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Responses of the wetland grass, Beckmannia syzigachne, to salinity and soil wetness: Consequences for wetland reclamation in the oil sands area of Alberta, Canada

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Responses of the wetland grass, *Beckmannia syzigachne,* to salinity and soil wetness: Consequences for wetland reclamation in the oil sands area of Alberta, Canada

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Abstract

Reclamation of the boreal landscape, including both wetlands and uplands integrated into complex watersheds, has presented a challenge over the past decade with few attempts. Relevant today is wetland/peatland reclamation on reclaimed landscapes positioned on saline sand deposits left on ‘in-pits’ from open pit oil sands mining. Part of the reclamation challenge lies in choosing characteristic species that are tolerant of conditions present on the reclaimed landscape. Species need to both survive harsh environmental conditions and facilitate succession from mineral-based wetlands (marshes) to peat-based ones (fens). A two-by-six factorial experiment was implemented in a greenhouse under two moisture levels: saturation to 2.5 cm below the soil level (high) and saturation to 7.5 cm below the soil level (low) and six salinity treatments: 5 mgL^{-1} Na^{+}, 400 mgL^{-1} Na^{+}, 850 mgL^{-1} Na^{+}, 1,250 mg L^{-1} Na^{+}, 1,850 mg L^{-1} Na^{+}, and 2,700 mg L^{-1} Na^{+}. Water level affected total biomass, with the low water level producing higher biomass. Sodium concentration affected biomass, root:shoot ratio, stomatal conductance, evapotranspiration, and photosynthetic rate; all responses were similar for the lower Na concentrations and declined after the 850 mgL^{-1} treatment. We conclude that *B. syzigachne* tolerates Na levels of 850 mg L^{-1} and survives with diminished performance at treatment of 850 mg L^{-1} up to 2,700 mg L^{-1}. With these salinity responses, along with broad tolerance to water levels, *B. syzigachne* has great potential as an early

colonizing annual species for conditions predicted to occur in many of the in-pit reclamation designs.

1. Introduction

The need for environmental repair has been long recognized and there have been attempts to restore many ecosystems (Hobbs et al., 2006); however, less well-studied ecosystems, such as the boreal peatlands, present a challenge for restoration. Peatlands are wetlands, characterized by accumulation of partially decomposed organic matter, that over millennia, form deposits of peat (Clymo et al., 1998). The boreal landscape of western Canada consists of a mosaic of upland forest and a variety of peatland types. Beneath this mosaic of forest and peatland is bitumen, a crude oil that is extracted through mining, disturbing the ecosystems and leaving a sterile contaminated landscape. Whereas in situations where some of the underlying peat remains intact (for example after removal of horticultural quality peat) efforts of restoration have been successful (Rochefort et al., 2003); after bitumen extraction, where all peat and mineral soil was removed, restoration is generally not possible as none of the original ecosystem components remain. Attempts to build entire new landscapes containing both wetlands and uplands are presently underway (Daly et al. 2012, Wytrykush et al., 2012). Part of the reclamation challenge, especially for wetlands, lies in choosing characteristic species that are also tolerant of conditions present on the reclaimed landscape. Such species need to both survive harsh environmental conditions and facilitate succession from mineral-based wetlands (marshes) to peat-based ones (fens). One species that fits both criteria is American sloughgrass (*Beckmannia syzigachne*), but tests of responses of this species this to salinity and wetness are not well elucidated in the literature.

Canada contains 1.235 million km^2 of peatlands (Joosten and Clarke, 2002) and two of the largest peatland complexes in the world (Vitt et al., 2005). In northern Alberta, oils sands are contained in the Mackenzie River Basin Peatland Complex beneath 142,200 km^2 of which 4,800 km can be surface mined (Government of Alberta, 2009). Oil sands production, the process of mining for bitumen, has already dramatically changed the boreal landscape of northern Alberta. These oil sands deposits are located beneath roughly one-fourth of Alberta's land. The deposits may be extracted by open pit mining, whereby rock and earth are removed and transported by vehicle, leaving a large pit (an in-pit). As of 2011, open pit mining accounted for 51% of the 1.7 million barrels per day of crude bitumen in Alberta (Government of Alberta, 2011). After a few decades, the oil sands deposits are consumed and the in-pits are filled with sterile, salty sand (Wytrykush et al., 2012). The filled in-pits will be a prominent feature on the future boreal landscape of Alberta.

Reconstruction of the in-pit areas has been attempted through introduction of non-peat forming (marsh) plants, but never species naturally occurring in peatlands. Additionally peatlands are complex ecosystems that have developed through successional processes over thousands of years (Bauer et al., 2003). Functionally and contrasted to marshes, fens are wetlands that actively accumulate organic matter that with time is maintained as a deposit of peat. Although, marsh reclamation of in-pits offers some guidance to the challenge of creating a peatland, specifically a fen (Harris, 2007), selection of appropriate species for fen development may be different than those for marshes. Marsh species are more resistant to contaminants (Hornung and Foote, 2007; Trites and Bayley, 2009a) and peatland floras, especially mosses, are typically not

tolerant of salinity (Boerner and Forman, 1975). Thus, the overlap occurrence of a few species in both marshes and fens is crucial to fen reclamation. Salinity, derived from the sand and extraction process, and from natural salinity of the region, limits the diversity of wetland species and slows succession from reclaimed marshes to fens (Ciborowski et al., 2011). Successfully reclaimed in-pits to fens would be comparable to natural fens in hydrology, chemistry, and flora. Natural fens receive water from precipitation and from either the surrounding uplands, from groundwater, or are in contact with aquatic ecosystems. The pore water chemistry of fens is variable but pH's as high as 8.5 are present in Albertan rich fens. The vegetation of fens is also variable; some site types having only field and ground layers (sedge-dominated) to an often well-developed shrub layer and in some cases an open canopy of trees. Fens are the dominant peatland type on the Alberta landscape and were also prevalent in most early developmental stages of western Canadian peatlands (Kuhry et al., 1992, 1993).

Developing specific plans for vegetating in-pits created by oil sands mining is needed for reclamation. Species attributes include 1) tolerance to high levels of both sodium and calcium, 2) tolerance to a range of water level conditions, 3) common on the natural landscape of northern Alberta, 4) reproduce and establish quickly, and 4) obtained easily in quantity from natural sites. Understanding tolerances of key species potentially available for reclamation of oil sands areas is an important part of future reclamation efforts. Recent studies by Trites and Bayley 2008, Pouliot et al. 2012, (reviewed in Daly et al. 2012), and Koropchak and Vitt 2013 are important beginnings.

Beckmannia syzigachne, or American sloughgrass, is a caespitose, annual or occasionally biennial grass species. It commonly produces abundant seeds that are large

and easily collected. Initial germination studies by Boe and Wynia (1985) show that slough grass does not appear to be limited by complex germination requirements, low forage yield, or poor seed production. The species has considerable geographic range, occurring in North America from southern Alaska to California, eastward in the northern portions of Ontario to Quebec and Nova Scotia, and southward to New Mexico through Kansas the U.S. Midwest and Northeast (NatureServe, 2009). Typically it is found in marshes, low wet ground or "sloughs", floodplains, pond shores, lakes, streams, ditches, and other types of open wetland habitats (Flora of North America, 2007).

Beckmannia syzigachne is associated with a number of rich fen site types in Alberta, found in transitional areas on both shallow organic soils as well as moist mineral soils. Beckmannia never occurs in large populations, and is rarely associated with stable, mature fen communities owing to its' annual/biennial life style. It produces abundant seeds that easily germinate in nature. When planted in experimental regimes in high densities, after two to three years nearly all of the individuals have disappeared (data from unpublished Syncrude reports). There is no evidence from these Syncrude trials that Beckmannia populations persist and negatively affect later successional species. Thus, this is a species that potentially could serve as a key early successional species in oil sands reclamation efforts. To understand whether *B. syzigachne* can be used in in-pit reclamation, we examined the responses of this species to a range of salinities under varying water levels that imitate the expected conditions present on in-pit constructed landscapes. Physiological responses (stomatal conductance, evapotranspiration, and net photosynthetic rate) give indication of a plant's health. Photosynthesis is limited by the diffusion of CO2 from the atmosphere to the chloroplasts. The magnitude of the

limitation is termed resistance; the reciprocal of resistance is conductance. With higher stomatal conductance, there is an increase in CO_2 assimilation and an increase in water loss (evapotranspiration) (Lambers et al., 2008). Thus arises the problem of compromise: both CO_2 and water vapor are diffusing through the stomata: CO_2 to the lower concentration inside the leaf from the atmosphere, and water vapor to the atmosphere from the high concentration inside the leaf. Plants balance the compromise by regulating stomatal conductance. Under a physiological stress such as salinity, the plant may have to conserve water and limit stomatal conductance and thus decreasing carbon assimilation. Stomata exert the greatest short-term control over plant water relations due to the steep concentration gradient between leaf and air (Lambers et al., 2008).

We undertook this experiment to test the tolerance of *Beckmannia syzigachne* to sodium under controlled greenhouse conditions. Since *Beckmannia* occurs under a range of soil moisture conditions we also tested whether differences in wet or dry soils affected performance under a range of sodium conditions. We chose to use both morphological and physiological measures to assess performance. Based on field observations from natural fens, we hypothesize that *Beckmannia syzigachne* will perform best in low-salinity and relatively dry conditions, but will tolerate both wetter conditions and high levels of Na.

2. Methods

Sixty *Beckmannia syzigachne* (Steud.) Fernald plants were grown from seed (collected in Fall of 2011 at Syncrude Canada Ltd. 57º 042’ N, -111º 658’ W) for two months and maintained in moist peat and watered with fresh water, then transplanted to

10 cm diameter pots in a mixture of two-thirds commercial *Sphagnum* peat and one-third coarse sand (to mimic reclamation site soil).

A two-by-six factorial experiment was implemented with each treatment combination having 5 replicates, Our choice of 5 replicates was dictated by the number of germinated plants. Two moisture levels were maintained: saturation to 2.5 cm below the soil level (high) and saturation to 7.5 cm below the soil level (low). Six salinity treatments were implemented: 5 mg L^{-1} Na^+(=26 μS cm^{-1}) - similar to natural rich fen waters (Wind-Mulder and Vitt, 2000), 400 mg L^{-1} Na^+(=2,309 μS cm^{-1}) - similar to process water used by Syncrude (unpublished data from Syncrude Canada, Ltd.). EC's from 500-2000 μS cm^{-1} have been termed sub-saline, while those having EC's above 2000 μS cm^{-1} are saline (S. Bayley pers. comm., Trites and Bayley 2008), 850 mg L^{-1} Na^+ (=4,830 μS cm^{-1}), 1250 mg L^{-1} Na^+ (=7,050 μS cm^{-1}), 1,850 mg L^{-1} Na^+(=8,750 μS cm^{-1}), and 2,700 mg L^{-1} Na^+(=11,710 μS cm^{-1}). Stock solutions were prepared using NaCl and stored in closed 20 L buckets. Salinity was expressed in terms of electrical conductivity and monitored throughout the experiment. Electrical conductivity and water levels were maintained at each level for the duration of the experiment as evapotranspiration removed water from the bins. DI water was added when electrical conductivity was higher than initial stock solutions and all water in the bins was replaced with stock solution every two weeks.

Plants were maintained under experimental conditions of salinity and moisture for 149 days (five months), We chose this length to mimic the broad boreal/temperate distribution of *Beckmannia*, with central/northern Albertan growing seasons around 125 days. Treatment conditions for each of the salinity/water level combinations were maintained by placement of plants in individual two-liter containers in a phytotron under ambient light and temperature conditions (light intensity of 200-350 μmol$m^{-2}s^{-1}$, 18-

22°C). Samples were randomly rearranged every 14 days and maintained under natural light conditions. Plants were fertilized twice (day 6 and 55) using 2 liters of a solution (prepared from 15-16-17 Peat-Lite Jack's Professional®) of 28.8 mg N per liter, 30.6 mg P per liter, 32.8 mg K per liter), to ensure limiting nutrients were not responsible for plant response and performance. Exchangeable nitrogen at natural benchmark sires in the oil sands area have values between 20 and 70 mg km^{-1} soil (J. Hartsock pers. comm.), while N, P, and K concentrations in natural fen pore waters are always below 5 mg L^{-1} (Vitt & Chee 1990). Our concentrations of N are comparable to those currently being applied to whole ecosystem experiments in the oil sands areas (pers. comm. J Graham). Net photosynthetic rates, evapotranspiration, and stomatal conductance of each plant were measured at 83 days, 118 days, and 146 days from the start of the experiment. All physiological data was normalized to leaf area. Physiological parameters were measured using CI-340 portable photosynthesis system in a 22.5 cm^2 cylindrical chamber during late morning and early afternoon (10 am to 2 pm; when PAR was highest). If net photosynthetic rate was measured at zero and leaves were brown and crisp, the plant was considered dead. At the end 149 days, the *B. syzigachne* plants were collected, rinsed of all foreign material, and dried at 60°C for 72 hours. Plant biomass was separated into roots and shoots, and weighed. Physiological measurements were pooled for the three collection dates in order to examine overall treatment effects (Na and water level), non-normal measurements were log transformed, and analyzed using two-way ANOVA in JMP® 9.0.1. The effect of treatment (Na) effects on physiological performance over time were were log transformed if non-normal, and analyzed using repeated measures two-way ANOVA in SPSS.

3. Results

3.1. Plant survival and biomass

Sodium treatments remained within 10-20% of the initial conductivity over the course of the experiment, with the exception of conductivity spikes with addition of fertilizer. *Beckmannia syzigachne* had 100% survival for four [Na^+] treatments (5 mg L^{-1}, 400 mg L^{-1}, 850 mg L^{-1}, and 1,250 mg L^{-1}) and 80% survival for two [Na^+] treatments (1,850 mg L^{-1}, and 2,700 mg L^{-1}). Both [Na^+] and water level affected total biomass (F = 18.65, $p < 0.001$; F = 5.50, p = 0.0232, respectively). Biomass was greater for the lower [Na^+] (5 mg L^{-1}, 400 mg L^{-1}, and 850 mg L^{-1}) and the low water level; biomass was lower for the higher [Na^+] (1,250 mg L^{-1}, 1,850 mg L^{-1}, and 2,700 mg L^{-1}) and high water level (Fig. 1A; Fig. 2). Water level did not affect root:shoot ratio, but [Na^+] did (F = 7.74, $p <$ 0.001), where there was a general decline in root:shoot ratio as [Na^+] increased (Fig. 1B).

3.2. Stomatal Conductance

Na concentration had a significant effect on stomatal conductance (F= 42.73, $p <$ 0.0001). Water level had no effect and there was no interaction (F= 2.52, p =0.119; F= 0.94, p = 0.119, respectively). The lower [Na^+] (5 mg L^{-1}, 400 mg L^{-1}, and 850 mg L^{-1}) had the higher rates of stomatal conductance, while the higher [Na^+] (1,250 mg L^{-1}, 1,850 mg L^{-1}, and 2,700 mg L^{-1}) had the lower rates of stomatal conductance (Fig. 1C). Time also affected stomatal conductance (F= 31.34, $p < 0.001$). Stomatal conductance was higher during day 83, than in days 118 and 146 (Fig. 3A).

3.3. Evapotranspiration Rate

Na concentration also had a significant effect on evapotranspiration (F= 35.74, p < 0.001), whereas water level had no effect and there were no interactions (F= 2.18, p

=0.146; F= 1.02, p = 0.416, respectively). The lower [Na^+] (5 mg L^{-1}, 400 mg L^{-1}, and 850 mg L^{-1}) had the higher rates of water loss, while the higher concentrations (1,250 mg L^{-1}, 1,850 mg L^{-1}, and 2,700 mg L^{-1}) had the lower rates of water loss (Fig. 1D). Time, water level, and sodium concentration interaction also affected water loss (F= 2.43, p = 0.017). The lower [Na^+] (5 mg L^{-1}, 400 mg L^{-1}, and 850 mg L^{-1}) had the higher rates of water loss during day 83 and 146, while the higher concentrations (1,250 mg L^{-1}, 1,850 mg L^{-1}, and 2,700 mg L^{-1}) had the lower rates of water loss during day 83 and 146 (Fig. 4). Water loss was greatest for all concentrations during day 118. High and low water treatment sporadically affected water loss throughout the days and sodium concentrations.

3.4. Photosynthetic Rate

The rate of photosynthesis showed a significant difference between Na treatments (F= 18.57, p < 0.001), whereas water level had no effect, nor was there an interaction (F= 0.72, p =0.4; F= 0.62, p = 0.68, respectively). The lower [Na^+] (5 mg L^{-1}, 400 mg L^{-1}, and 850 mg L^{-1}) had the higher rates of photosynthesis, while the higher concentrations (1,250 mg L^{-1}, 1,850 mg L^{-1}, and 2,700 mg L^{-1}) had the lower rates (Fig. 1E). Time also affected photosynthetic rate (F= 58.08, p < 0.001). Photosynthetic rate was higher during day 83, than in days 118 and 146 (Fig. 3B).

3.5. Water Use Efficiency

Na concentration affected the water use efficiency of *B. syzigachne* (F= 2.89, p = 0.025), whereas water level had no effect, nor was there an interaction (F= 1.05, p < 0.31; F= 1.21, p = 0.319, respectively) (Fig. 1F). Water use efficiency was higher in the 400 mg L^{-1} sodium concentration, than in the 5 mg L^{-1}, 850 mg L^{-1}, and 1,250 mg L^{-1}) (Fig.

9). Time also affected water use efficiency ($F= 11.34$, $p < 0.001$). Water use efficiency was higher during day 83, than in days 118 and 146 (Fig. 3C).

Overall *B. syzigachne* was not affected by the water level treatments, responding similarly to both saturated and unsaturated soil conditions. Also, overall survival was good; four of the sixty plants died, two at 1,850 Na mg L^{-1} both high and low water levels and two at 2,700 Na mg L^{-1} both high and low water levels; however, performance was affected by salinity, both in terms of biomass and physiological performance. Like biomass, all three of the physiological performance measures were reduced as salinity increased. The greatest changes were consistently observed between the 850 and 1,250 Na mg L^{-1} treatments. As stomatal conductance decreased, so did evapotranspiration and photosynthetic rates. At 850 mg L^{-1}, photosynthetic rates were 74% of the 5 mg L^{-1} control, dropping to 46% at the 1,250 mg L^{-1} treatment. Similar declines were present in the stomatal conductance, evapotranspiration, and water use efficiency. At 850 Na mg L^{-1}, stomatal conductance was 69% of the 5 Na mg L^{-1} control, dropping to 33% at the 1250 mg L^{-1} treatment. At 850 Na mg L^{-1} at 83, 118, and 146 days under high water treatment, evapotranspiration was 65-70% of the 5 Na mg L^{-1} controls, dropping to 33-40% at the 1,250 mg L^{-1} treatment. At 850 Na mg L^{-1} at 83 and 146 days under low water treatment, evapotransporation was over 100% of the 5 Na mg L^{-1} control (and 50% of the 5 Na mg L^{-1} control at 118 days), dropping to 60-65% at the 1,250 mg L^{-1} treatment (and 32% of the 5 Na mg L^{-1} control at 118 days).

All the *Beckmannia syzigachne* plants physiologically performed the best during the 83-day reading. During the 118 day and 146 day, stomatal conductance was less than 50% of the 83 day performance. During the 118 day and 146 day, photosynthesis was

less than 60% of the 83 day performance. During the 118-day and 146 day, evapotranspiration was less than 50% and 84% of the 83-day performance, respectively. During the 118 day and 146 day, water use efficiency was less than 87% and 68% of the 83 day performance, respectively.

4. Discussion

Salinity of water in western boreal peatlands ranges from very low (< 1 mg L^{-1}) to around 10 mg L^{-1} (Vitt and Chee, 1990), with the exception of saline fens, which can be over 2,000 mg L^{-1} (Vitt et al., 1993). The salinity within peat, from natural alkaline fens, ranges from 100 mg kg^{-1} to ~1,000 mg kg^{-1} (Vitt and Chee, 1990). Trites and Bayley (2009a & 2009b) found the electroconductivity of natural boreal wetlands to range from 600 μS cm^{-1} to 13,500 μS cm^{-1} and oil sands wetlands to range from 500 μS cm^{-1} to 3,300 μS cm^{-1}. At Syncrude Canada's current in-pit reclamation landscape (referred to as the "Sandhill Watershed") electroconductivity ranges from 500-4,000 μS cm^{-1}; and two years after revegetation began, the Na concentrations of pore water have ranged from 30-400 mg L^{-1} **(**M. House, *unpublished results***)**. It is unclear how salinity will change from future upwelling from the deeper sands over time. A modeled conservative estimate of salinity conditions at the Sandhill reclamation would range between 73 mg L^{-1} during the first 10 years and 390 mg L^{-1} throughout the 45-year time span (BGC Engineering Inc., 2008). The upper end of this range is much greater than found in natural rich fens, but similar to that in local saline fens.

Comparison to other boreal wetland species can be made to *B. syzigachne*, such as *Typha latifolia*, an emergent aquatic plant, commonly found in disturbed and early

successional habitats in a wide range of environmental conditions (Liefers, 1983). A similar experiment with *T. latifolia* was conducted in a greenhouse under six initial sodium concentrations (0, 300, 600, 1,200, and 2,400 mg L^{-1}). Koropchak and Vitt (2012) found decreases in plant health, survivorship, growth, and biomass of *T. latifolia* as sodium concentration increased. The greatest decrease occurring between 300 and 600 mg L^{-1} Na treatments, whereas *B. syzigachne* showed decreased performances and biomass after 850 mg L^{-1}. This implies a greater potential as a reclamation species. Similar results were obtained by Pouloit et al. (2012) where they grew four peat-forming fen species, under greenhouse conditions, in process waters. They found no impacts for any of the four species in morphological attributes at sodium concentrations up to 569 mg L^{-1}.

Carex aquatilis is another promising reclamation species that has been compared on oil sands wetlands to sites indirectly affected by industry to natural sites in Northern Alberta (Mollard et al., 2012). Sodium concentrations on oil sands sites was 271 ± 141 mg L^{-1}; on indirectly affected sites, 100 ± 65 mg L^{-1}; and on natural sites, 15.7 ± 6.6 mg L^{-1}. Overall, *C. aquatilis* had similar physiological performance (net photosynthesis and transpiration rates) on oil sands contaminated wetlands when compared to populations on natural wetlands, although there was reduced morphological performances and higher photochemical efficiency (Mollard et al., 2012). Given the physiological and morphological performances of *B. syzigachne* diminish after 850 mg L^{-1} Na, its potential as a reclamation species on oil sands is as good if not better than *C. aquatilis*. Given the different life history traits of these two species, but somewhat similar tolerances to sodium, we recommend introducing both species together early on in reclamation. The

annual, *Beckmannia* with caespitose growth form providing quick cover to the site and the rhizomatous, long-lived perennial, *C. aquatilis*, providing long-term stability. These two species, used together, will provide similar, quick plant colonization for wetland reclamation similar to that currently used in suburban yards and highway roadsides.

We conclude that *Beckmannia syzigachne* tolerates Na levels of 850 mg L^{-1} and survives with diminished performance at treatment 850 mg L^{-1} up to 2,700 mg L^{-1}. With these salinity responses along with broad tolerance to water levels, *B. syzigachne* has great potential as an early colonizing species for conditions predicted to occur in many of the in-pit reclamation designs.

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Figure legends

Fig. 1. Influence of sodium (Na) treatment on total dry weight biomass (**A**), root:shoot ratio (**B**), stomatal conductance (**C**), evapotranspiration (**D**), photosynthetic rate (**E**), and water use efficiency (**F**) of *Beckmannia syzigachne* plants. For panels A-E, the white line represents the mean, the black line represents median, the error bars show the minimum and maximum values of the data set, the box below the median represents the first quartile and the box above the median represents the third quartile. Panel F represents the mean and standard error. Within a panel, significant differences are indicated by different letters.

Fig. 2. Influence of water level on total dry weight biomass of *Beckmannia syzigachne* plants. See legend of Fig. 1 for details on the box and error bars. Significant differences are indicated by different letters.

Fig. 3. Stomatal conductance (**A**), photosynthetic rate (**B**), and water use (**C**) for *Beckmannia syzigachne* plants as a function of time. For panels A and B, see legend of Fig. 1 for details on the box and error bars. Panel C represents the mean and standard error. Within a panel, significant differences are indicated by different letters.

Fig. 4. Influence of sodium (Na) treatment, time, and water level on evapotranspiration of *Beckmannia syzigachne* plants. Data represent the mean and standard error. Significant differences are indicated by different letters.

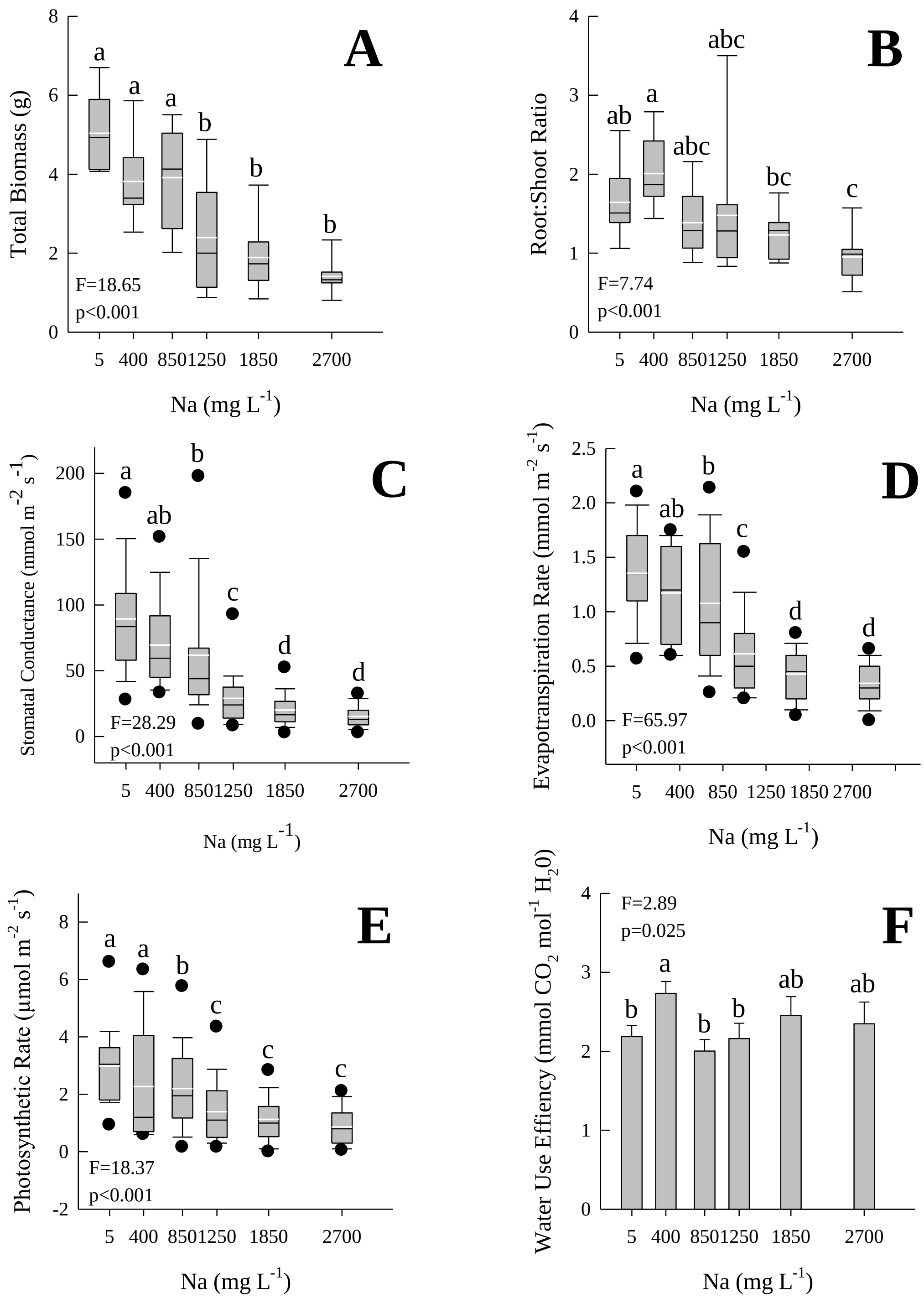

A
Total Biomass (g)
F=18.65
p<0.001
a a a b b b
Na (mg L-1)
5 400 850 1250 1850 2700
B
Root:Shoot Ratio
F=7.74
p<0.001
ab a abc abc bc c
Na (mg L-1)
C
Stomatal Conductance (mmol m-2 s-1)
F=28.29
p<0.001
a ab b c d d
Na (mg L-1)
D
Evapotranspiration Rate (mmol m-2 s-1)
F=65.97
p<0.001
a ab b c d d
Na (mg L-1)
E
Photosynthetic Rate (µmol m-2 s-1)
F=18.37
p<0.001
a a b c c c
Na (mg L-1)
F
Water Use Effiency (mmol CO2 mol-1 H20)
F=2.89
p=0.025
b a b b ab ab
Na (mg L-1)

Figure 1

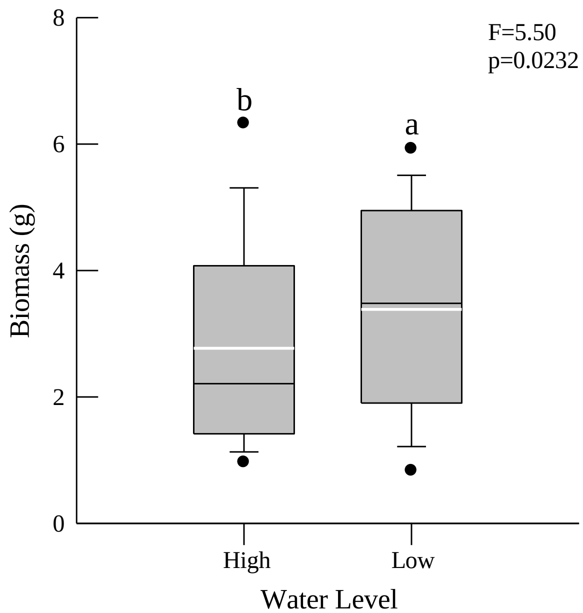
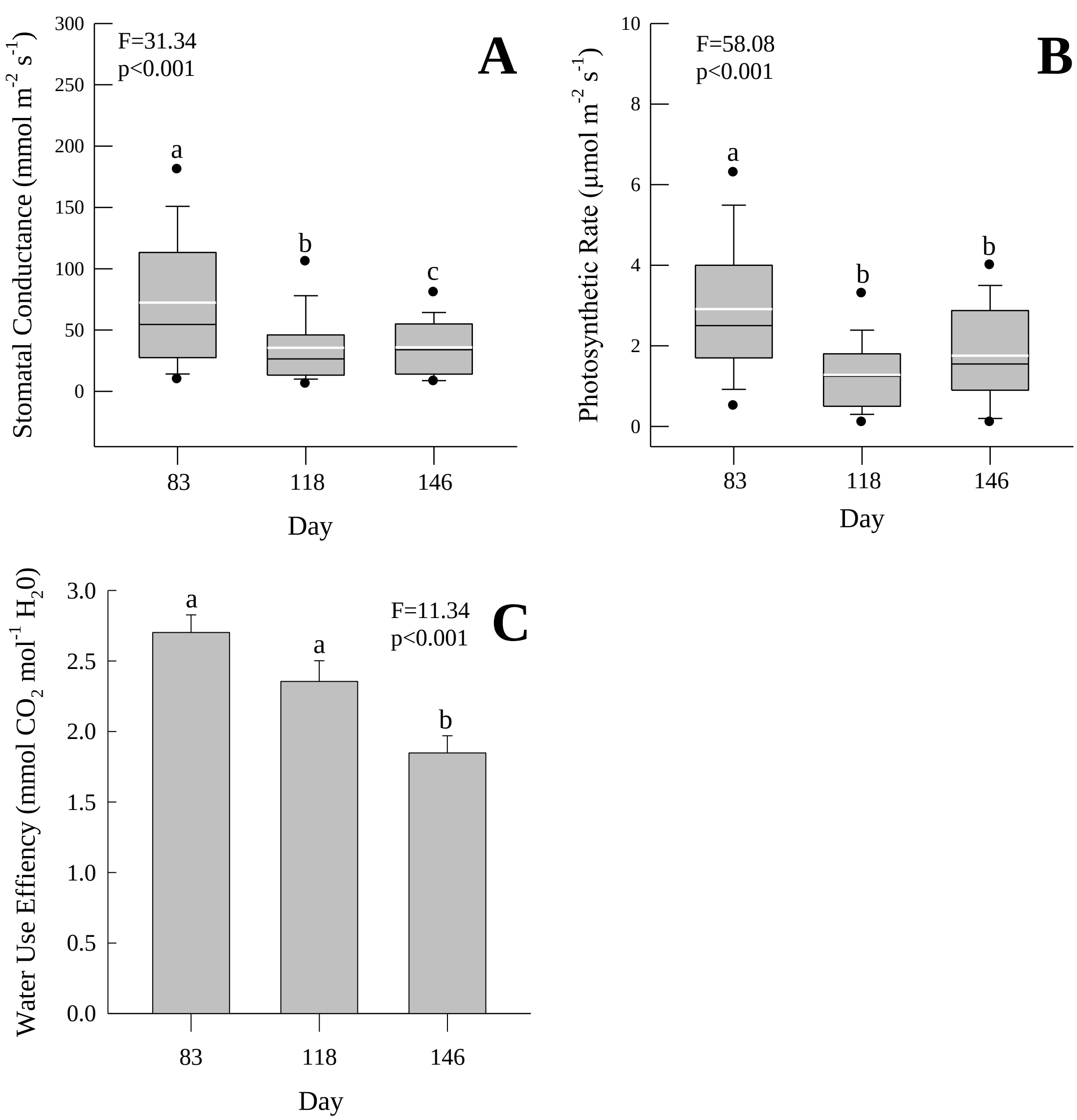
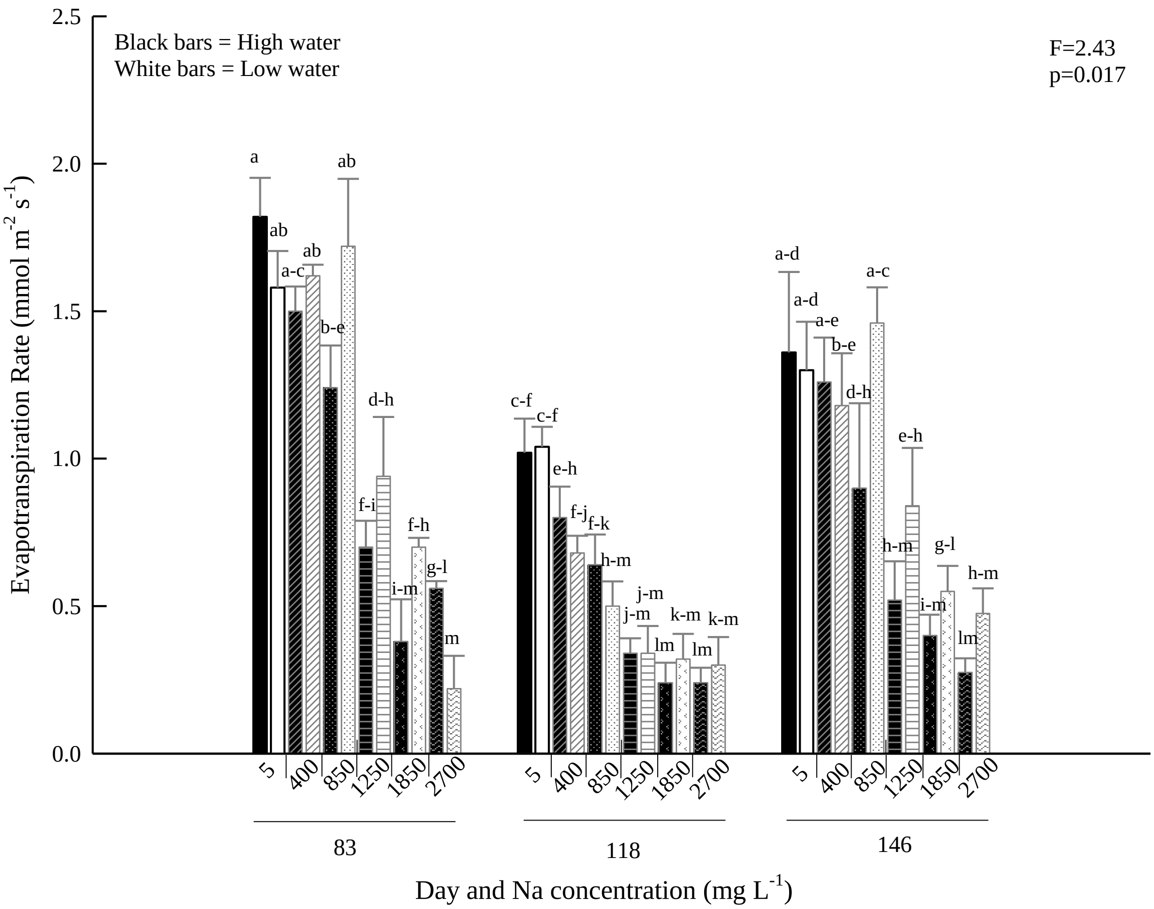


Figure 2



A
F=31.34
p<0.001
Stomatal Conductance (mmol m-2 s-1)
300
250
200
150
100
50
0
a
b
c
83
118
146
Day
B
F=58.08
p<0.001
Photosynthetic Rate (µmol m-2 s-1)
10
8
6
4
2
0
a
b
b
83
118
146
Day
C
F=11.34
p<0.001
Water Use Effiency (mmol CO2 mol-1 H20)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
a
b
83
118
146
Day

Figure 3



Black bars = High water
White bars = Low water
F=2.43
p=0.017
Evapotranspiration Rate (mmol m-2 s-1)
2.5
2.0
1.5
1.0
0.5
0.0
a
ab
a-c
ab
b-e
ab
f-i
d-h
i-m
f-h
g-l
m
c-f
c-f
e-h
f-j
f-k
h-m
j-m
j-m
lm
k-m
lm
k-m
a-d
a-d
a-e
b-e
d-h
a-c
h-m
e-h
i-m
g-l
lm
h-m
5
400
850
1250
1850
2700
83
118
146
Day and Na concentration (mg L-1)

Figure 4