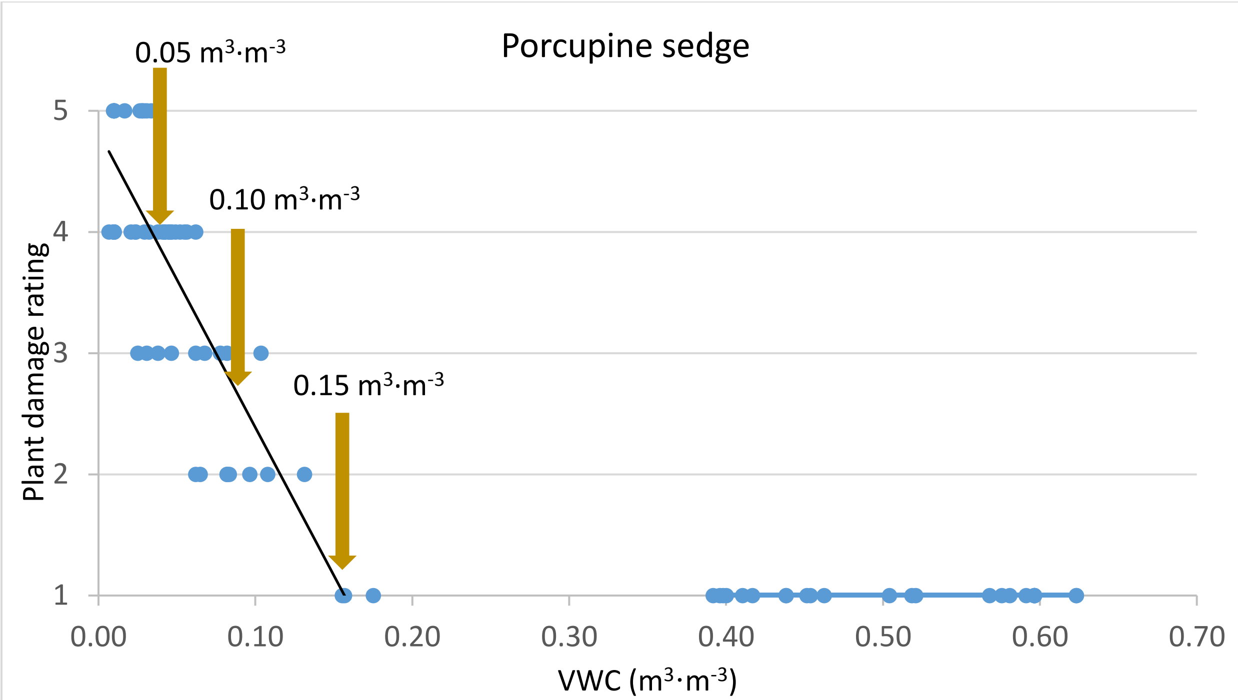

Figure 2-4. Typical visual plant damage rating (1= no plant damage; 2= start of leaf wilt; 3= greater than 50% of plant wilting; 4= leaf dieback; 5= plant dead) for a given substrate volumetric water content. Volumetric water content (VWC) measurements and visual plant damage ratings were taken every other day from 3 July to 3 Aug, 2015 (only data from 3 July to 15 July is shown) from sedges growing in a greenhouse on the NDSU campus, Fargo, ND.

Cyclical flood-drought study. Sedges were divided into equal-sized divisions, within species, based on shoot counts. Each division of yellow fox sedge, plains oval sedge, Gray's sedge, porcupine sedge, palm sedge, Pennsylvania sedge, and long-beak sedge contained 30, 30, 7, 15, 15, 30, and 4 shoots, respectively. Sedges were allowed to establish for 3 months until the start of the experiment. Environmental conditions in the greenhouse were monitored with three sensors (VP-4, Decagon Devices, Pullman, WA) spaced throughout the greenhouse collecting relative humidity, temperature, and vapor pressure data every five minutes from 28 Nov. 2015 to 15 May 2016. Data from all three sensors were averaged together and can be found in the Appendix (Fig. A1). The greenhouse was heated when temperatures dropped below 18 ^{o}C and cooled when temperatures reached 25 ^{o}C. The average temperature during the study was 23 ^{o}C. Treatments were initiated on 26 Nov. (run 1), 20 Jan. (run 2), and 6 Mar. (run 3).

***Treatments and data collection*.** Treatments consisted of two flood periods, two or seven days, followed by a dry down period to one of three VWC setpoints as established in the preliminary study: 0.15, 0.10, and 0.05 $m^3 \cdot m^{-3}$ (i.e. substrate matric potentials of -40, -300, -14,800 kPa, respectively) for a total of 6 treatments with each treatment having 3 plants. A well-watered control (n = 3) was maintained for comparison. Control plants were watered as needed to keep the VWC above 0.15 $m^3 \cdot m^{-3}$ (Appendix fig. A2-A7). Sedges were flooded for two or seven days by placing the 2.9 L container with sedge into another 2.9 L container lined with a 26.8 cm x 27.3 cm plastic bag (SC Johnson, Racine, WI). Tap water was added until a 2 cm layer was above the substrate surface. Water was added daily to maintain this depth. At the end of the flood cycle, the outer pot with plastic bag was removed and sedges were allowed to drain. Substrate VWC readings were taken daily at the same time each day on each plant starting 24 h after the end of the flood cycle, using the hand held GS3 volumetric water content sensor. Once the substrate VWC reached the respective threshold, flooding was repeated (Fig. 2-5 and 2-6). This cycle continued until the seven-day flood and 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment went through four complete cycles at which point the experiment was terminated. Shoot height, shoot count, and dry weight of shoots and roots were measured. A visual damage rating (1-4 scale; 1= 0-25% dieback, 2= 26-50% dieback, 3= 51-75% dieback, 4= 76-100% dieback) was assigned to each plant based on the amount of foliage dieback. Evapotranspiration (ET) per day, total biomass water use efficiency (WUE), and days of dry down were also calculated. Height was determined by grasping the plant foliage and extending upward until it was held straight. Height was measured from the soil surface to the highest living portion of leaf tissue. Shoot counts were determined by counting all living shoots that were at least 1.25 cm above the substrate surface. Shoots were severed at the substrate surface and roots were washed clean of substrate. Shoots and roots were placed into separate paper bags and oven dried at 65 ^{o}C for 72 hours. After drying, shoots and roots were removed from paper bags and weighed using an electronic balance (EORW60, Ohaus Corporation, Pine Brook, NJ) to determine dry weights. Total biomass was calculated by adding together root mass and shoot mass. Evapotranspiration per day was calculated by determining the difference in VWC from the beginning to the end of each dry down cycle. The sum of the differences was multiplied by the volume of substrate in the container to determine total grams of water removed. Total grams of water removed from the container was divided by the total number of days spent in dry down to determine grams of water removed per day. Total biomass WUE was calculated by dividing the total grams of water removed from the container by total biomass to determine grams of water needed to produce/maintain one gram of total biomass. Days of dry down was calculated by taking the sum of the days needed to complete each dry down cycle divided by the total number of dry down cycles to determine the average number of days needed per dry down cycle.

Experimental design and statistical analysis

The experiment was arranged as a randomized complete block design with a 7 x 2 x 3 factorial arrangement consisting of seven species, two flood periods, and three levels of VWC with three single plant replicates per species. The experiment was run three times. Data were pooled for analysis after determining the variance of each run were similar by comparing the error mean square values (within a factor of 10). Prior to analysis, all data except visual damage rating, ET per day, total biomass WUE, and days of dry down were expressed as percent of the control and subjected to analysis of variance (Proc MIXED, SAS 9.4; SAS Institute, Cary, NC).

Experimental run was considered a random effect and species, flood, and drought as fixed effects. Treatment means were separated using Tukey's honestly significant difference. Means were considered significant at the $P < 0.05$ level. All data except for plant height, shoot count, visual damage rating, and ET per day were $\log_{10}$ transformed prior to analysis to standardize the variance and back transformed for presentation of data.

Results

Relative shoot height. The main effects of species and drought setpoint were significant for relative shoot height. All species exhibited reduced shoot height under all treatments relative to their respective control (Fig. 2-7). However, plains oval sedge and Gray's sedge had significantly less of a decrease in shoot height than all other species. There was no difference in relative shoot height among yellow fox sedge, porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge. Regardless of species and flood duration, sedges had significantly less relative shoot height at the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment compared to the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-8). There was no difference between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments.

Relative shoot count. There was a significant species by drought setpoint interaction for shoot count. Within a sedge species, the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment had significantly fewer shoots compared to the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments for porcupine sedge, palm sedge, and Pennsylvania sedge (Fig. 2-9). There was no significant difference between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments for these species. Within a species, there was no significant difference in shoot counts among the 0.05, 0.10, and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments for yellow fox sedge, plains oval sedge, Gray's sedge, and Sprengel's sedge. The 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment for yellow fox sedge, plains oval sedge, and

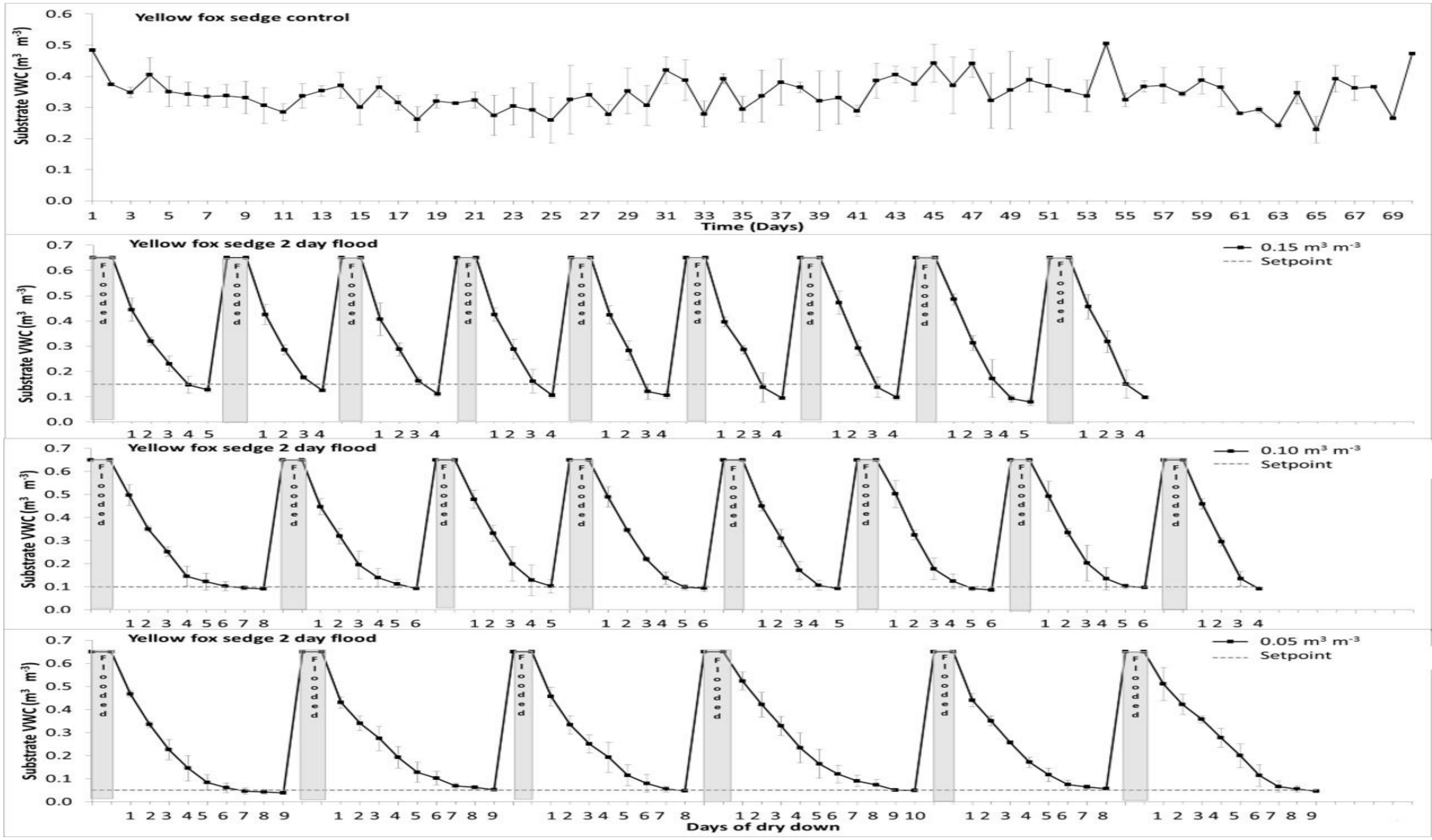

Figure 2-5. Example of substrate volumetric water contents (VWC) from control and 2-day flood with drought setpoints 0.15, 0.10, and 0.05 $m^3 \cdot m^{-3}$ for yellow fox sedge. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

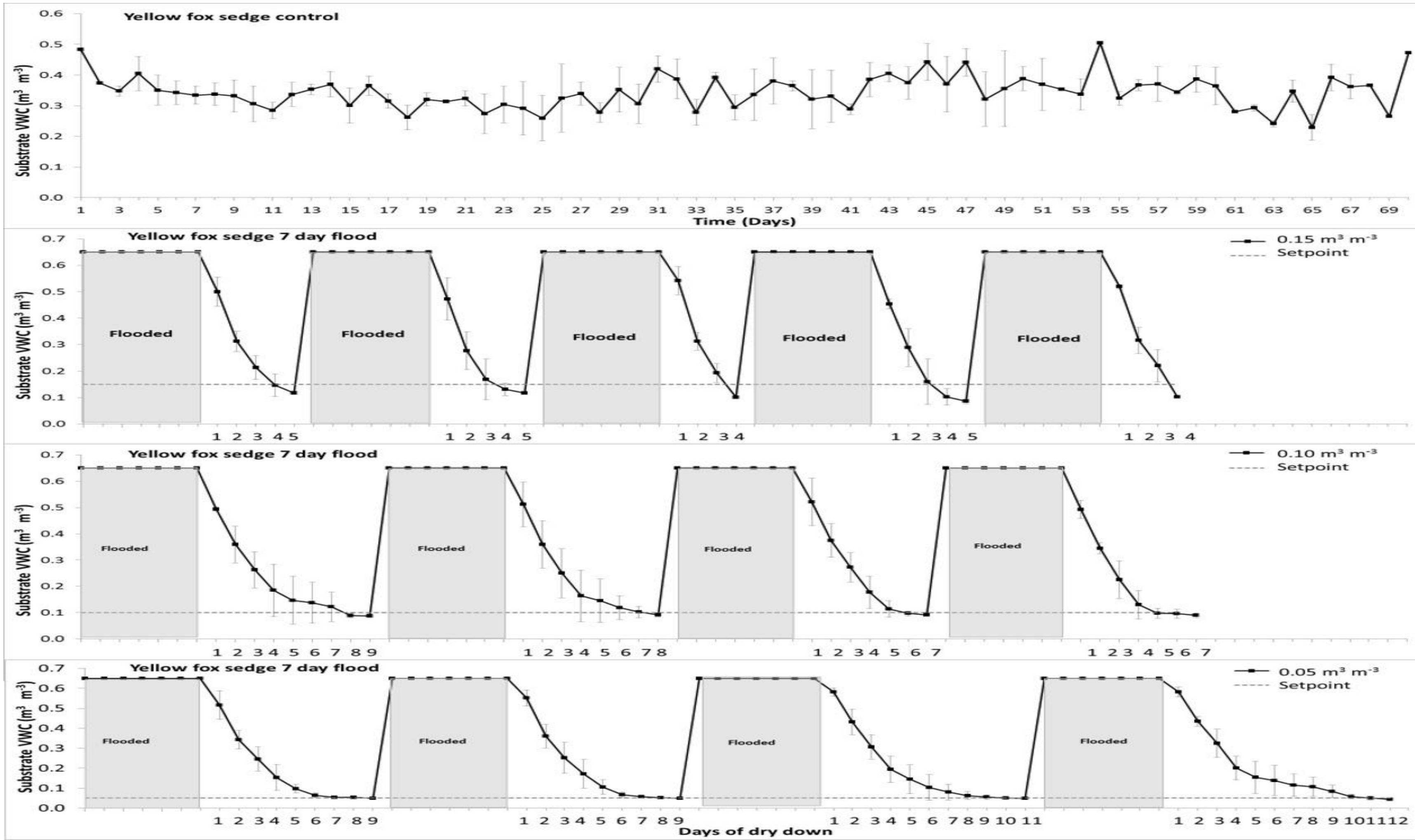

Figure 2-6. Example of substrate volumetric water contents from control and 7-day flood with drought setpoints 0.15, 0.10, and 0.05 $m^{3} \cdot m^{-3}$ for yellow fox sedge. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

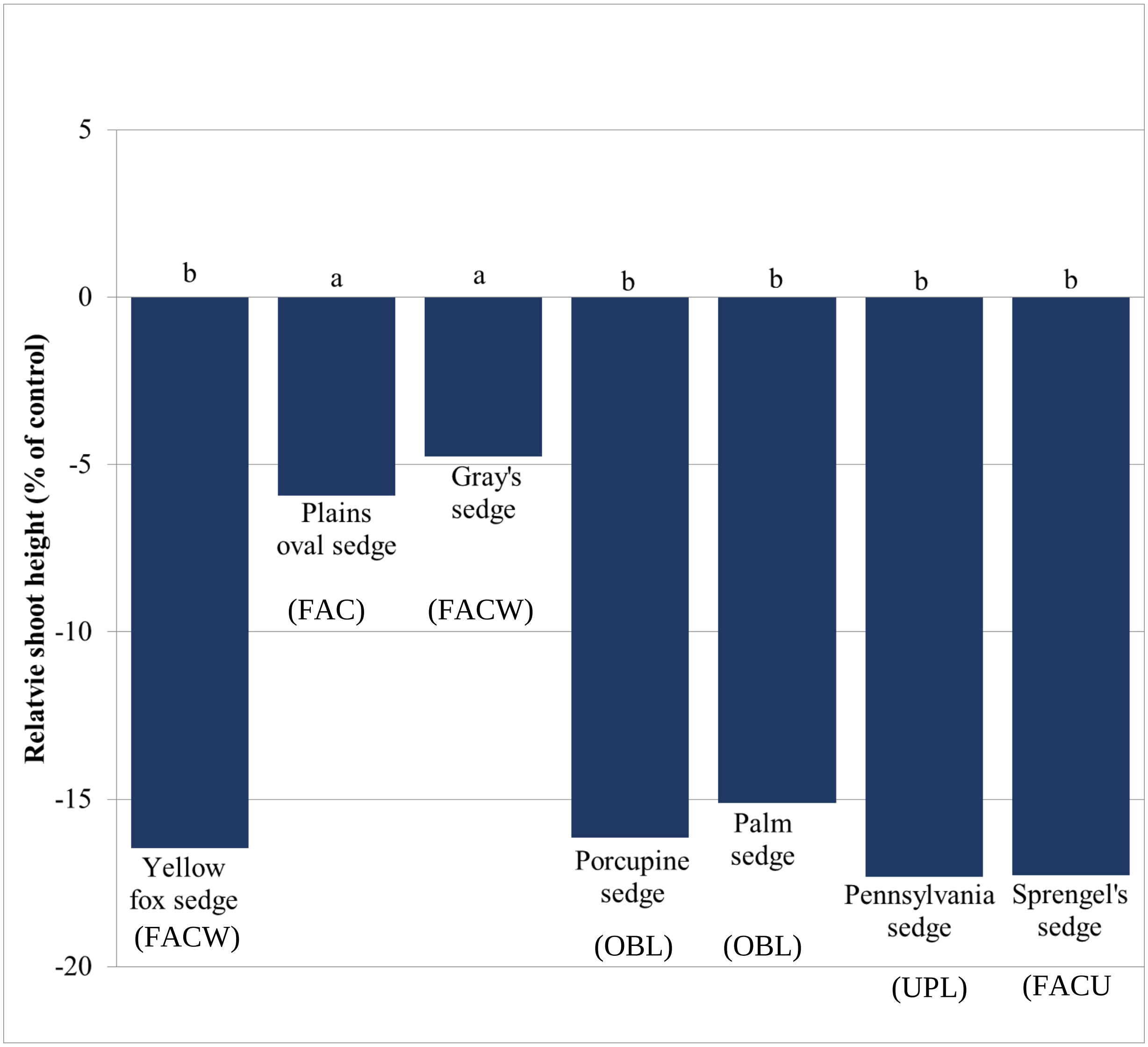

Figure 2-7. Shoot height as a percentage of the control of seven sedge species averaged across flood and drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate volumetric water content (VWC). Mean (n = 54) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at P< 0.05.

Gray's sedge had a positive relative shoot count compared to the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment for porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge. No significant differences among species were observed at the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments except for Sprengel's sedge and Pennsylvania sedge. Sprengel's sedge was significantly lower than plains oval sedge at the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC and yellow fox sedge at the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments. Pennsylvania sedge at the 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatment was significantly lower than plains oval sedge at the 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatment.

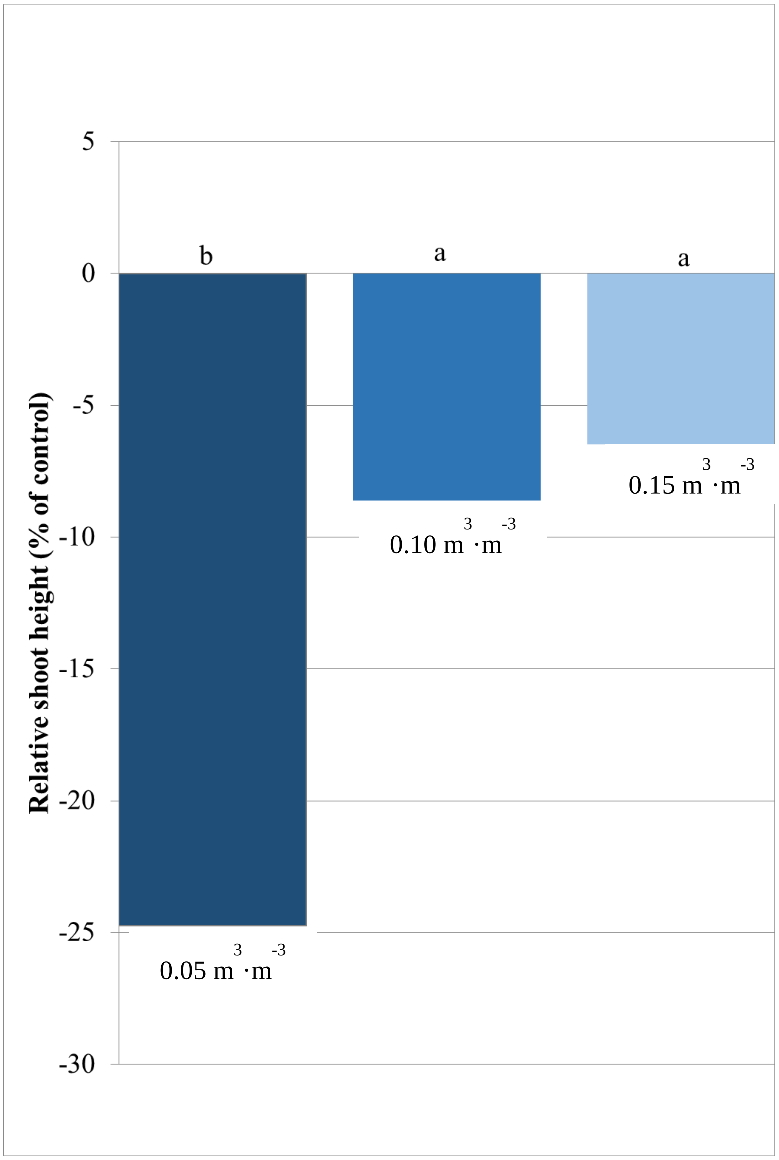

Figure 2-8. Relative shoot heights for the drought setpoints 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate volumetric water contents when averaged across sedge species and flood duration. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate volumetric water content (VWC). Mean (n = 126) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

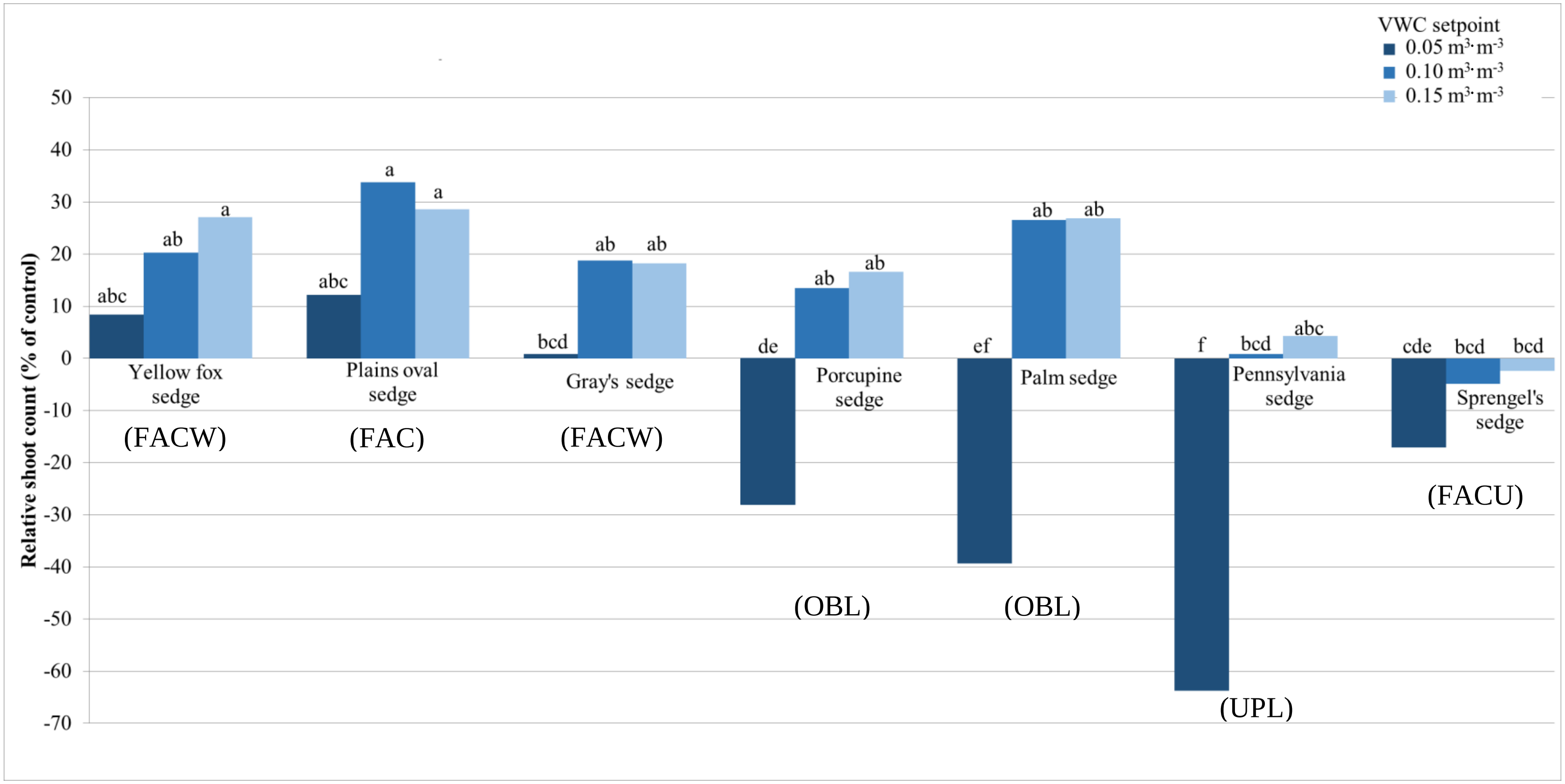

Figure 2-9. Shoot count as a percentage of the control for seven sedge species subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate volumetric water content (VWC). Mean (n = 18) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

Relative shoot mass. The main effects of species, flood duration, and drought setpoint were significant for relative shoot mass. Plains oval sedge had significantly higher relative shoot mass compared to all other species (Fig. 2-10). Sprengel's sedge had significantly less relative shoot mass compared to all other sedges except porcupine sedge. Relative shoot mass was significantly increased for the 7-day flood period compared to the 2-day flood period (Fig. 2-11). Among drought setpoints, the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment produced significantly less relative shoot mass compared to the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-12). There was no significant difference in relative shoot mass between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments.

Relative root mass. There was a species by flood duration interaction and a drought setpoint main effect for relative root mass. The species by flood duration interaction only occurred for Pennsylvania sedge where the 2-day flood duration treatment had significantly greater relative root mass compared to the 7-day flood treatment (Fig. 2-13). Within a species, there were no significant differences between the 2-day and 7-day flood duration treatments for the other sedge species. The 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment had significantly less relative root mass compared to the 0.10 and the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-14). There were no significant differences between the 0.10 and the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments.

Relative total biomass. The main effects, species and drought setpoint, were significant for total biomass. Plains oval sedge had significantly more relative total biomass compared to porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge, but not yellow fox sedge or Gray's sedge (Fig. 2-15). Palm sedge had the lowest relative total biomass but only significantly lower compared to plains oval sedge, yellow fox sedge, and Gray's sedge. The 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment had significantly less relative total biomass compared to the

0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-16). There were no significant differences between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments.

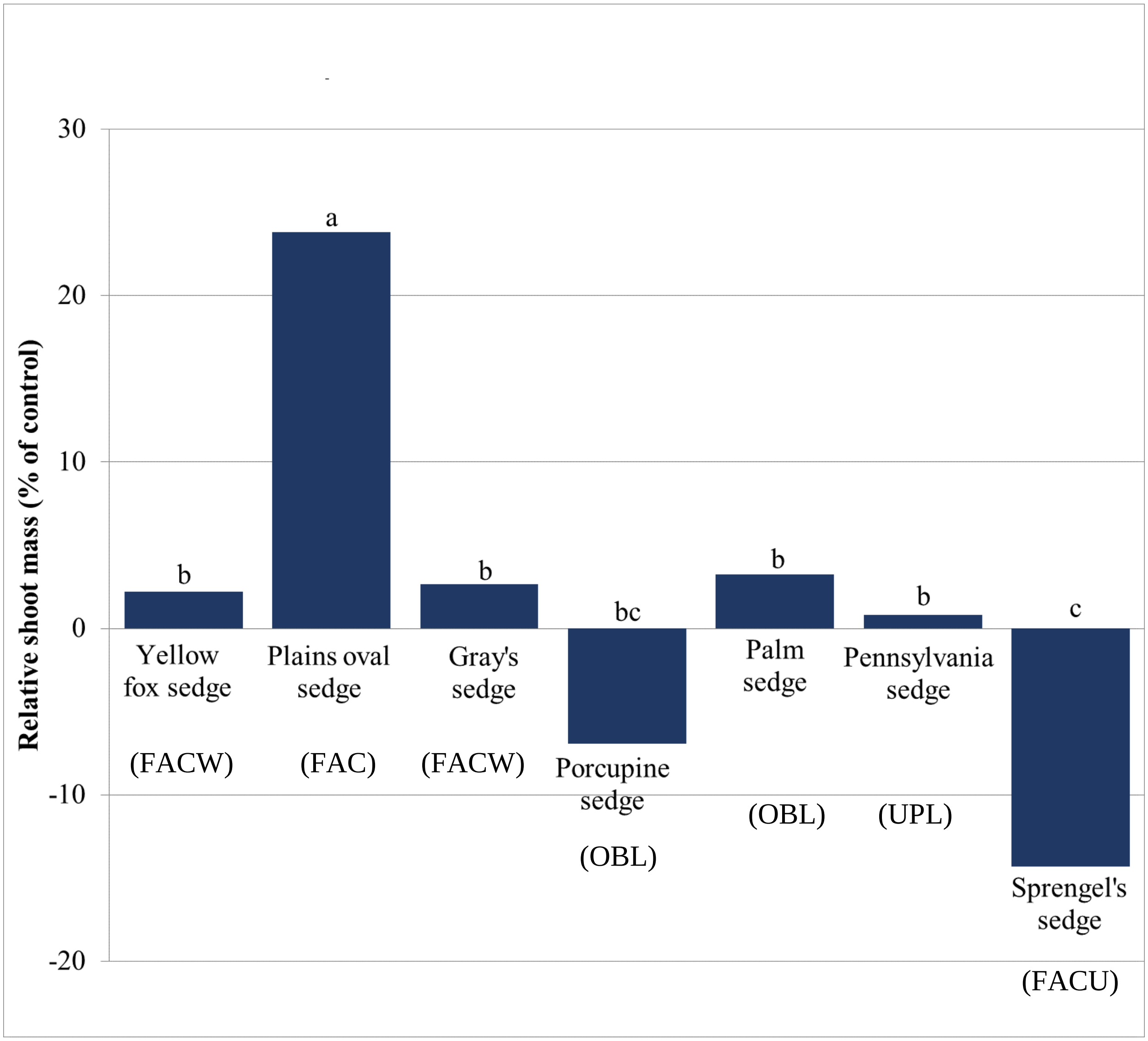

Figure 2-10. Shoot mass as a percent of the control for seven sedge species subjected to cyclical flood and drought periods. Mean values are averaged across flood and drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 54) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

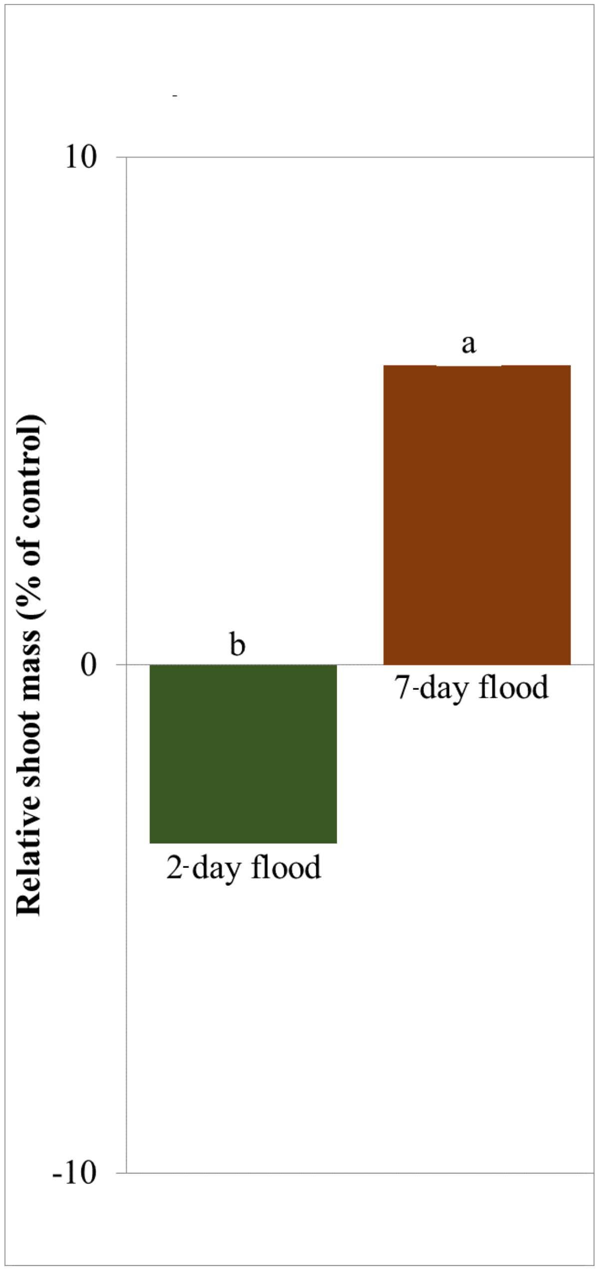

Figure 2-11. Relative shoot mass of sedges subjected to cyclical flood and drought periods. Mean values are averaged across drought treatments and sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 189) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

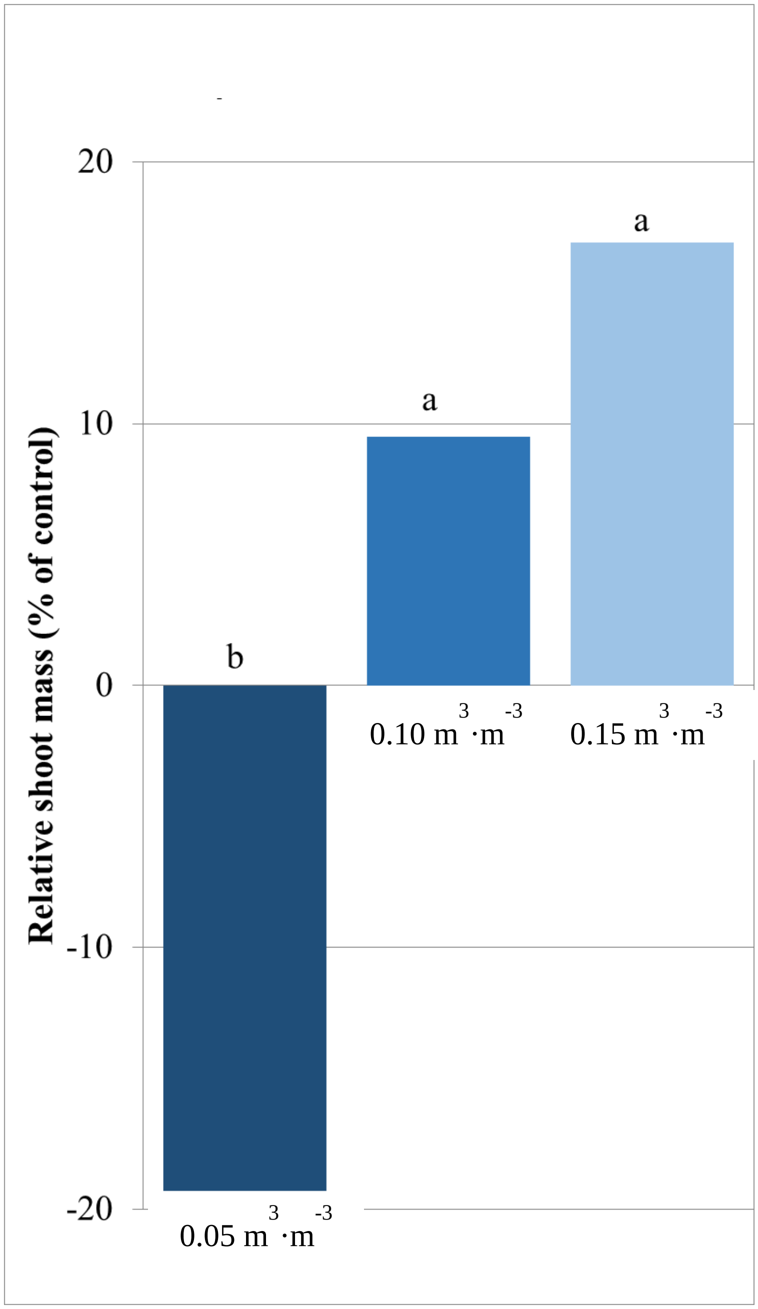

Figure 2-12. Relative shoot mass of sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments and sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 126) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

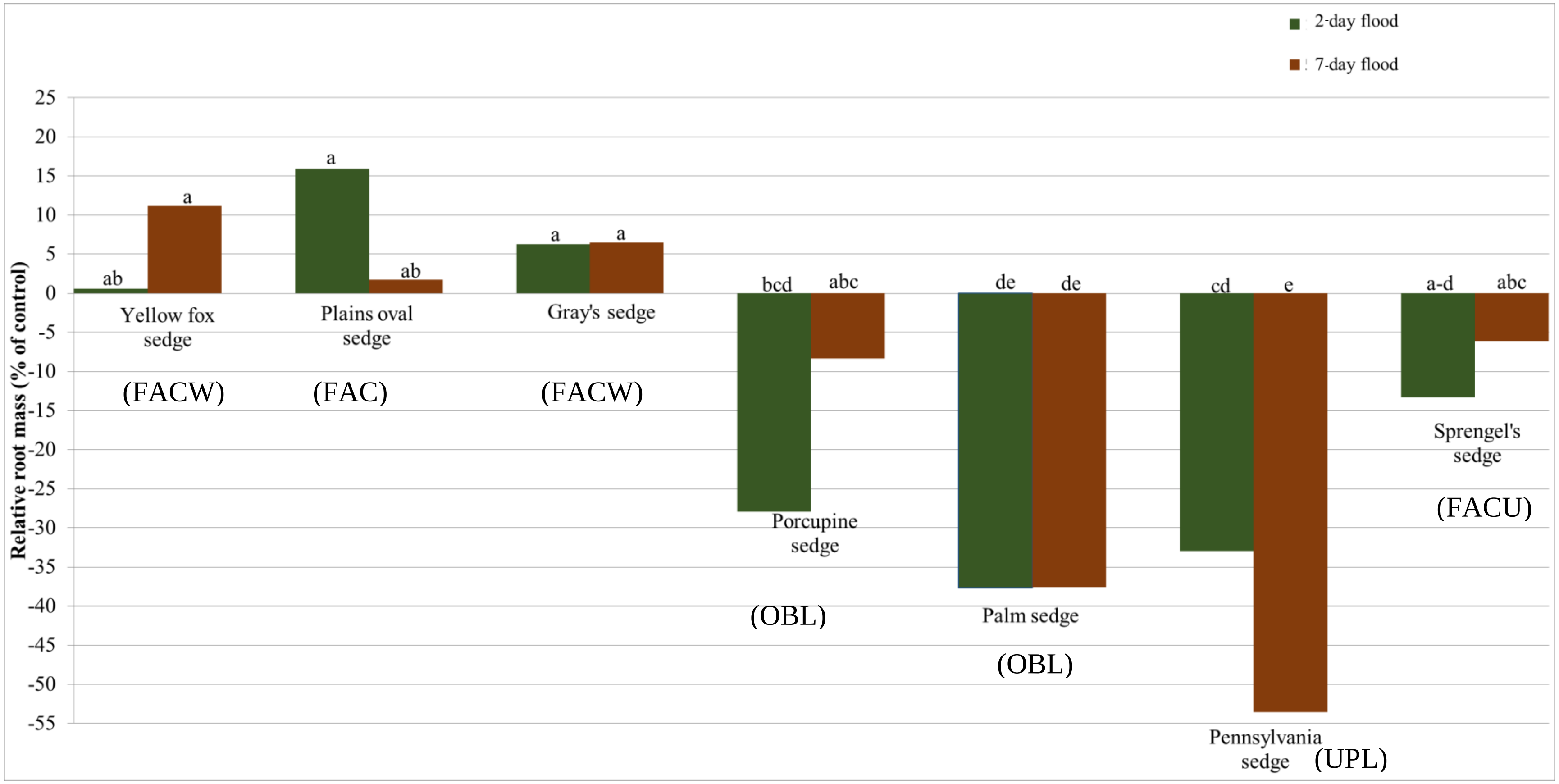

Figure 2-13. Root mass as a percent of the control of seven sedges subjected to cyclical flood and drought periods. Mean values are averaged across drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 27) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

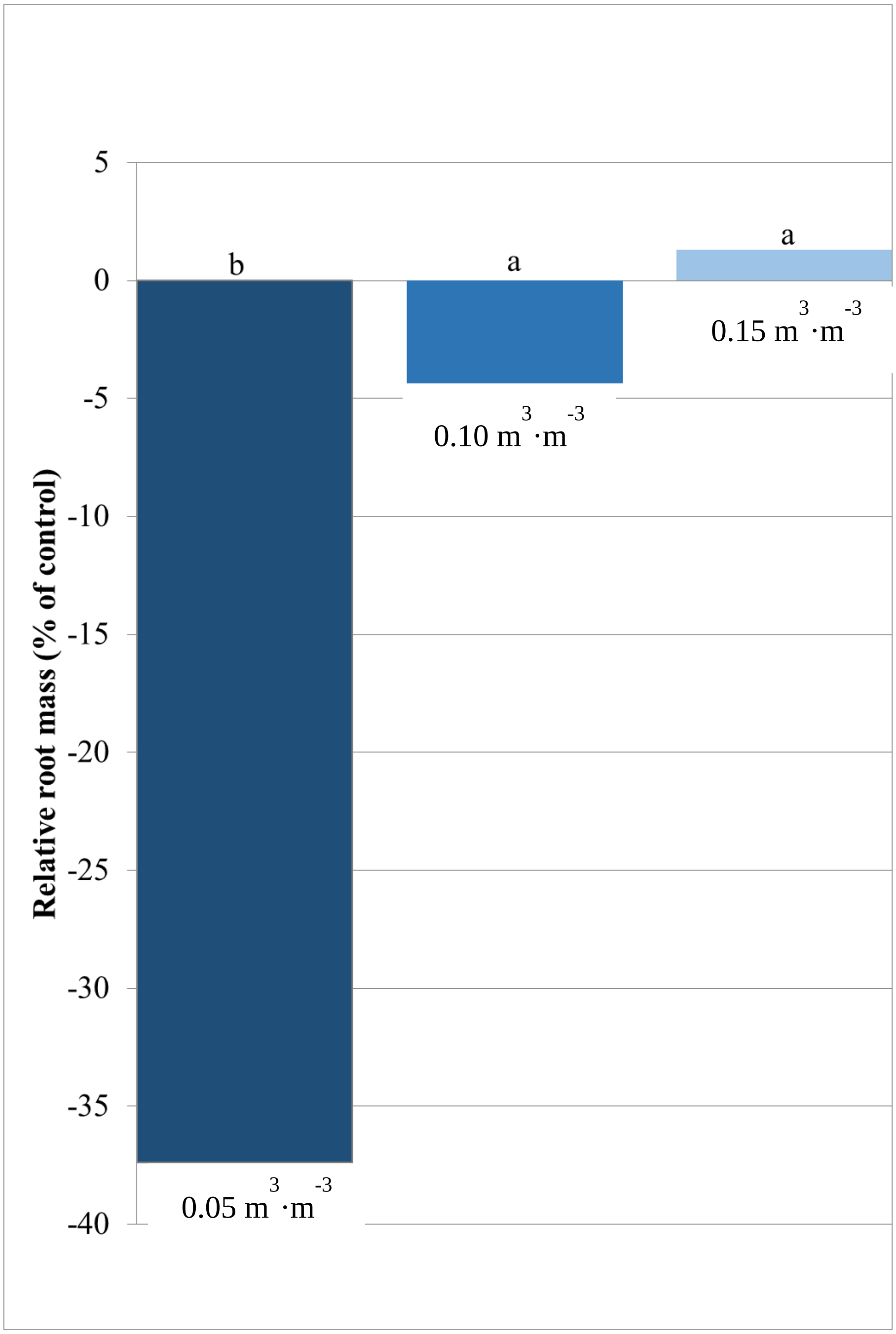

Figure 2-14. Root mass as a percent of the control of sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments and sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 126) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

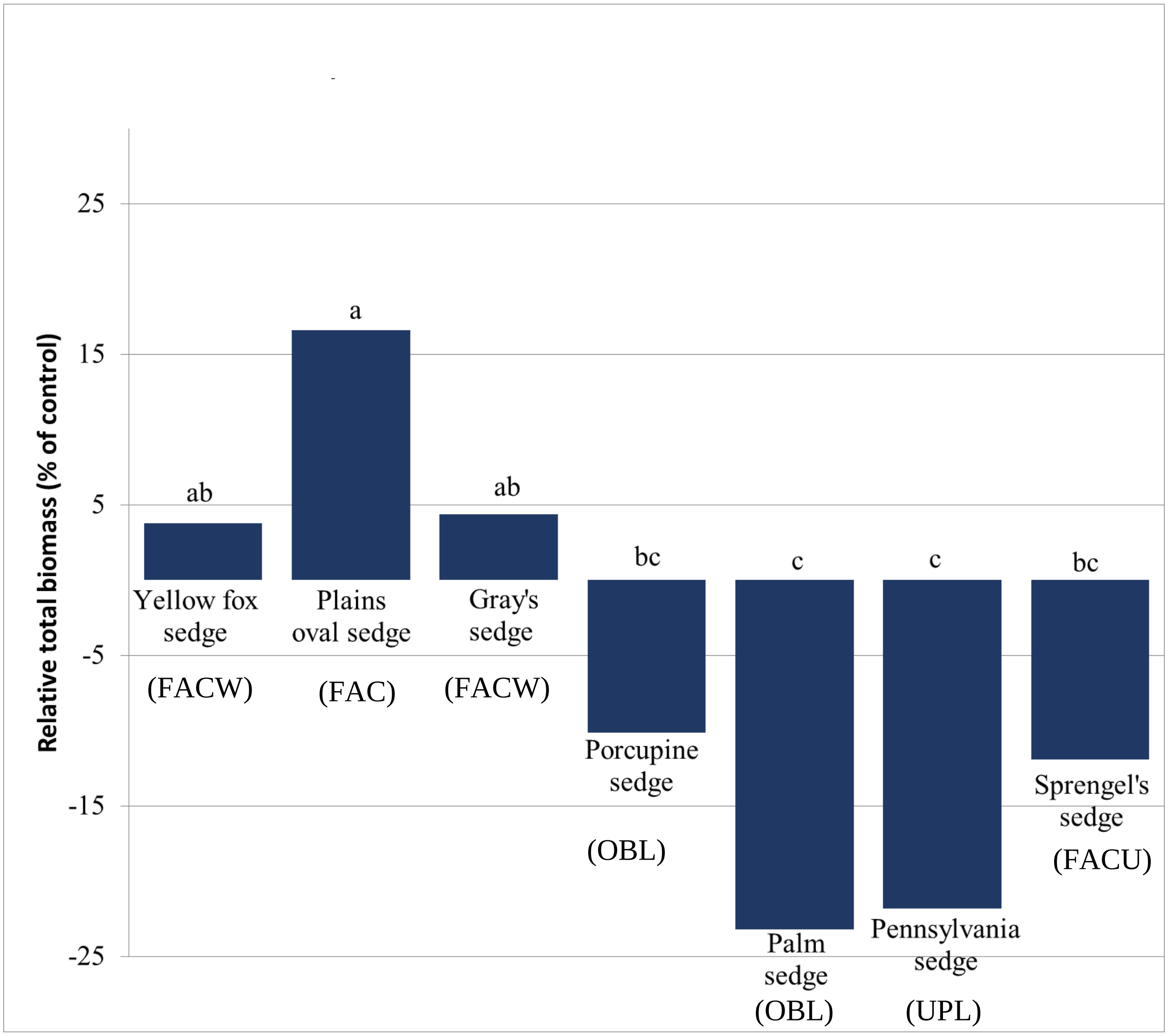

Figure 2-15. Total biomass as a percent of the control of seven sedge species subjected to cyclical flood and drought periods. Mean values are averaged across flood and drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 54) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

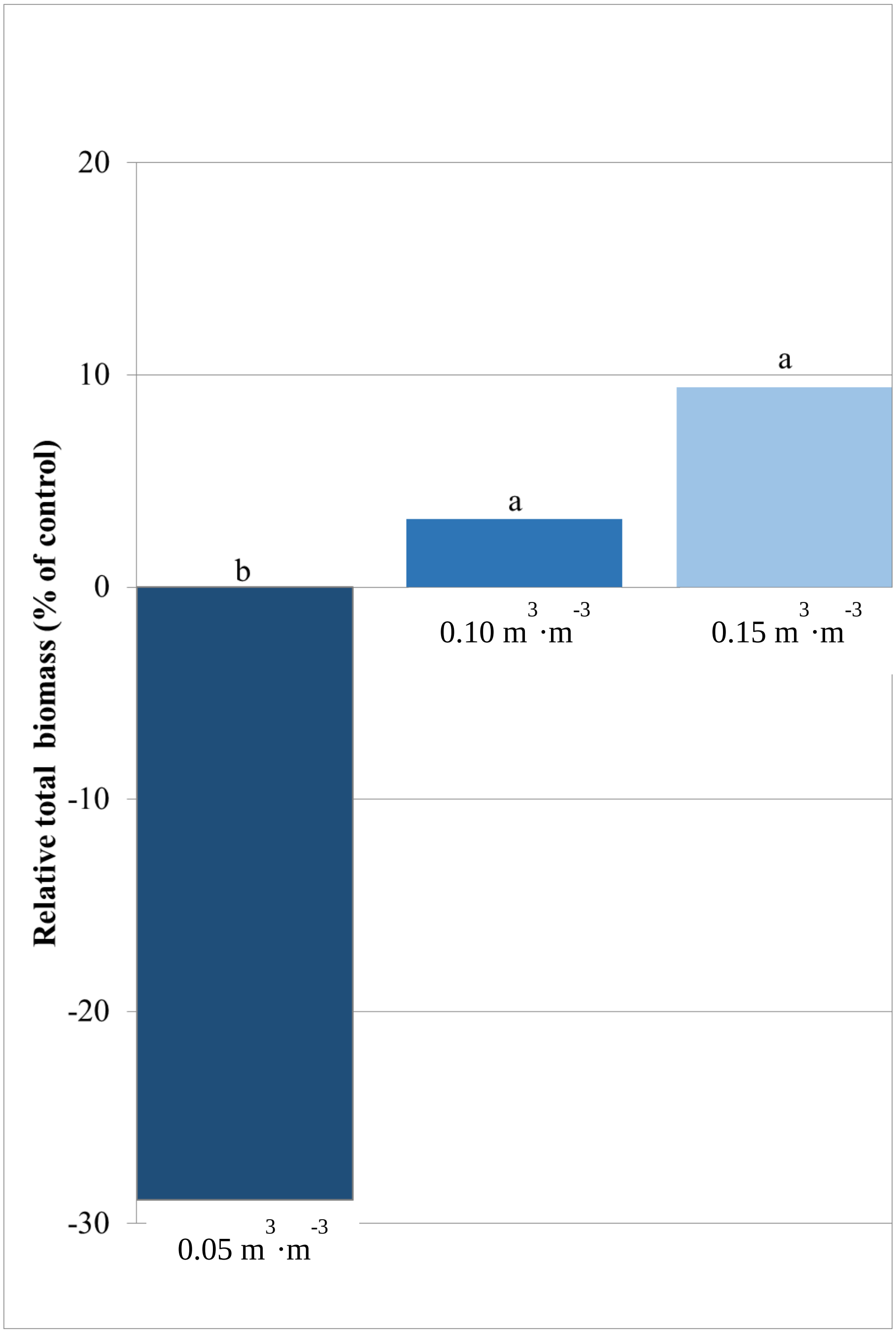

Figure 2-16. Relative total biomass of sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments and sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 126) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

Visual damage rating. A three-way interaction occurred for visual damage rating among species, flood duration, and drought setpoint for yellow fox sedge and Gray's sedge. The 2-day flood duration with 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment for yellow fox sedge had a significantly higher visual damage rating compared to the 2-day flood duration with 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatment and the 7-day flood duration with 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment (Fig. 2-17). The 2-day flood duration with 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment for Gray's sedge had a significantly higher visual damage rating compared to the 2-day and 7-day flood duration with 0.10 $m^3 \cdot m^{-3}$ and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments. The visual damage rating for the 7-day flood duration with 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment for yellow fox sedge and Gray's sedge was not significantly different compared to all other treatments of yellow fox sedge and Gray's sedge. The 2-day and 7-day flood duration with 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatments for palm sedge and Pennsylvania sedge had a significantly higher visual damage rating compared to the 2-day and 7-day flood duration with 0.10 $m^3 \cdot m^{-3}$ and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments for each species. There was no difference among treatments for plains oval sedge and Sprengel's sedge.

Evapotranspiration. A species by drought setpoint and a species by flood duration interaction occurred for evapotranspiration (ET) per day of dry down. The species by drought interaction only occurred for Sprengel's sedge where the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment was significantly higher compared to the 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatment (Fig. 2-18). For all other species, there was no difference between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments. For all species, the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment had significantly less ET per day compared to the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments. Palm sedge had the highest ET per day for the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment, although not significantly

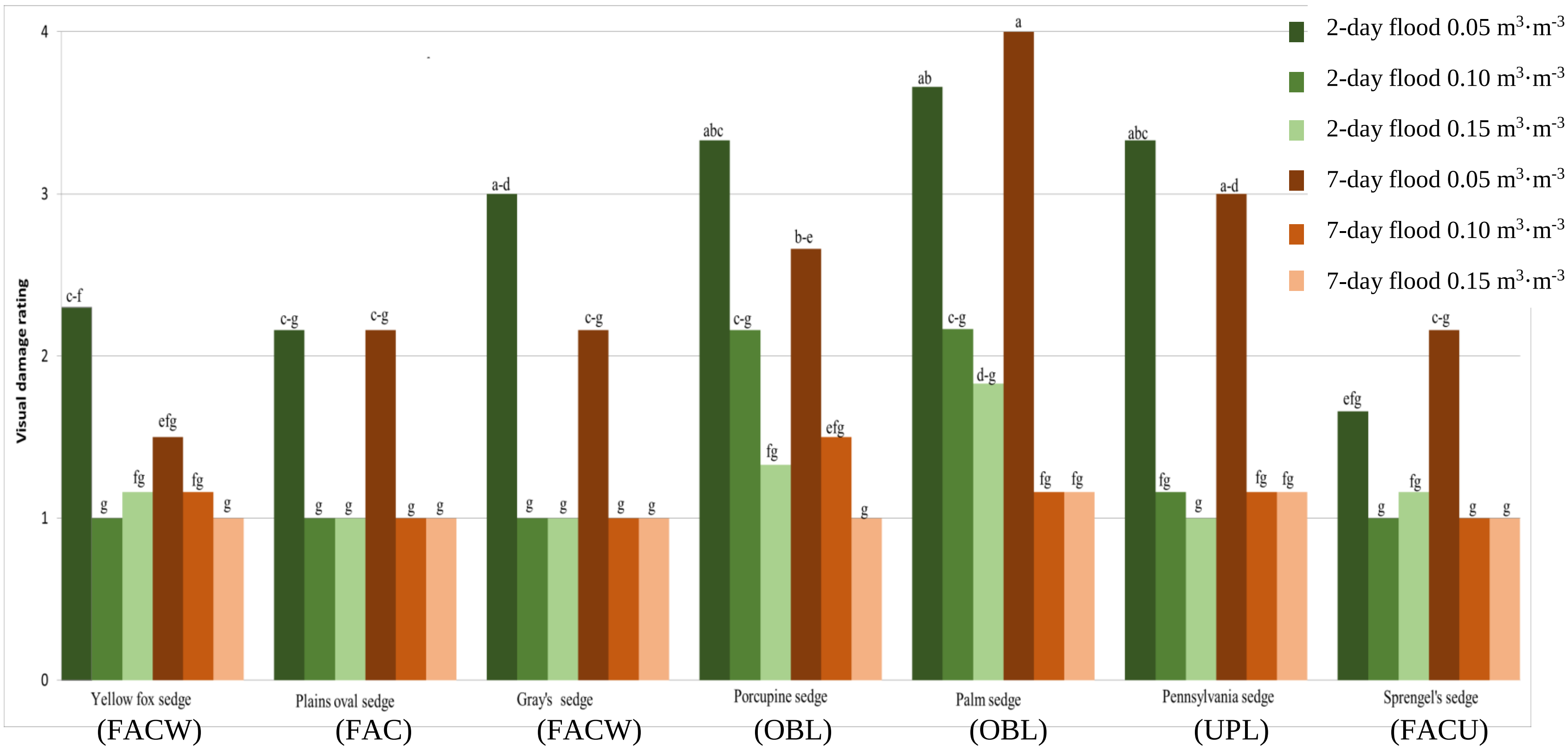

Figure 2-17. Visual damage rating (1-4 scale; 1= 0-25% dieback, 2= 26-50% dieback, 3= 51-75% dieback, 4= 76-100% dieback) of sedges subjected to cyclical flood and drought periods. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 9) values labeled with different lower case letters were significantly different by Tukey-Kramer honestly significant difference test at $P < 0.05$.

higher compared to porcupine sedge and yellow fox sedge at the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment. The species by flood duration interaction only occurred for porcupine sedge where the 2-day flood treatment had significantly less ET per day of dry down compared to the 7-day flood treatment (Fig. 2-19). There was no significant difference between the 2-day and 7-day flood durations for the other species. Among species, porcupine sedge flooded for 7-days had the highest ET, although not significantly higher compared to yellow fox sedge flooded for 7-days, plains oval sedge flooded for 2-days or 7-days, and palm sedge flooded for 2-days or 7-days. Pennsylvania sedge flooded for 7-days had the lowest ET and was significantly lower compared to all other sedge species regardless of flood duration. There was no significant difference between Pennsylvania sedge flooded for 2-days or 7-days.

Water use efficiency. A flood duration by drought setpoint interaction and a species by flood duration interaction occurred for total biomass water use efficiency (WUE). The post hoc analysis of the species by flood duration treatments using Tukey's revealed the 2-day flood duration was always significantly higher compared to the 7-day flood duration treatment regardless of species, therefore the species main effect is presented. The 2-day flood treatment, regardless of drought setpoint, had a significantly higher total biomass WUE compared to the 7-day flood treatment (Fig. 2-20). Within a flood duration, the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment was always higher than the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments but not always significantly higher. There was no significant difference between the 2-day flood and 0.05 and 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatments but the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment was significantly higher than the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment. The 7-day flood, 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment was significantly higher than the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments. There were no differences between the 0.10 and 0.15 $m^3 \cdot m^{-3}$

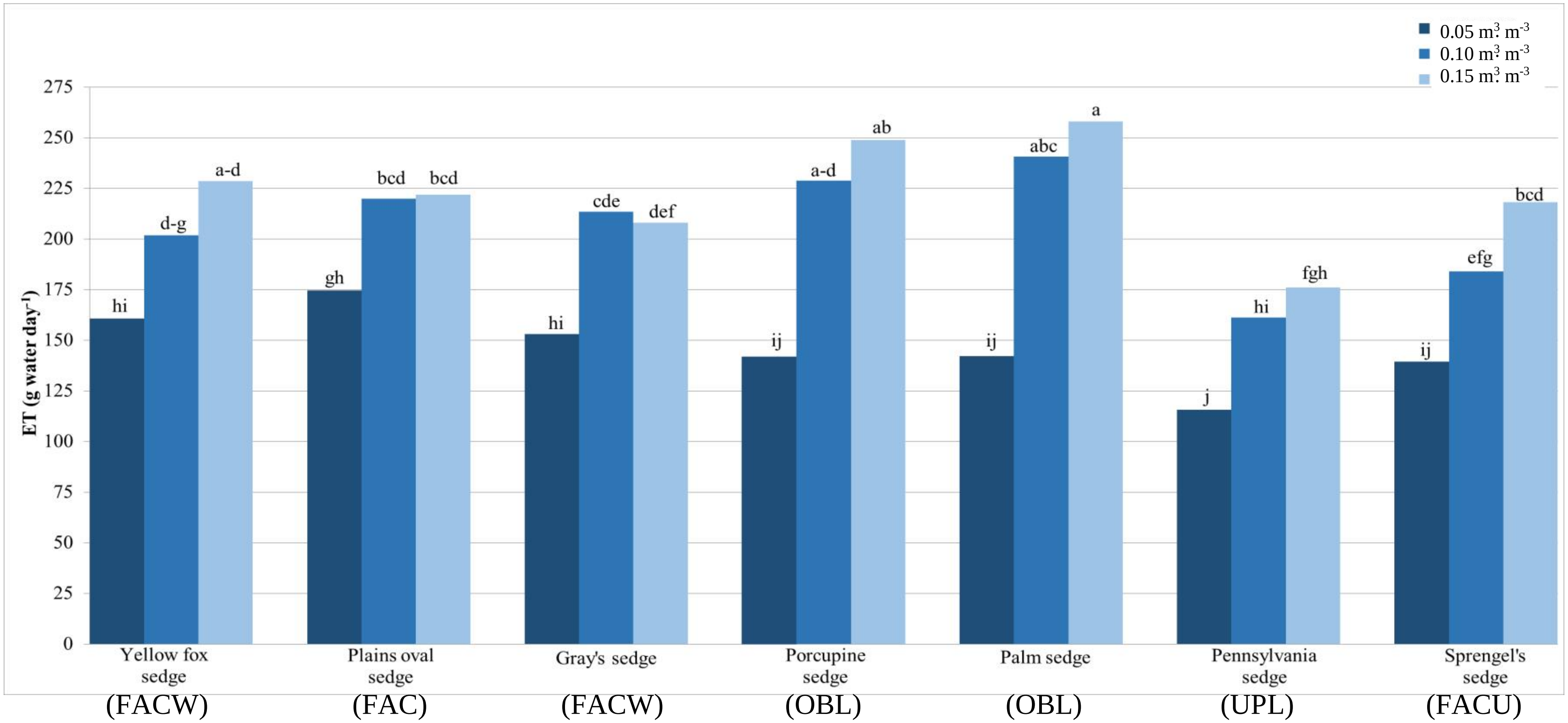

Figure 2-18. Evapotranspiration (ET) per day during dry down of sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 18) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

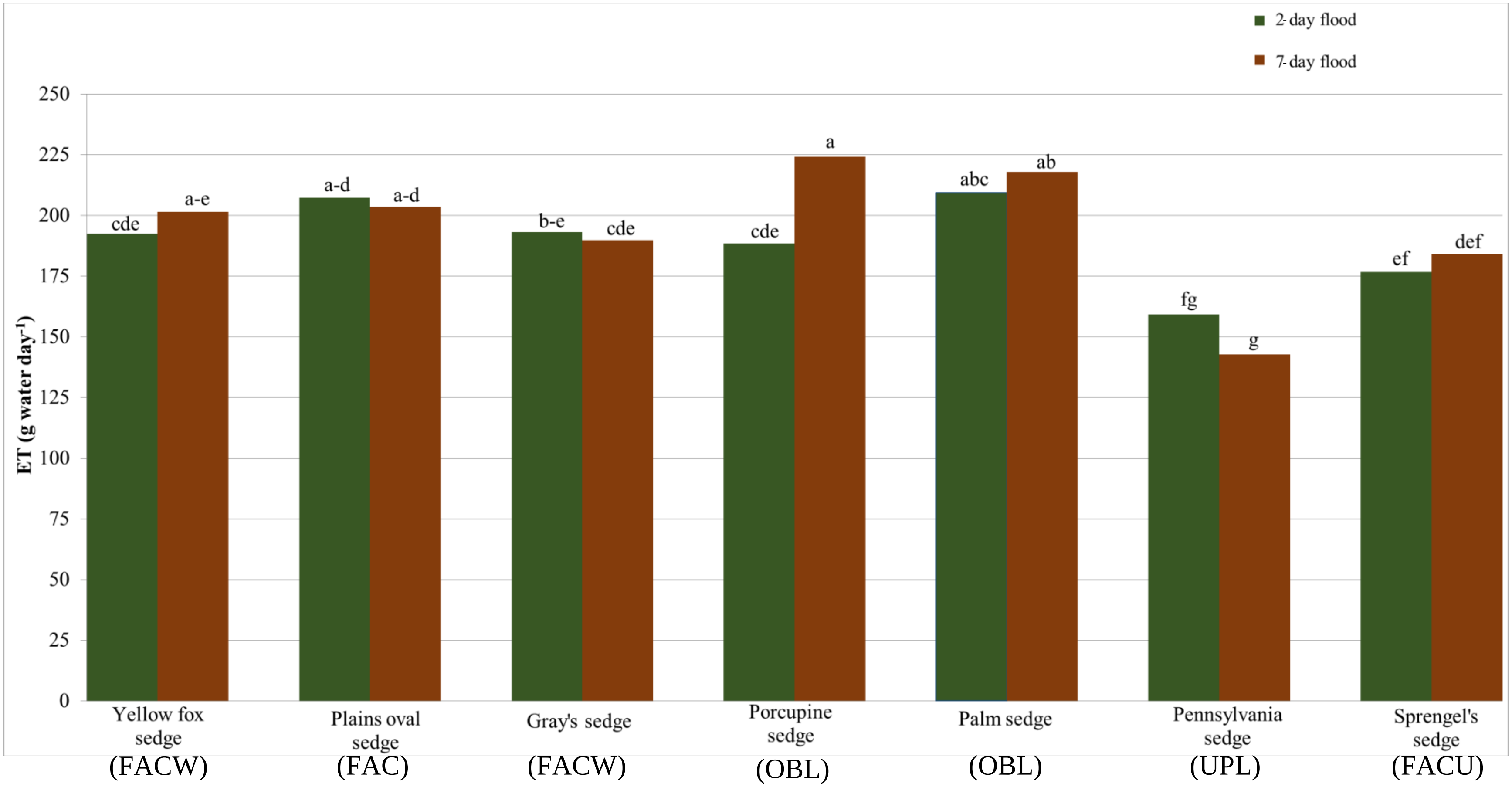

Figure 2-19. Evapotranspiration (ET) per day during dry down of sedges subjected to cyclical flood and drought periods. Mean values are averaged across drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 27) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

substrate VWC treatments regardless of flood duration. Among species, Pennsylvania sedge had the highest total biomass WUE and was significantly higher than all other species (Fig. 2-21). Sprengel's sedge was the second highest and significantly higher than all other sedges except Pennsylvania sedge. There was no difference among yellow fox sedge, plains oval sedge, and Gray's sedge. Porcupine sedge was significantly lower compared to all other sedge species except palm sedge which was significantly lower compared to all sedge species.

***Days of dry down*.** There was a species by flood duration and a species by drought setpoint interaction for days of dry down. The post hoc analysis of the species by flood duration treatments using Tukey's revealed there was no difference within a species between the 2-day and 7-day flood treatments. The post hoc analysis of the species by drought setpoint treatments using Tukey's revealed significant differences but these differences were less than one day. The main effect of flood was also significant but the means were less than one day, therefore only species and drought main effects are presented. Among species, Pennsylvania sedge required significantly more time to dry down compared to all other species (Fig. 2-22). Sprengel's sedge required significantly more time to dry down compared to all other species except Pennsylvania sedge. Days of dry down were similar among yellow fox sedge, plains oval sedge, Gray's sedge and porcupine sedge. Although a significant difference occurred between plains oval sedge and Gray's sedge, this difference is less than one day. Palm sedge required significantly less number of dry down days compared to all other sedge species. The number of days needed for dry down was significantly higher for the 0.05 m^3 m^{-3} substrate VWC treatment compared to the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-23). The 0.10 $m^3 \cdot m^{-3}$ substrate VWC treatment was significantly higher compared to the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment.

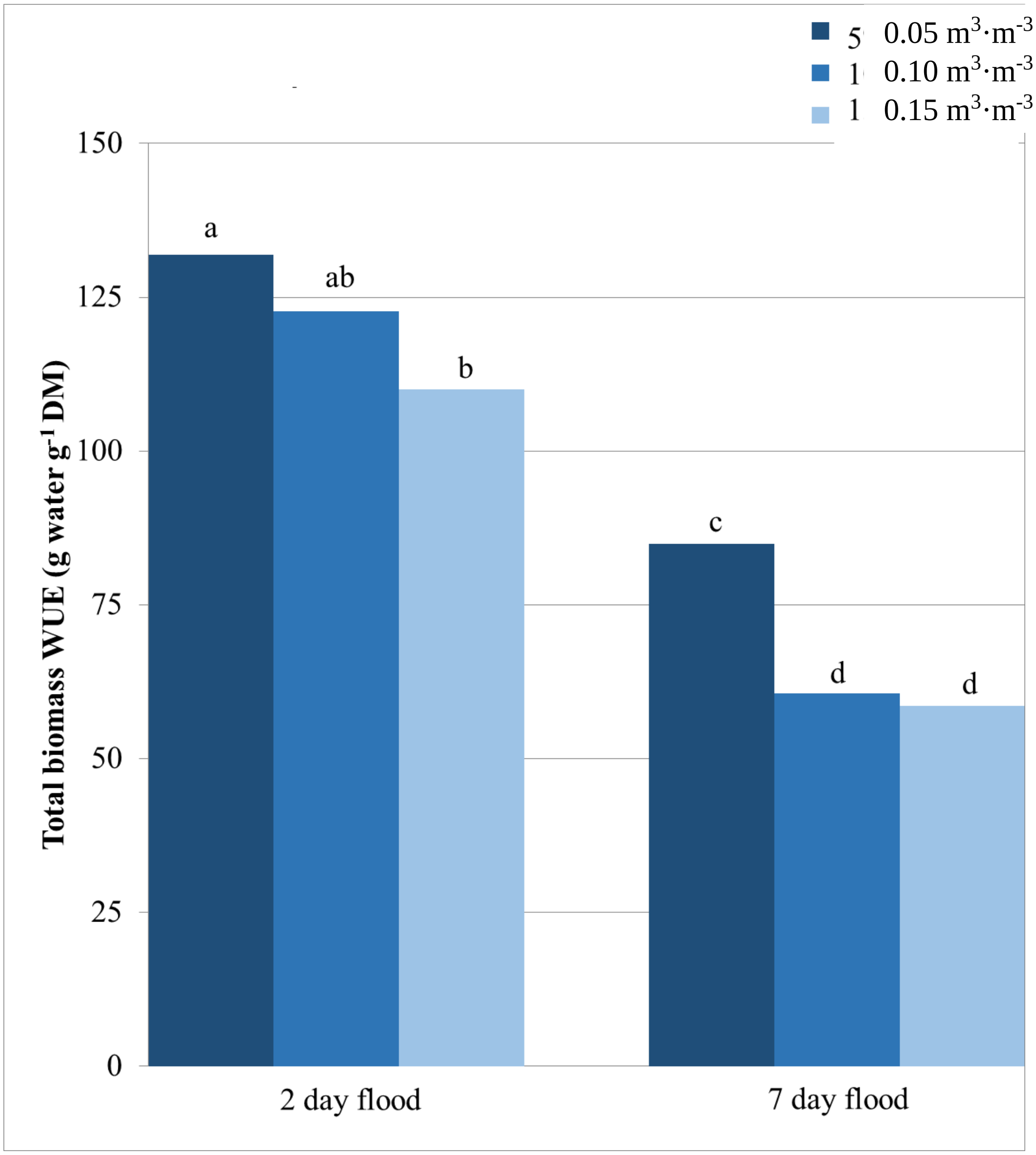

Figure 2-20. Total biomass water use efficiency (WUE) of sedges subjected to cyclical flood and drought periods. Mean values are averaged across sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3·m^{-3}$ substrate VWC. Mean (n =63) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

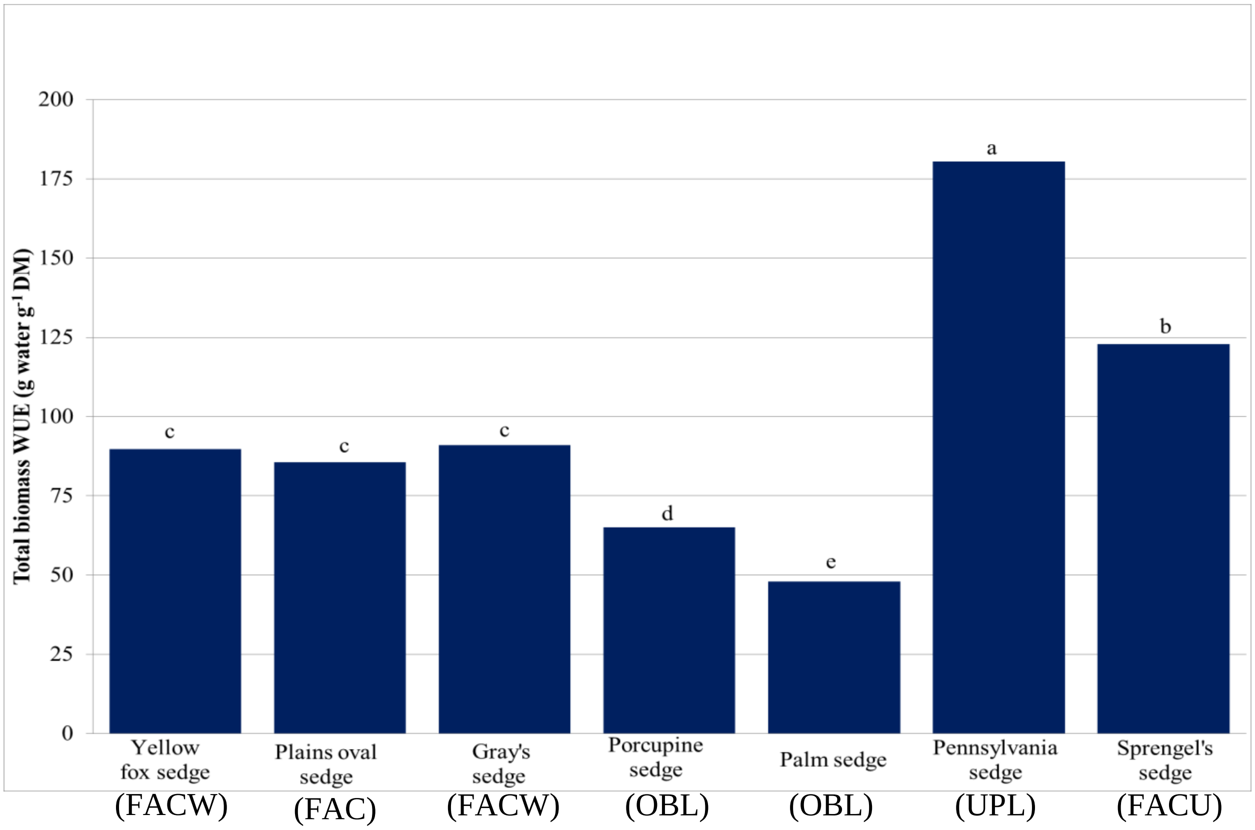

Figure 2-21. Total biomass water use efficiency (WUE) of sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood and drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n = 54) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

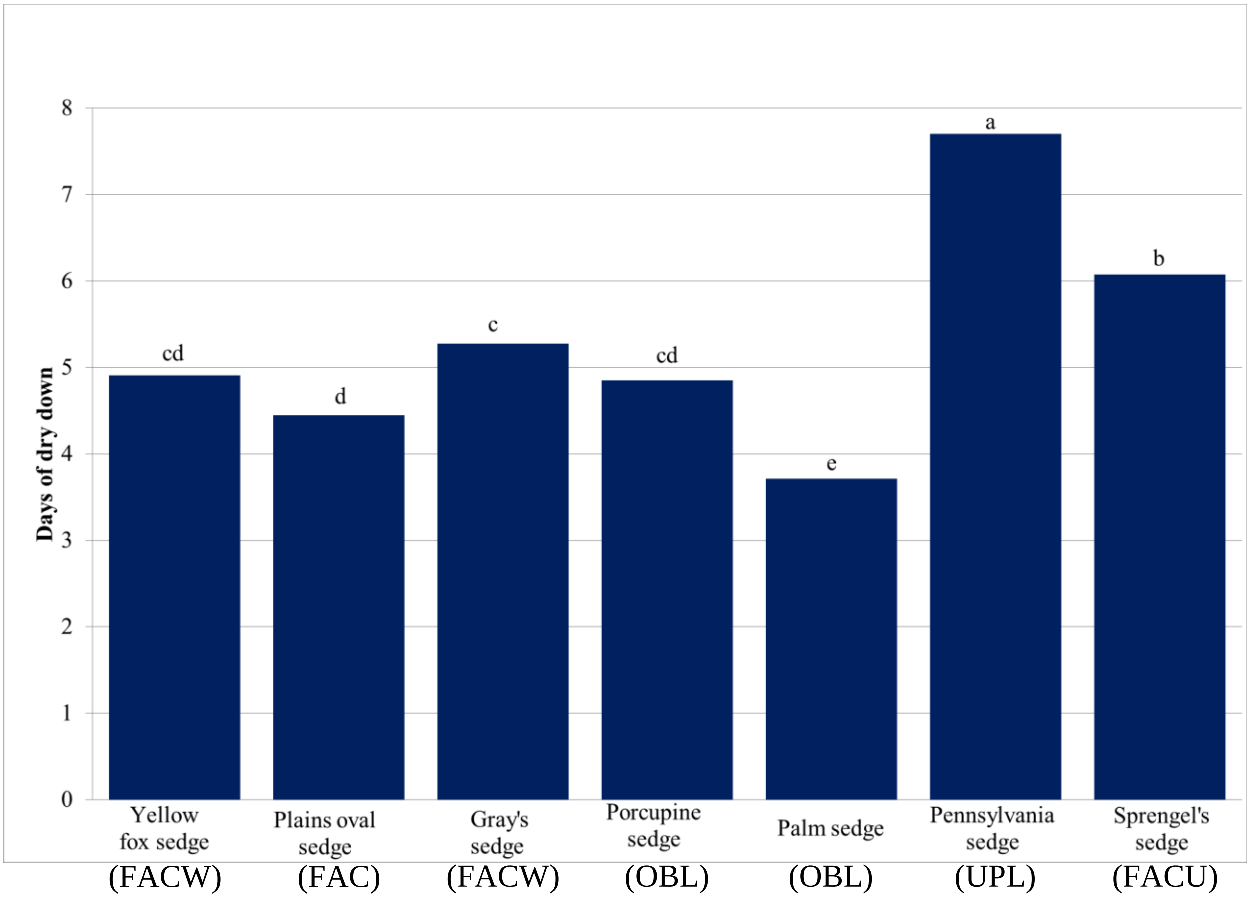

Figure 2-22. Days of dry down for sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood and drought treatments. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n =54) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

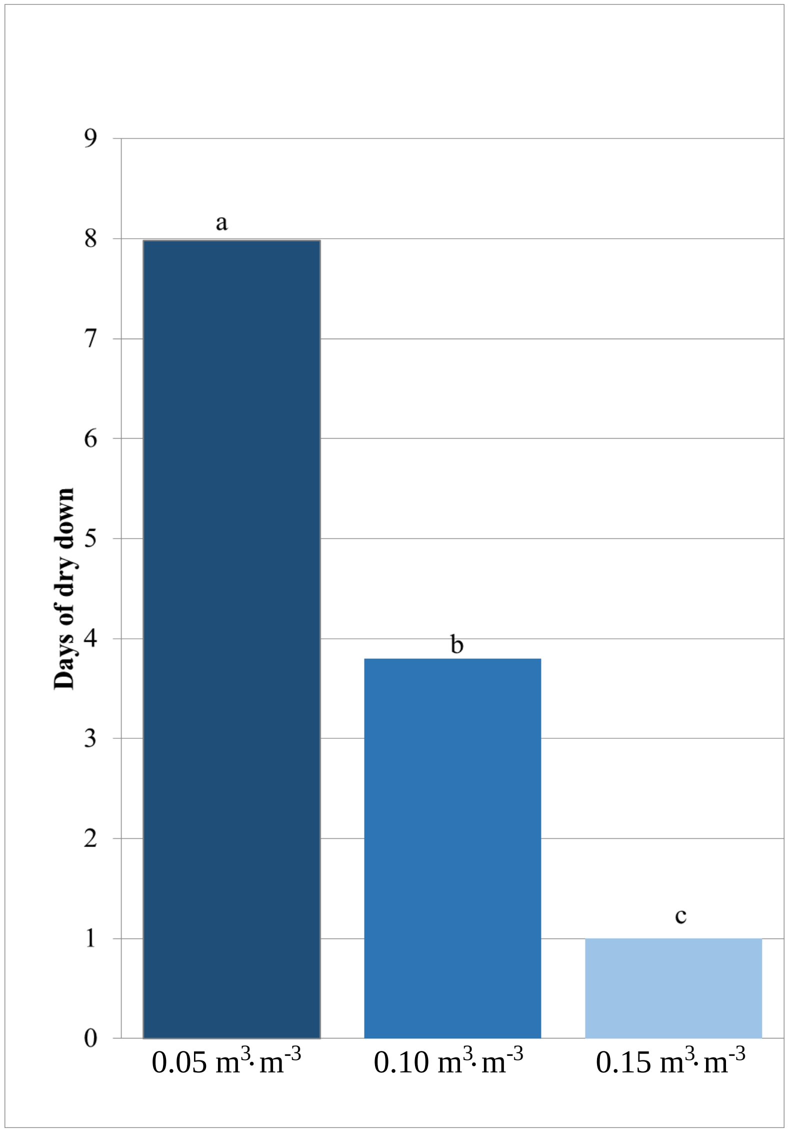

Figure 2-23. Days of dry down for sedges subjected to cyclical flood and drought periods. Mean values are averaged across flood treatments and sedge species. Sedges were flooded for two or seven days and allowed to dry down to 0.05, 0.10 or 0.15 $m^3 \cdot m^{-3}$ substrate VWC. Mean (n =126) values labeled with different lower case letters were significantly different by Tukey's honestly significant difference test at $P < 0.05$.

Discussion

All sedge species exhibited a decrease in height relative to their respective controls that were maintained under optimal conditions (Fig. 2-7). This was expected, as drought stress affects plants by reducing cell division and expansion (Farooq et al., 2012). Plains oval sedge and Gray's sedge exhibited less of a height reduction compared to the other sedge species, thus indicating that both species were better able to handle the stress of cyclical flooding and drought. Figure 2-8 further demonstrates the effect that extreme drought had on the shoot height of all species that were subjected to the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment. Under the driest VWC treatment, relative shoot height was reduced almost 25% compared to the controls. Plants grown at the drought setpoints of 0.10 and 0.15 $m^3 \cdot m^{-3}$ showed a slight decrease in relative shoot height that was not significant between the two treatments. Timeliness of inducing cyclical flooding in the 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatment was more difficult because of the speed in which the substrated dried from one day to the next. This often resulted in substrates reaching VWCs below the 0.15 $m^3 \cdot m^{-3}$ setpoint before flooding could be induced.

The most extreme drought setpoint adversely affected relative shoot count for porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge while yellow fox sedge, plains oval sedge, and Gray's sedge continued to grow under all three setpoints (Fig. 2-9). Yellow fox sedge and Gray's sedge are facultative wetland plants (FACW) while plains oval sedge is a facultative (FAC) plant. These are intermediate wetland indicator categories that denote plants that usually occur in wetlands but also may occur in non-wetland areas (Lichvar, 2014). This is in contrast to the obligate wetland plants (OBL), porcupine sedge and palm sedge and the facultative upland (FACU) and upland (UPL) plants, Sprengel's sedge and Pennsylvania sedge. Plants in the OBL wetland indicator category are almost always found in wetlands while plants in the FACU and UPL wetland indicator categories are rarely found in wetlands (Lichvar, 2014). The ability to grow in transition areas may explain the versatility of yellow fox sedge, plains oval sedge, and Gray's sedge and why they were less affected by the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment. Relative shoot mass was positive compared to the controls for all sedge species except for porcupine sedge and Sprengel's sedge (Fig. 2-10). Plains oval sedge had significantly higher relative shoot mass compared to all other sedge species indicating that it can still grow despite the stresses of cyclical flood and drought. Regardless of species and drought setpoint, relative shoot mass was significantly increased when sedges were flooded for 7-days compared to only 2-days (Fig. 2-11). Similar results were found by Moog and Janiesch (1990) where two of the three sedge species had increased shoot mass after 40 d of anaerobic growth compared to the aerobic control. Similar to relative plant height, relative shoot mass was significantly reduced for the 0.05 $m^3 \cdot m^{-3}$ substrate VWC treatment but no differences were observed between the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments (Fig. 2-12).

Relative root mass was negative compared to the controls for porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge under the 2-day and 7-day flood durations but positive for yellow fox sedge, plains oval sedge, and Gray's sedge (Fig. 2-13). These results are similar to the results for relative shoot count suggesting that the root systems of FACW and FAC sedges are better able to handle cyclical flood and drought compared to porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge. Pennsylvania sedge was the only species that had significantly less relative root mass for the 7-day flood duration compared to the 2-day flood duration. Pennsylvania sedge is an upland (UPL) sedge species and therefore would be expected to decline under prolonged flood conditions. Similar results were found by Moog and Janiesch (1990) for longbract sedge (*C. extensa* Goodenough) (authors report longbract sedge commonly grows in dry and sandy soils near the coastline) where 40 d of anaerobic growth reduced root weight compared to the aerobic control. The reduction in relative root mass for porcupine sedge and palm sedge, both OBL species, is likely due to the effect of drought. Similar to relative shoot mass, relative root mass was reduced as the VWC was reduced (Fig. 2-14). Relative total biomass was negative compared to the controls for porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge and positive for yellow fox sedge, plains oval sedge and Gray's sedge suggesting the UPL, FACU, and OBL sedges were less able to handle stress from cyclical flood and drought (Fig. 2-15). Similar to relative root mass, relative total biomass was reduced as the VWC was reduced (Fig. 2-16).

The visual damage rating was minimal among all sedge species at the 0.10 and 0.15 $m^3 \cdot m^{-3}$ substrate VWC treatments regardless of flood duration (Fig. 2-17). As the substrate dried down to 0.05 $m^3 \cdot m^{-3}$, the visual damage rating was always higher, although not always significant, for all sedge species. Overall, sedges are quite adaptable. The 0.05 $m^3 \cdot m^{-3}$ VWC treatment was an extreme drought and would result in an unacceptable visual damage rating for all sedge species. Therefore, irrigation during times of drought may be necessary to keep visual damage at an acceptable level. Evapotranspiration decreased for all sedge species as the substrate VWC decreased from 0.15 to 0.05 $m^3 \cdot m^{-3}$. This is also illustrated in fig. 2-5 which shows yellow fox sedge flood and drought cycles based on drought setpoint. As the substrate VWC decreases, ET also decreases and more time is needed for dry down. Flood duration had little effect on ET except for porcupine sedge where the two-day flood had significantly less ET per day compared to the seven-day flood. This is likely due to the difference in root loss between the two-day and seven-day flood treatments (Fig. 2-13). Although there was a similar difference in relative root mass loss between the 2-day flood and 7-day flood treatments for Pennsylvania sedge it was not enough to cause a significant difference in ET per day. However, the reduction in root mass was likely responsible for Pennsylvania sedge having the lowest ET per day among species for the 7-day flood treatment. Palm sedge lost over 35% relative root mass regardless of flood duration, however, rates of ET per day during dry down were among the highest of all the sedge species (Fig. 2-18 and 2-19) suggesting the extensive loss in root mass did not harm root function.

Overall, ET rates per day were similar among sedge species illustrating that small sedges, such as Pennsylvania sedge, can remove a fair amount of water from a rain garden. Sedges with high ET rates would be beneficial to rain gardens in areas prone to frequent rain events (e.g. less than 48 h apart) because more water could be held by the rain garden.

Total biomass WUE (i.e. grams of water needed to produce/maintain one gram of dry matter) was significantly higher for the two-day flood treatment compared to the seven-day flood treatment regardless of drought setpoint (Fig. 2-20). The WUE was only calculated during the dry down period between flood cycles and therefore WUE during flooding was not calculated. It is reasonable to assume that growth occurred during flood treatments and likely resulted in the total biomass WUE being lower in the seven-day flood compared to the two-day flood treatment. As expected, total biomass WUE decreased as the substrate VWC increased from 0.05 to 0.15 $m^3 \cdot m^{-3}$, although the differences were not always significant. Among species, total biomass WUE was highest for Pennsylvania sedge and Sprengel's sedge and lowest for porcupine sedge and palm sedge (Fig. 2-21). Palm sedge had the lowest total biomass WUE, suggesting the loss in relative root mass when flooded for two or seven days did not negatively affect root function. There was no difference among yellow fox sedge, plains oval sedge, and Gray's sedge. The differences in total biomass WUE align closely with the wetland indicator categories. Obligate sedges had the lowest WUE, followed by FAC and FACW sedges, while FACU and UPL sedge had the highest WUE. Similar to WUE, days of dry down between flood cycles was highest for Pennsylvania sedge and Sprengel's sedge and lowest for palm sedge (Fig. 2-22). There was little difference among yellow fox sedge, plains oval sedge, Gray's sedge, and porcupine sedge. As the substrate VWC decreased from from 0.15 to 0.05 $m^3 \cdot m^{-3}$, the days needed for dry down increased (Fig. 2-23). This can also be observed in fig. 2-5 which shows yellow fox sedge flood and drought cycles based on drought setpoint. As the substrate VWC decreases, the days needed for dry down increases.

Based on the results of this study, plains oval sedge, yellow fox sedge, and Gray's sedge are extremely versatile plants for the challenging rain garden environment. These species may be planted at any elevation in the rain garden given their ability to gain in relative root mass under 2-days or 7-days of flooding. Sprengel's sedge had a slight negative relative root mass under 2-days and 7-days of flooding and should be planted at higher elevations where flooding will occur for less than two days. Pennsylvania sedge lost over 30% relative root mass when flooded for 2-days and therefore should be planted on the highest elevation of the rain garden. As obligate wetland plants, porcupine sedge and palm sedge should be planted in the deepest part of the rain garden where soils will occasionally be water-logged.

Conclusion

Drought generally reduced relative plant height, shoot count, shoot mass, root mass, total biomass, ET per day, and total biomass WUE. Drought generally increased the visual damage rating and days of dry down. The sedge species; yellow fox sedge, plains oval sedge, and Gray's sedge were better able to handle cyclical flood and drought compared to porcupine sedge, palm sedge, Pennsylvania sedge, and Sprengel's sedge. All sedge species performed well if the substrate VWC did not drop below 0.10 $m^3 \cdot m^{-3}$. Sedges planted in raingardens may need supplemental water during times of extended drought.

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CHAPTER III. PERIGYNIA REMOVAL IMPROVED GERMINATION IN TWO NATIVE SEDGE SPECIES

Introduction

Plants used for stormwater management practices (e.g., bioretention basins and rain gardens) need to be tolerant of fluctuating water levels, prolonged periods of saturated soil, drought, sediment, and pollutants (Shaw and Schmidt, 2003). Native plants are often recommended for stormwater management purposes because of their ability to adapt to challenging local conditions and are less prone to disease and drought stress (Shaw and Schmidt, 2003; Stange and Jensen, 2007). Sedges (*Carex* L. spp.), an herbaceous perennial, are commonly recommended in the north central U.S. because several species are native to this region and many species have the ability to tolerate fluctuating water levels (Bannerman and Considine, 2003; Lichvar, 2013; Shaw and Schmidt, 2003).

Yellow fox sedge (*C. annectens* Bicknell), porcupine sedge (*C. hystericina* Muhl. Ex Willd), plains oval sedge (*C. brevior* Mack) and palm sedge (*Carex muskingumensis* Schwein) are native to the north central U.S., recommended for rain gardens and are readily available from native plant nurseries (HHRCDC, 2017; Rodie et al., 2010; Schmidt et al., 2007; Shaw and Schmidt, 2003; USDA-NRCS, 2015). For small projects (i.e. residential rain gardens), transplants are often used (Bannerman and Considine, 2003) while direct seeding larger projects (i.e. bioretention ponds), may be more economical (Jones et al., 2004).

Sedge achenes are frequently difficult to germinate and may exhibit physiological dormancy (Baskin and Baskin, 2014). Common strategies to overcome physiological dormancy in sedges include cold, moist-stratification and after-ripening (Schütz, 2000). Sedges with physiological dormancy may have achenes that germinate, when mature, over a narrow range of environmental conditions (i.e. conditional dormancy) whereas nondormant achenes would germinate over a broader range of environmental conditions (Baskin and Baskin, 2014; Kettenring and Galatowitsch, 2007a). Plains oval sedge and porcupine sedge have conditionally dormant achenes but will germinate readily with a diurnally fluctuating 27/15 ^{o}C temperature regime (Kettenring and Galatowitsch, 2007a, b). A study by Schütz and Rave (1999) showed palm sedge achenes that were recently harvested required cold, moist-stratification (4 ^{o}C for 6 m) and light to achieve 89% germination while achenes receiving no cold, moist-stratification only achieved 0.9% germination. In contrast to the Schutz and Rave (1999) study, a pilot study for this project showed that palm sedge germinates without the need for cold, moist-stratification. No germination studies have been published on yellow fox sedge.

While much work has been done on overcoming physiological dormancy in sedges, little work has been done on accelerating the speed of germination. Whether planting seed in the greenhouse for transplant production or direct seeding into a bioretention basin, quick germination and subsequent plant establishment is critical. Removing the perigynium, a bladder–like sac that adheres to the pericarp of the achene, has decreased germination time and increased percent germination of some sedges. Nebraska sedge (*C. nebrascensis* Dewy) germination was increased from 38 to 60% and time needed to reach 50% of total germination was reduced by removing perigynia (Hoag et al., 2001). In another study, removing the perigynia increased germination of Nebraska sedge and Northwest Territory sedge (*C. utriculata* Boott) when achenes were grown in the light and reduced time needed to reach 50% germination of germinated achenes by 4 to 9 days (Jones et al., 2004). Germination of Pennsylvania sedge (*C. pensylvanica* Lam.) was significantly improved from approximately 12 to 32% when perigynia were removed and achenes were grown in the light (McGinnis and Meyer 2011). Perigynia removal also increased germination of awlfruit sedge (*C. stipata* Muhl) from 21 to 58% six weeks after planting (Hough-Snee and Cooper, 2011). Although physiological dormancy breaking techniques have been established for several sedge species, germination is not uniform and may occur over the course of 8 weeks. It would be beneficial if germination time could be shortened after dormancy requirements have been satisfied. The objective of this study was to determine if perigynia removal would increase percent germination and decrease time needed to reach 50% germination of yellow fox sedge, porcupine sedge, plains oval sedge, and palm sedge achenes incubated at diurnally fluctuating temperatures of 27/15 ^{o}C.

Materials and methods

Achenes for the experiment were harvested from a collection of open-pollinated native sedge plants that were maintained in a garden plot located on the North Dakota State University Campus, Fargo, USA, (latitude 46^{O} 52’ 38” N). To facilitate optimal seed production, nitrogen was applied as urea (46N-0P-0K) at a rate of 97.6 kg ha^{-1} on 16 August, 2014 and 48.8 kg ha^{-1} on 5 May, 2015. Sedges were watered as needed with overhead irrigation to prevent wilting and weeds were controlled. Mature achenes of plains oval sedge, yellow fox sedge, porcupine sedge, and palm sedge were harvested on 2, 11, and 23 July and 25 Aug., 2015, respectively. Achenes of a species were considered mature when they turned from green to brown, were easily removed from the spike, and when cut laterally with a razor blade (10 seeds per species), the contents were firm. Empty achenes were separated from filled achenes using an air column separator (New Brunswick General Sheet Metal Works, New Brunswick, NJ) and stored dry in paper bags at 21 ^{o}C until the start of experiment. Achene storage time at the start of the experiment ranged from 19 to 22 weeks. Achene viability was tested on 5 November, 2015 using a 1% solution of 2,3,5-triphenyltetrazolium chloride (TZ) (Chemproducts, Portland, OR) following the protocol described in Miller (2010). Fifty achenes of each species were placed in 88 ml paper cups (AJM Packing Corp, Bloomfield Hills, MI) filled with 40 ml of tap water and soaked for 24 hours. After soaking, achenes were cut laterally above the embryo, placed in 88 ml paper cups filled with 10 ml of 1% TZ solution, and placed in the dark at 21 ^{o}C for 48 h. Achenes were removed from the TZ solution and the embryo was examined for staining. The achene was considered viable if the entire embryo was stained. Viability percentages for plains oval sedge, yellow fox sedge, porcupine sedge, and palm sedge were 62, 60, 62, and 72%, respectively. Perigynia were removed from achenes by rubbing between thumb and palm of hand. The friction created by rubbing between thumb and palm of hand removed the perigynia but did not scarify the exterior of the achene.

Pure live seed was calculated by taking the desired pure live seed count and dividing this number by the estimated viability. A total of 25 pure live seed of each species with and without perigyina were placed into 6.0 x 1.5 cm^2 petri dishes (VWR International, Batavia, IL) containing one 5.5 mm diameter filter paper (Whatman grade 1, GE Healthcare UK Limited, Buckinghamshire, UK). Filter paper was moistened with reverse osmosis water and more was added as needed during the study. Each petri dish was placed inside of a 7.6 x 10.2 cm^2 plastic bag (Darice, Inc. Strongsville, OH) to prevent excessive evaporation. Achenes were placed in a growth chamber (Conviron PGW40, Controlled Environments Ltd., Winnipeg, Manitoba, Canada) and grown for four weeks under 108 $\mu mol \cdot m^{-2} \cdot s^{-1}$ irradiance (measured at seed level with the LI-250 quantum sensor, LI-COR, Inc., Lincoln, NE) for 12-hours from cool, white fluorescent light, with alternating 27 ^{o}C, 10-hour days/15 ^{o}C, 10-hour nights with a 2-hour transition period between temperatures. Germination counts were taken every other day for 28 d and germinated achenes were removed. Germination was defined by emergence of radical and hypocotyl. At the conclusion of the study, germination was greater than the estimated viability predicted by initial TZ testing. All non-germinated achenes from each petri dish were collected and viability was determined using the method described previously. Total number of viable achenes per petri dish was determined by taking the sum of germinated and non-germinated but viable achenes (based on second TZ test). Germination percentage for each petri dish was calculated by dividing the number of germinated achenes by the number of viable achenes. Time to 50% germination was calculated for each petri dish by adding up the number of days needed to reach 50% of maximum germination.

Experimental design and statistical analysis

The experiment was arranged as a completely random design with a factorial arrangement consisting of each species with perigynia intact or removed and replicated four times. The entire experiment was repeated one week later. Data from both experimental runs were combined for analysis after determining the variance of each run were similar by comparing the error mean square values (within a factor of 10). Data was subjected to analysis of variance (Proc MIXED, SAS 9.4; SAS Institute, Cary, NC). Treatment means were separated using Tukey's honestly significant difference. Means were considered significant at the $P < 0.05$ level. Germination proportions were $\log_{10}$ transformed prior to analysis to standardize the variance. Germination proportions were backtransformed and are reported as percentages.

Results and discussion

There was a significant species by perigynia interaction. Removing the perigynia significantly increased germination from 51 to 93% for yellow fox sedge (Fig. 3-1). Perigynia removal did not significantly increase percent germination of palm sedge, plains oval sedge, or porcupine sedge. These three species exceeded 90% germination regardless of perigynia status.

Time to 50% germination was significantly reduced from 21 to 17 d and 15 to 10 d by removing perigynia for yellow fox sedge and porcupine sedge, respectively (Fig. 3-2). Perigynia removal did not significantly decrease time to 50% germination for palm sedge and plains oval sedge.

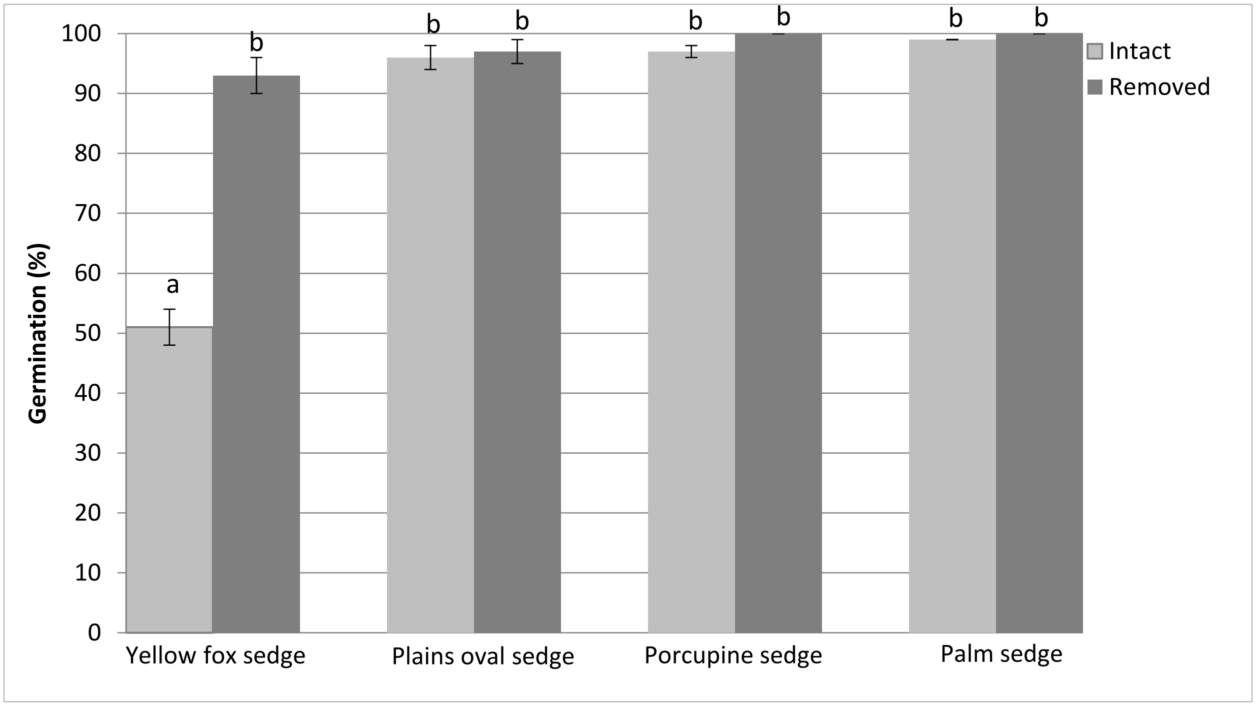

Figure 3-1. The effect of perigynia removal on percent achene germination of four sedge species after 4 weeks of incubation. Half of achenes had their perigynia left intact while the other half was removed. Error bars represent standard error. Mean values labeled with different lower case letters were significantly different according to Tukey's honestly significant difference test at $P < 0.05$.

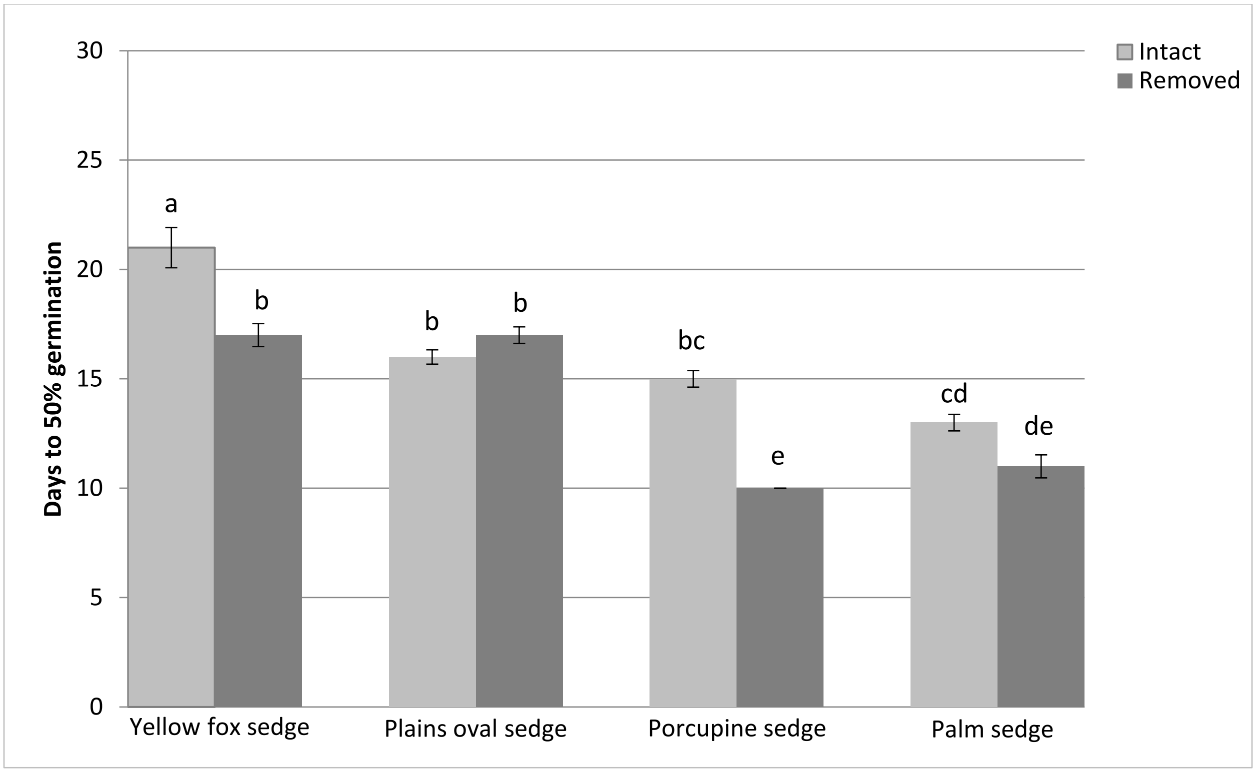

Figure 3-2. The effect of perigynia removal on time to 50% achene germination of four sedge species. Half of achenes had their perigynia left intact while the other half was removed. Error bars represent standard error. Mean values labeled with different lower case letters were significantly different according to Tukey's honestly significant difference test at $P < 0.05$.

Our study suggests that increased percent germination and decreased time to 50% germination by removing perigynia is species specific. The reason why perigynia removal increased germination percentage and decreased time to 50% germination in some sedge species is unclear. One possible explanation is that some sedge species have chemical compounds within the perigynia that inhibit germination. Removing the perigynia would remove the inhibitory compounds and facilitate germination. Jones et al. (2004) suggests that an intact perigynium reduces light reception by the achene. Therefore, sedges with a strict light requirement may be sensitive to the light absorbed by the perigynium. Removing the perigynium may increase light reception by the achene allowing for increased germination percentage and a decrease in the time needed to reach 50% germination.

The amount of light reception by the achene may help explain why some sedge species in our study had an increase in germination and a decrease in time needed to reach 50% germination when perigynia were removed. Kettenring et al. (2006) found that achenes of plains oval sedge needed 14 minutes of white light for germination to 50% while porcupine sedge needed 8.37 h. Both species achieved 100% germination after a 3 w incubation at a 14 h daily exposure of white light. In our study, the time needed to reach 50% germination was significantly decreased for porcupine sedge but not for plains oval sedge. At the end of our 4-w study, percent germination was the same for both species whether perigynia was left intact or removed. Schütz and Rave (1999) found greater than 80% germination of palm sedge, with perigynia intact, when incubated at a constant temperature of 30 ^{o}C in the dark after achenes were stratified for six months. In our study, perigynia removal did not affect percent germination and time needed to reach 50% germination for palm sedge.

Conclusion

The results of our study suggest perigynia removal is an effective strategy to increase percent germination of yellow fox sedge and reduce time needed to reach 50% germination of yellow fox sedge and porcupine sedge. Quicker germination in the greenhouse may result in less time needed to produce saleable transplants. Likewise, perigynia removal may speed germination when achenes are sown into a bioretention basin. Reduced germination time will allow for quicker establishment and reduced competition from weeds.

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APPENDIX

Table A1. Relative shoot count, shoot mass, root mass, and total biomass of four sedge species subjected to continuous flood or drought grown in a greenhouse on the NDSU campus, Fargo, ND from 3 July to 3 Aug, 2015.

Species	Treatment	Relative shoot count (% of control)	Relative shoot mass (% of control)	Relative root mass (% of control)	Relative total biomass (% of control)
Yellow fox sedge	Flood	2 b[z]	22 bc	-40 b	-18 b
Yellow fox sedge	Drought	-28 cd	-28 d	-62 cde	-50 c
Plains oval sedge	Flood	45 a	18 c	-34 b	-7 b
Plains oval sedge	Drought	-26 c	-39 d	-73 e	-58 c
Porcupine sedge	Flood	55 a	48 a	20 a	29 a
Porcupine sedge	Drought	-24 c	-27 d	-54 bcd	-46 c
Palm sedge	Flood	-7 bc	43 ab	-46 bc	-16 b
Palm sedge	Drought	-44 d	-39 d	-67 de	-57 c

[z]Values in the same column with different letters are significantly different at $P < 0.05$ according to Tukey-Kramer honestly significant difference test.

Table A2. Relative plant height across four sedge species subjected to continuous flood or drought grown in a greenhouse on the NDSU campus, Fargo, ND from 3 July to 3 Aug, 2015.

Treatment	Relative plant height (% of control)
Flood	3 a[z]
Drought	-5 b

[z]Values in the same column with different letters are significantly different at $P < 0.05$ according to Tukey-Kramer honestly significant difference test.

Table A3. ANOVA for shoot height.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	320	8.38	<.0001
Flood duration	1	320	3.1	0.0795
Drought duration	2	320	62.56	<.0001
Species*Flood	6	320	2	0.0655
Species*Drought	12	320	0.73	0.7262
Flood*Drought	2	320	0.62	0.5379
Species*Flood*Drought	12	320	1.19	0.2869

Table A4. ANOVA for shoot count.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	323	19.52	<.0001
Flood duration	1	323	2.15	0.1431
Drought duration	2	323	75.84	<.0001
Species*Flood	6	323	1.31	0.2522
Species*Drought	12	323	5.3	<.0001
Flood*Drought	2	323	2.16	0.1171
Species*Flood*Drought	12	323	0.75	0.7018

Table A5. ANOVA for shoot mass.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	328	10.42	<.0001
Flood duration	1	328	12.48	0.0005
Drought duration	2	328	75.19	<.0001
Species*Flood	6	328	1.45	0.1961
Species*Drought	12	328	1.42	0.1541
Flood*Drought	2	328	1.05	0.3502
Species*Flood*Drought	12	328	0.96	0.4918

Table A6. ANOVA for root mass.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	328	24.64	<.0001
Flood duration	1	328	0.07	0.7975
Drought duration	2	328	54.48	<.0001
Species*Flood	6	328	3.18	0.0047
Species*Drought	12	328	1.68	0.0689
Flood*Drought	2	328	2.37	0.0954
Species*Flood*Drought	12	328	0.85	0.5947

Table A7. ANOVA for total biomass.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	319	13.23	<.0001
Flood duration	1	319	2.79	0.0959
Drought duration	2	319	68.21	<.0001
Species*Flood	6	319	2.11	0.0514
Species*Drought	12	319	1.65	0.0781
Flood*Drought	2	319	1.73	0.1789
Species*Flood*Drought	12	319	0.73	0.7208

Table A8. ANOVA for visual damage rating.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	205	18.21	<.0001
Flood duration	1	205	10.04	0.0018
Drought duration	2	205	209.34	<.0001
Species*Flood	6	205	1.84	0.092
Species*Drought	12	205	4.84	<.0001
Flood*Drought	2	205	0.17	0.8478
Species*Flood*Drought	12	205	2.04	0.0221

Table A9. ANOVA for evapotranspiration per day.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	328	32.43	<.0001
Flood duration	1	328	3.48	0.063
Drought duration	2	328	272.07	<.0001
Species*Flood	6	328	4.81	0.0001
Species*Drought	12	328	5.69	<.0001
Flood*Drought	2	328	0.59	0.5559
Species*Flood*Drought	12	328	1.65	0.0779

Table A10. ANOVA for total biomass water use efficiency.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	327	139.6	<.0001
Flood duration	1	327	473.83	<.0001
Drought duration	2	327	36.98	<.0001
Species*Flood	6	327	2.49	0.0228
Species*Drought	12	327	1.62	0.0834
Flood*Drought	2	327	8.37	0.0003
Species*Flood*Drought	12	327	1.07	0.3861

Table A11. ANOVA for days of dry down.

Effect	Num DF	Den DF	F Value	Pr > F
Species	6	328	66.32	<.0001
Flood duration	1	328	9.2	0.0026
Drought duration	2	328	431.04	<.0001
Species*Flood	6	328	2.73	0.0133
Species*Drought	12	328	7.43	<.0001
Flood*Drought	2	328	1.94	0.1449
Species*Flood*Drought	12	328	1.3	0.2144

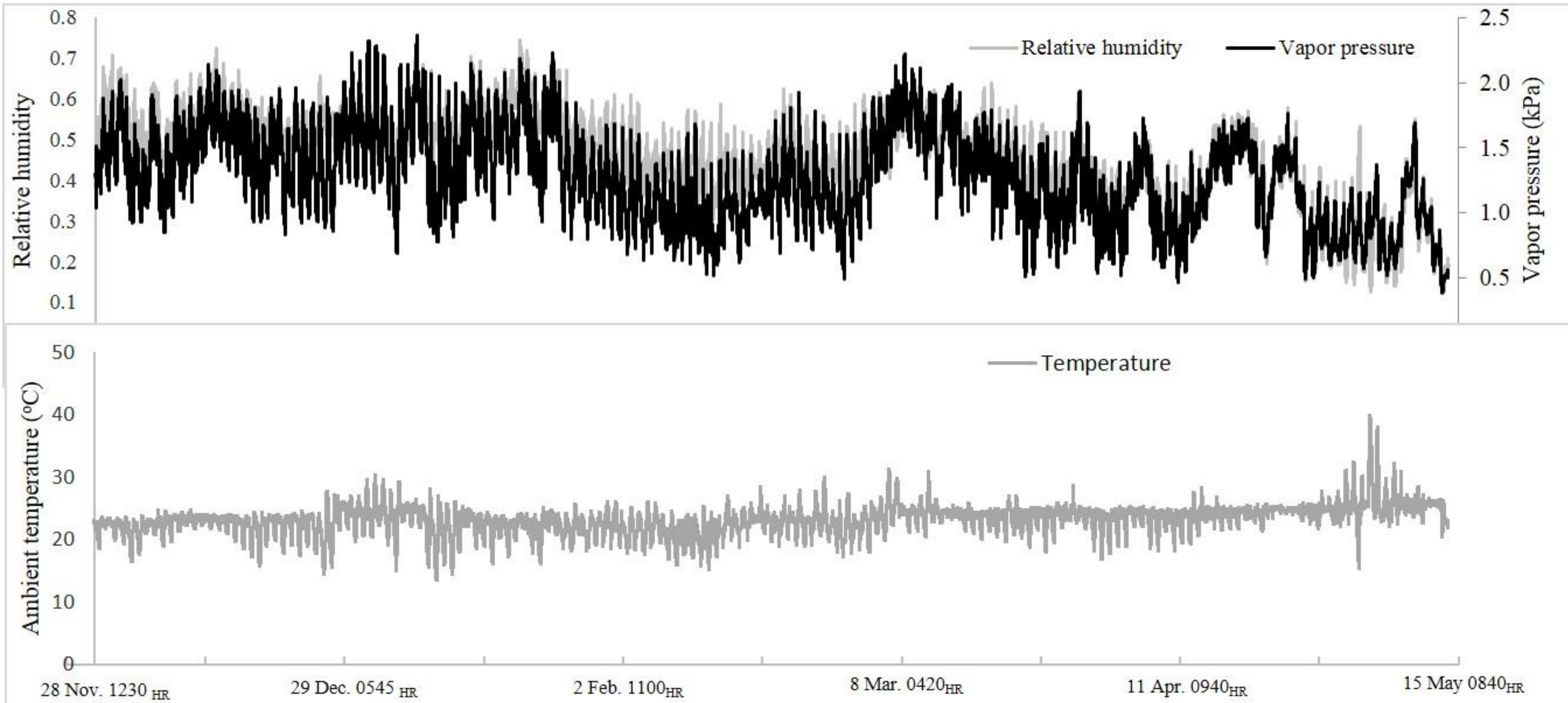

Figure A1. Environmental conditions during a greenhouse study conducted from 28 Nov. 2015 to 15 May 2016.

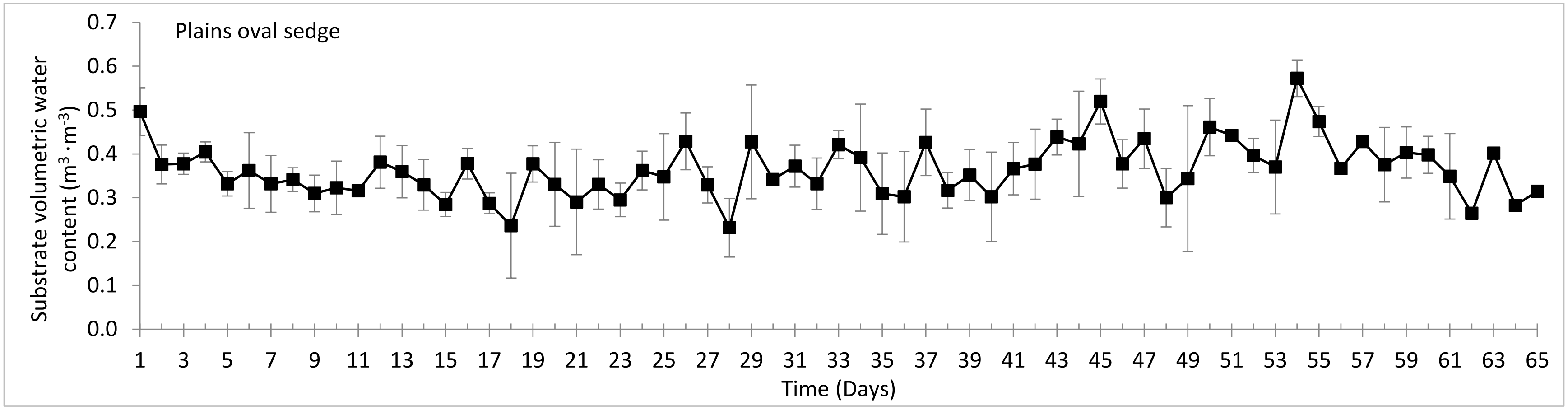

Figure A2. Substrate volumetric water contents of plains oval sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

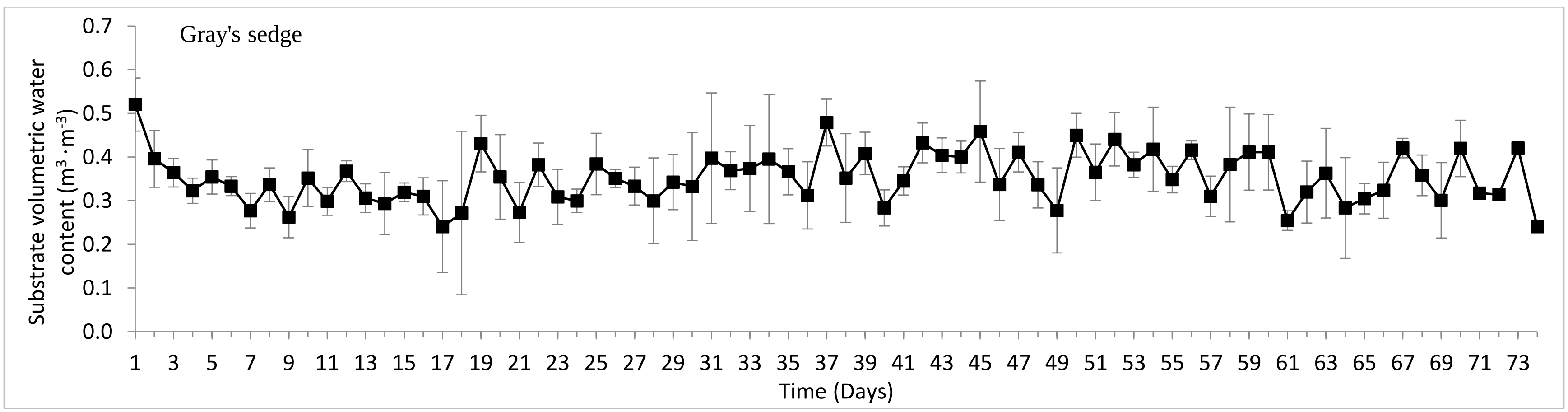

Figure A3. Substrate volumetric water contents of Gray's sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

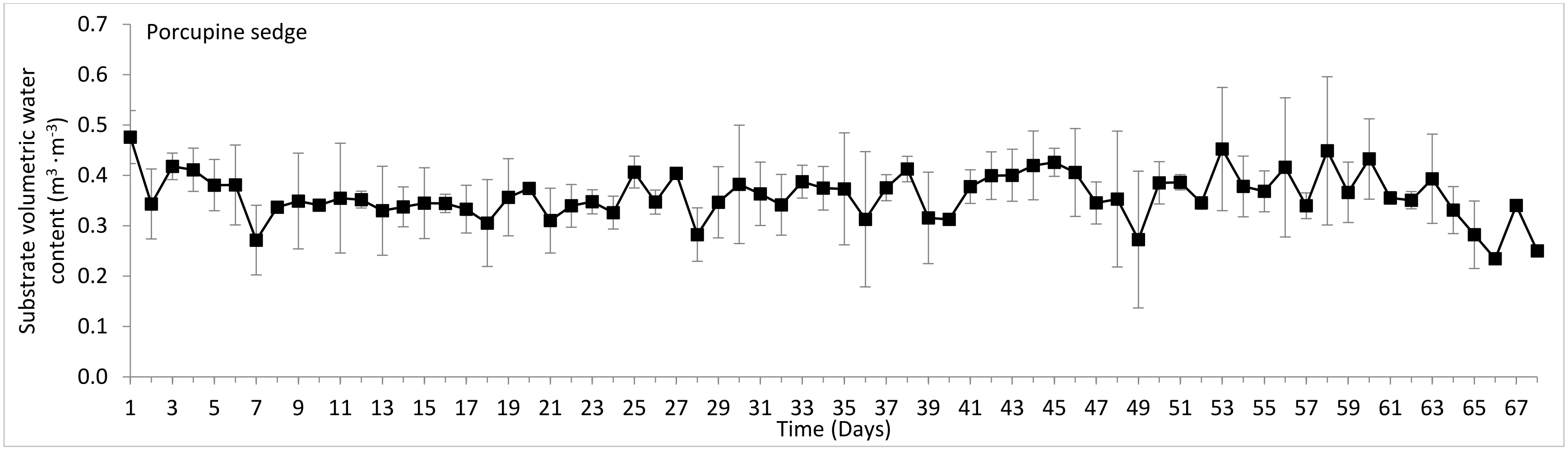

Figure A4. Substrate volumetric water contents of porcupine sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

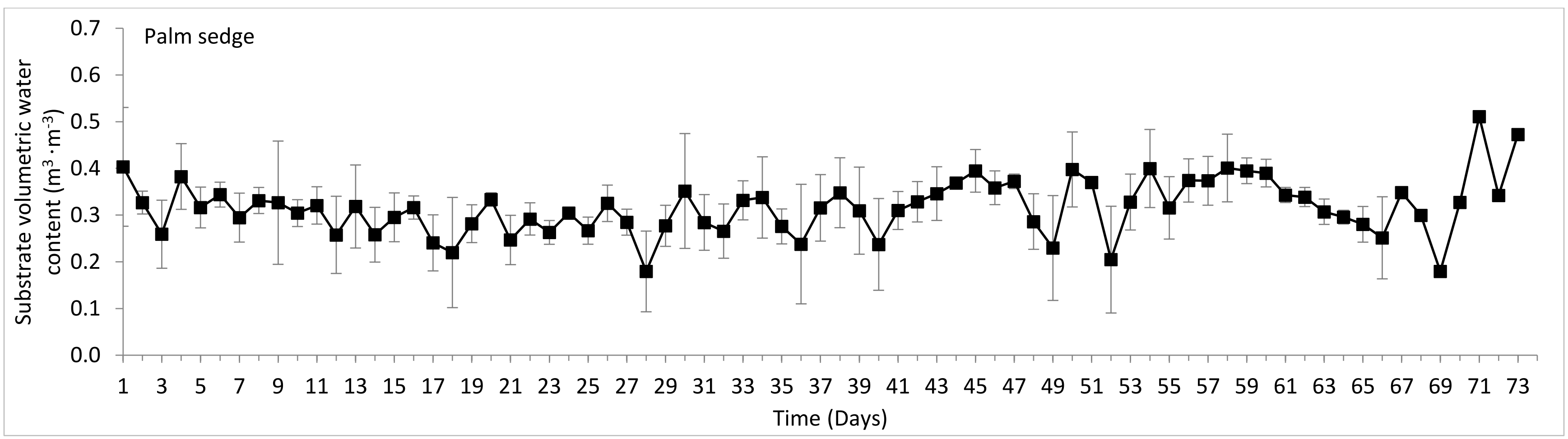

Figure A5. Substrate volumetric water contents of palm sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

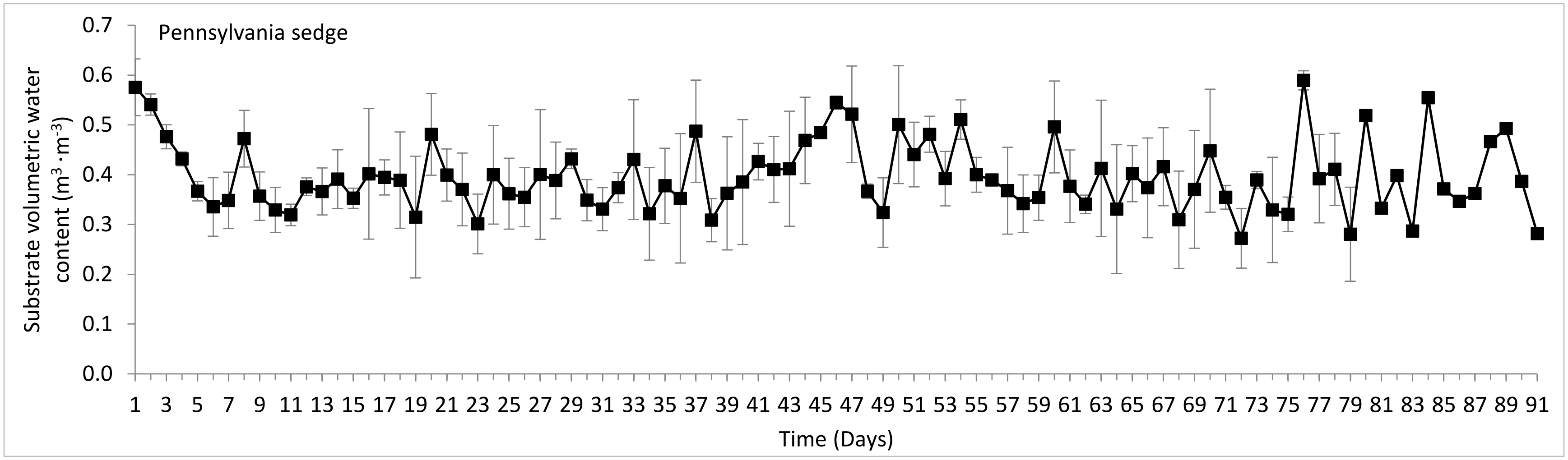

Figure A6. Substrate volumetric water contents of Pennsylvania sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.

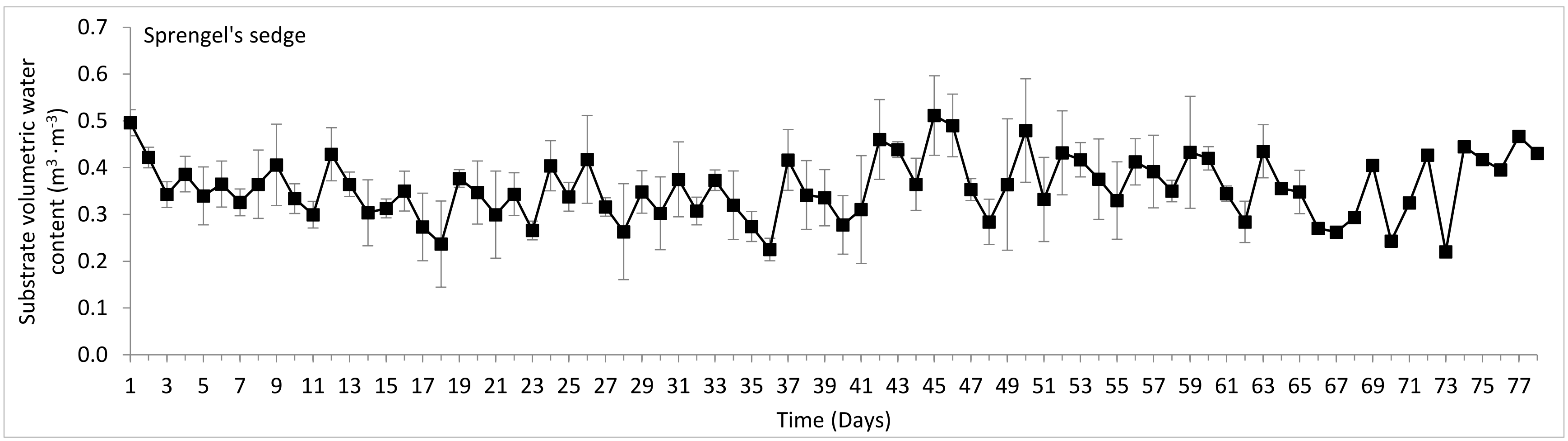

Figure A7. Substrate volumetric water contents of Sprengel's sedge from the control treatment. Error bars indicate standard deviations. All replicates did not take the same amount of time to dry down, therefore some data points are less than n = 9.