Plant Science xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Tolerance of switchgrass to extreme soil moisture stress: Ecological implications

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ARTICLE INFO

Article history:
Received 28 August 2009
Received in revised form 2 September 2009
Accepted 4 September 2009
Available online xxx

Keywords:
Biofuel
Drought
Flooding
Panicum virgatum
Soil moisture stress

ABSTRACT

Switchgrass (*Panicum virgatum* L.), a native of eastern and central North America, is a leading candidate as a dedicated biofuel feedstock in the US due to its broad adaptability, rapid growth rate, and ability to grow in low production soils. To begin to characterize the important agronomic and ecological traits related to environmental tolerance of switchgrass, we evaluated fitness under stressful growing conditions. We assessed the germination, establishment, performance, and reproductive potential of four common accessions, both upland and lowland ecotypes, at various levels of soil moisture availability (moisture deficit to flooded) in the greenhouse. Seeds emerged and established (55–90% survival) under all soil moisture conditions (−0.3 MPa to flooded). Transplants of lowland ecotypes performed as well in flooded conditions as in field capacity controls, though flooding reduced performance of upland ecotypes. Drought treatments (−4.0 and −11.0 MPa) reduced tiller length and number, leaf area, and biomass production by up to 80%. However, once established, all plants survived at −4.0 MPa and had the same proportion of tillers in flower as at field capacity. The ability of switchgrass to germinate, establish, and flower in low moisture and flooded conditions, particularly lowland ecotypes, may increase the range of environments suitable for biofuel cultivation, and can serve as a baseline for further ecological studies and genetic improvement.

1. Introduction

The United States has set an ambitious goal of integrating biofuels into the nation's energy portfolio, which includes 61 billion liters of non-grain-based liquid fuels by 2022 [1]. It is estimated that 22–61 million hectares of land will be required for cellulosic feedstock cultivation to meet this mandate [2,3], and by 2050 cellulosic biomass will be cultivated on an estimated 1500 million hectares globally [4]. Much of the area for dedicated biofuel production must occur on less productive marginal land, which will require crops with tolerance to stressful conditions [5]. The leading candidates for biofuel crops are perennial rhizomatous grasses which possess the agronomically desirable traits of broad climatic tolerance, rapid growth rates, high yields, growth on low production soils, and few natural enemies [6].

Despite growing interest in using biomass crops for energy production, little is known about the basic biology and physiological ecology of many of these species [2]. Therefore, there exists the need to characterize the physiological and environmental tolerances of each biofuel crop to identify ecosystems most suitable for agronomic production. Additionally, economic viability of these crops may require that genetic modification play a considerable role [5]—making basic physiological studies important baselines for future crop improvement. Once described, these factors can be integrated into risk analysis and bioclimatic, agronomic, and economic models [7], thus leading to safer and more sustainable use of these potentially important crops [2].

To be competitive with conventional energy sources and curb supplantation of food crops, biofuel cultivation will likely be relegated to less productive soils and will require minimal inputs of water, fertilizer, and pesticides [8]. Water availability will be a major limiting factor to cultivating biofuel crops in the midwestern and western US [9], owing to diminishing availability of surface and ground water, and constricting water rights. Biofuel crops are being bred and genetically modified for enhanced abiotic stress tolerance traits (e.g., drought, heat, cold, metal, salt) that will expand the available cultivatable area [5].

Switchgrass (*Panicum virgatum*) is a leading dedicated biofuel feedstock candidate in the US due to its broad adaptability, rapid growth rate, and ability to grow in low production soils [10]. Switchgrass is a warm-season rhizomatous perennial formerly common in the North American tallgrass prairie, with a native range spanning from the Atlantic Coast to the Rocky Mountains, and from northern Mexico to southern Canada, though it is not native to California and other western states [11]. Two distinct ecotypes of this C_4 grass are recognized: lowland tetraploids,

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0168-9452/$ – see front matter © 2009 Published by Elsevier Ireland Ltd.
doi:10.1016/j.plantsci.2009.09.003

primarily from the southern extent of the native range; and upland octaploids, primarily from the mid to northern extent of the native range [10]. The ecotypes tend to occupy different edaphic conditions: upland ecotypes are associated with mesic to xeric environments, while lowland ecotypes are associated with hydric soils and are common in floodplains [12]. Several dozen cultivated varieties of each ecotype are commercially available, most of which are high-yielding selections from native populations [10]. The species includes tremendous variation in performance relative to environmental variables [13], though lowland ecotypes typically produce larger yields than upland ecotypes [10]. Although no studies have examined this in detail, evidence suggests that upland ecotypes would outperform lowland types under low soil moisture availability, and vice versa under excess soil moisture [12,14].

A previous study has demonstrated that much of eastern North America is highly suitable for switchgrass production, though the Mediterranean climate of California is unsuitable without irrigation—both of which are related to available soil moisture (Barney and DiTomaso, unpublished data). Therefore, the objective of this study was to quantify the soil moisture stress tolerance of switchgrass. By evaluating currently available switchgrass cultivars, we are establishing the baseline for tolerance to soil moisture environments, which future genotypes—whether genetically modified or not—can be compared against. In this study, we evaluated fitness and reproductive potential of two cultivars each of the upland and lowland switchgrass ecotypes under soil moisture availability ranging from extreme drought to flooded conditions. In a second experiment we evaluated emergence and establishment potential under these extreme conditions.

2. Materials and methods

To evaluate the soil moisture stress tolerance of currently available switchgrass cultivars we implemented two greenhouse studies. The first experiment was designed to evaluate the tolerance of established plants to soil moisture conditions ranging from extreme drought to flooding. The second experiment was designed to evaluate if seeds introduced to these extreme conditions could germinate and establish.

2.1. Experimental design

We used two common cultivars of each switchgrass ecotype, including the lowland types Alamo (Texas) and Kanlow (Oklahoma), and the upland types Cave-In-Rock (Illinois) and Blackwell (Kansas). Seeds were obtained from commercial vendors or breeders. Both experiments were conducted in a greenhouse at the University of California, Davis, with a 29/18($\pm$2) °C day/night cycle where humidity was allowed to vary and ranged between 18 and 69%. In the transplant experiment, sodium lamps were used to maintain a 14-h photoperiod.

2.1.1. Transplant stress tolerance

Seeds from each cultivar were sown in flats filled with UC mix (50% washed sand, 50% sphagnum peat moss) on 17 January 2008. One seedling was transplanted per 7.6 l pot filled with UC mix 4 weeks after emergence.

Soil moisture treatments were implemented 2 weeks after transplanting, when switchgrass was on average 68.0 $\pm$ 0.8 cm long and had 3.3 $\pm$ 0.1 tillers. Treatments were meant to represent a range of conditions, and not correspond to any specific environment. Treatments were applied in a block design, and are unbalanced due to a planned incremental harvest that was not implemented because of a lack of stress response in some treatments. Soil moisture treatments included flooding (n = 80), drought (n = 47), extreme drought (n = 31), and a stress-free control (n = 49). The control treatment was maintained at field capacity (20–35% moisture v/v, 0.0 MPa) by irrigating each pot with 480 ml water day^{-1}. The flooded treatment was imposed by sealing pot drain holes and irrigating with 480 ml day^{-1}, resulting in standing water 2–5 cm above the soil surface. Drought (5% moisture, −4.2 MPa) was achieved by adding 64 ml day^{-1}. We stopped watering a subsample of the drought treatment pots after 7 weeks to create an extreme drought treatment (3% moisture, −11.0 MPa). Watering rates were determined volumetrically and corresponding soil water potentials were measured using a WP4 Dewpoint Potentiometer (Decagon Devices, Pullman, WA). Pots were irrigated in mid-morning with drip emitters; 2 days fertigation (N:P:K = 236:52:341 ppm) were followed by 1 day of deionized water.

2.1.2. Germination and establishment potential

Following the results of the previous experiment, we were interested in evaluating the moisture conditions under which switchgrass can emerge and establish. Therefore, we included the following four treatments: control (same as above), flooded (same as above), 10% (−0.3 MPa) and 20% (−0.01 MPa) soil moisture treatments.

Seeds of the same four cultivars were sown in plug trays (72 cells, 60 cm^3 each) filled with UC mix and lined with a plastic flat on 3 July 2008. One seed was placed in each cell and covered with 0.5 cm potting media. Trays were arranged in a completely randomized design with 5 replications (each tray equaled 1 experimental unit with 72 subsamples). Control and flood (1 cm standing water above soil line) treatments were sub-irrigated with 750 and 1500 ml four times a day, respectively. Drought treatments were maintained gravimetrically with water additions every other day. There were a total of 4 cultivars with 4 treatments and 5 replications for a total of 80 trays.

2.2. Data collection

2.2.1. Transplant stress tolerance

The experiment was terminated 11 weeks after treatments began, after all cultivars had either flowered or senesced, at which time we recorded the final number of tillers, length (soil surface to the end of the longest leaf on the tallest tiller), and percentage of tillers flowering. Aboveground biomass was cut at the soil surface and separated into shoots and leaves, and leaf area was determined with a LiCor 3100 leaf area meter (LiCor, Lincoln, NE). Roots and rhizomes were washed of media. All plant parts were dried at 70 °C for 10 days and weighed. Presence of rhizomes was recorded, and root-to-shoot ratios (R:S) were calculated. Specific leaf area was calculated as leaf area per unit leaf dry mass (cm^2 g^{-1}).

Gas exchange measurements were performed 1–2 April (4 weeks after treatment initiation) to assess physiological response to soil moisture stress when soil water potential was −1.5 MPa in the drought treatment. Readings were taken only on flooded, control and drought treatments, as the extreme drought treatment had not yet been initiated. Measurements were conducted with a LiCor 6400 open gas exchange system (LiCor, Lincoln, NE) calibrated to deliver saturating light conditions (2000 μmol m^{-2} s^{-1} over 400–700 nm) and ambient CO_2 (380 ppm) with a leaf temperature of 27–30 °C. After equilibration, measurements were collected for 2 min at 5-s intervals on one randomly chosen plant from each treatment listed above in each block (four replications per treatment) on the youngest fully expanded leaf on the longest tiller. Stomatal conductance, transpiration (E), and net CO_2 assimilation (A) were recorded, and photosynthetic water-use efficiency was calculated as A/E.

2.2.2. Germination and establishment potential

Seedling emergence was recorded six times a week for 5 weeks. Establishment was determined as the percentage of emerged

Table 1
Mixed-model ANOVA results (F-values) for nine ecological traits[a] for switchgrass cultivars (Alamo, Kanlow, Blackwell, Cave-In-Rock) grown under moderate drought, extreme drought, flooded conditions, and a control.

Source	Length	Tiller number	Proportion tillers flowering	Leaf area	Specific leaf area	Aboveground biomass	Belowground biomass	Total biomass	R:S
Ecotype (E)	10.7**	3.2	67.3***	1.1	1.4	0.0	0.0	0.0	0.1
Cultivar [E]	16.9***	5.0**	24.1***	2.9	2.3	23.8***	14.3***	23.6***	0.3
Treatment (T)	84.7***	126.1***	9.8***	118.3***	6.8**	146117.9***	9166.5***	214873.5***	139.1***
E × T	1.2	2.5	1.5	3.6*	0.4	3.2*	4.5**	4.5**	1.8

[a] Leaf area and specific leaf area were not analyzed for the extreme drought treatment.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

seedlings that survived. Percent seedling emergence and emergence date were calculated for each flat (experimental unit) as the average of all 72 cells.

2.3. Data analysis

All data (transplant and emergence studies) were analyzed using a mixed-model ANOVA with ecotype, cultivar nested within ecotype, soil moisture treatment, and ecotype–soil moisture interaction as fixed effects and block as a random effect. Dependent variables were checked for normality and homoskedasticity and transformed as necessary. Final leaf length and area were Log_{10} transformed, final tiller number was Log_e transformed, and root:shoot was square root transformed. Aboveground and total biomass were highly heteroskedastic and required a modified z-transformation (S. Steinmaus, personal communication): $[(obs - mean_{trt})/s^2_{trt}] + mean_{trt}$. Main effect means were compared with Tukey HSD tests. Since we were interested in differences between ecotypes under stressful conditions (flood and drought) we performed orthogonal pairwise contrasts between ecotypes within the flood, drought, and extreme drought treatments. We used a protected P-value of $\alpha = 0.05/3 = 0.017$ for ecological traits, and $\alpha = 0.05/2 = 0.025$ for ecophysiological traits, as the extreme drought treatment had not yet been implemented. The presence of rhizomes and inflorescences was assessed using nominal logistic regression with the independent variables as above. All analyses were performed with JMP v7 (SAS, Cary, NC). All means and standard errors are presented as untransformed values.

3. Results

3.1. Transplant stress tolerance

Soil moisture profiles differed only slightly among cultivars, with drought treatments reaching ∼5% moisture (−4.0 MPa), and extreme drought further drying to ∼3% (−11.0 MPa) (data not shown). The stress-free control started at ∼35% moisture and was reduced to between 16 and 22% by the end of the experiment, but with a negligible change in soil water potential (∼0.01 MPa). All cultivars in the flooded treatment required supplemental watering starting 8 weeks after treatment initiation to maintain standing water conditions.

No typical signs of stress (e.g., chlorosis, leaf curling, wilting) were observed in control, flooded, or drought treatments. However, all cultivars under extreme drought experienced leaf senescence and eventual necrosis with no live tissue visible at harvest, though root systems appeared intact.

3.2. Ecological traits

Most ecological traits differed across cultivars (Table 1), with Alamo yielding 45% more total biomass, 30% more leaf area, and 16% longer culms, but 75% fewer flowering tillers than other cultivars across all soil moisture treatments (Fig. 1). Interestingly, only length and proportion of flowering tillers differed between ecotypes (Table 1), with lowland types producing longer culms but fewer flowering tillers (Fig. 1(a) and (d)). All traits varied across moisture treatments (Table 1), with individuals in the flooded treatments typically performing as well as or better than the controls (Figs. 2 and 3). However, individuals in both drought treatments were shorter, with lower leaf area and specific leaf area, and produced fewer tillers and less biomass (Figs. 2 and 3). The root-to-shoot ratio was much higher for switchgrass in the drought treatments compared to the control or flooded treatments (Fig. 3(d)). Interestingly, soil moisture environment had no effect on rhizome production ($\chi^2 = 5.14$, $P = 0.16$), though uplands were 15-fold more likely to flower than lowlands ($\chi^2 = 56.7$, $P < 0.0001$) under a 14-h photoperiod.

As expected, lowland types outperformed upland types in the flood treatment in tiller length, tiller number, leaf area, and biomass (Figs. 2 and 3), but yielded fewer flowering tillers (Fig. 2(d)). Contrary to expectations, uplands did not outperform lowlands under either drought condition for any trait, except for proportion of flowering tillers (Fig. 2(d)).

3.3. Ecophysiological parameters

Only net photosynthetic rate differed among cultivars (Table 2, Fig. 4(a)), with Kanlow 30% higher than all other cultivars. Net

Table 2
Mixed-model ANOVA results (F-values) for four ecophysiological traits for switchgrass cultivars (Alamo, Kanlow, Blackwell, Cave-In-Rock) grown under control, flooded and moderate drought conditions. Data were collected before the extreme drought treatment began.

Source	Net photosynthesis	Stomatal conductance	Transpiration	Photosynthetic water-use-efficiency
Ecotype (E)	4.2*	2.6	0.0	10.9**
Cultivar [E]	4.6*	2.1	1.3	1.4
Treatment (T)	36.7***	20.2***	18.5***	5.9**
E × T	1.0	0.9	2.0	0.7

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

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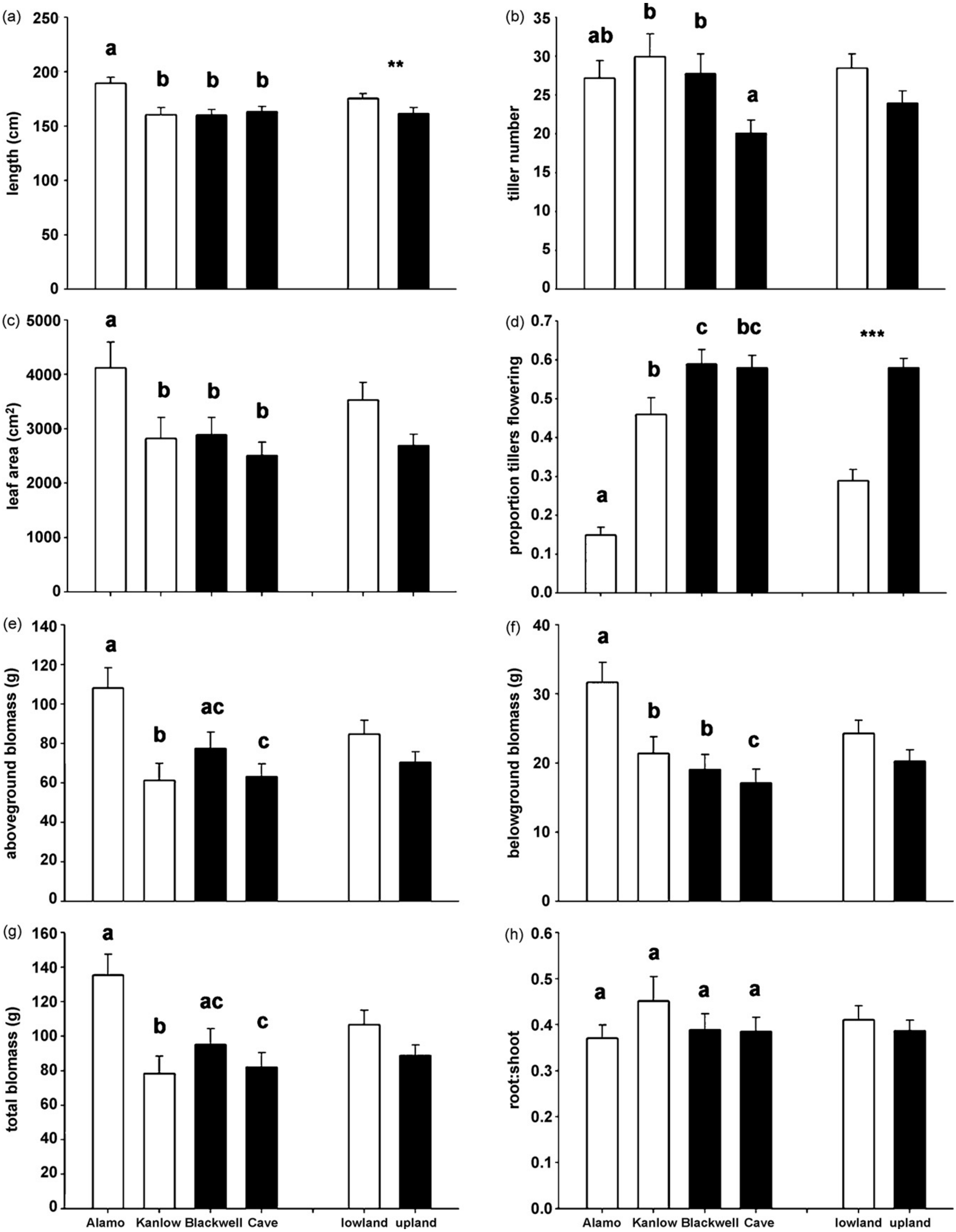

Fig. 1. Cultivar and ecotype means and standard errors for the ecological traits (a) length, (b) tiller number, (c) leaf area, (d) proportion of tillers flowering, (e) aboveground biomass, (f) belowground biomass, (g) total biomass, and (h) root-to-shoot ratio. White bars indicate lowland ecotypes, and black bars represent upland ecotypes. Cultivars
Q1 with different letters are significantly different at $P < 0.05$, and an asterisk represents ecotypic differences ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$).

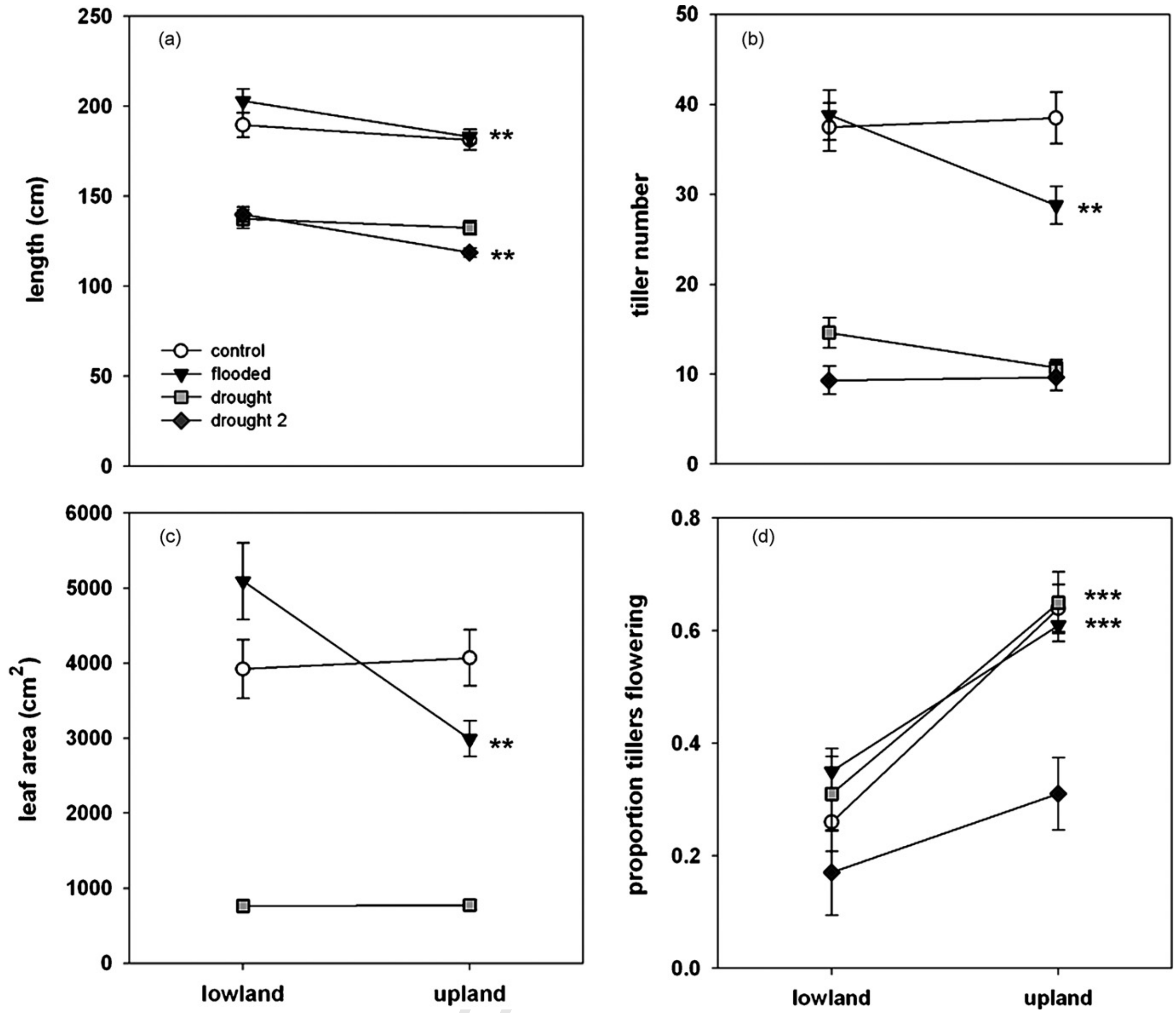

Fig. 2. Final length (a), final tiller number (b), leaf area (c), and proportion of tillers flowering (d) for lowland (Alamo, Kanlow) and upland (Blackwell, Cave-In-Rock) switchgrass under flooded, control, drought (5–10% soil moisture = drought), and extreme drought (<5% soil moisture = drought 2) soil moisture treatments. Leaf area was not calculated for extreme drought treatments due to complete leaf senescence prior to harvest. Reaction norms followed by an asterisk (*) and probability are ecotypically Q2 different ($P < 0.017$) within a treatment. Contrasts were performed for flood, moderate drought, and extreme drought treatments only (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$).

photosynthetic rate and photosynthetic water-use-efficiency were 17 and 34% higher, respectively, in lowland than upland types (Table 2, Fig. 4). No ecotypic differences were observed within drought treatments for any ecophysiological parameter, though lowland types tended to outperform upland types. Surprisingly, neither photosynthetic rate, stomatal conductance, nor transpiration rate was different among lowland and upland types under flooded conditions (Fig. 5(a)–(c)), although photosynthetic water-use-efficiency was higher in lowlands (Fig. 5(d)).

3.4. Germination and establishment potential

Seeds of both ecotypes emerged under all moisture treatments, but seeds in the flooded and 10% moisture treatments took longer to emerge than those in the control ($P < 0.01$; Fig. 6(a)). Percent emergence was reduced 3-fold under flooded conditions, and 10-fold under 10% moisture compared to control conditions ($P < 0.0001$; Fig. 6(b)). Establishment rates were high (>95%) except under 10% moisture where only 55% of emerging plants survived ($P < 0.0001$; Fig. 6(c)).

4. Discussion

Under greenhouse conditions, switchgrass displays broad tolerance to soil moisture conditions. To varying degrees, both lowland and upland ecotypes germinated, established, and flowered under low soil moisture (≤−0.3 MPa) and flooded conditions. Lowland ecotypes outperformed upland ecotypes under flooded conditions for the ecological traits of tiller production and tiller length, leaf area, biomass, and photosynthetic water-use-efficiency. Surprisingly, lowland switchgrass accessions performed as well under flooded conditions as in stress-free control conditions while upland accessions experienced only mild performance reductions, suggesting that switchgrass is a facultative wetland species. However, contrary to our expectations, upland types did not outperform lowland types under the drought conditions imposed in this study. Both lowland and upland types suffered severe reductions (75–80%) in biomass yield, tiller number, and leaf area with water stress at −4 MPa compared to the controls. Based on our results, lowland ecotypes can survive

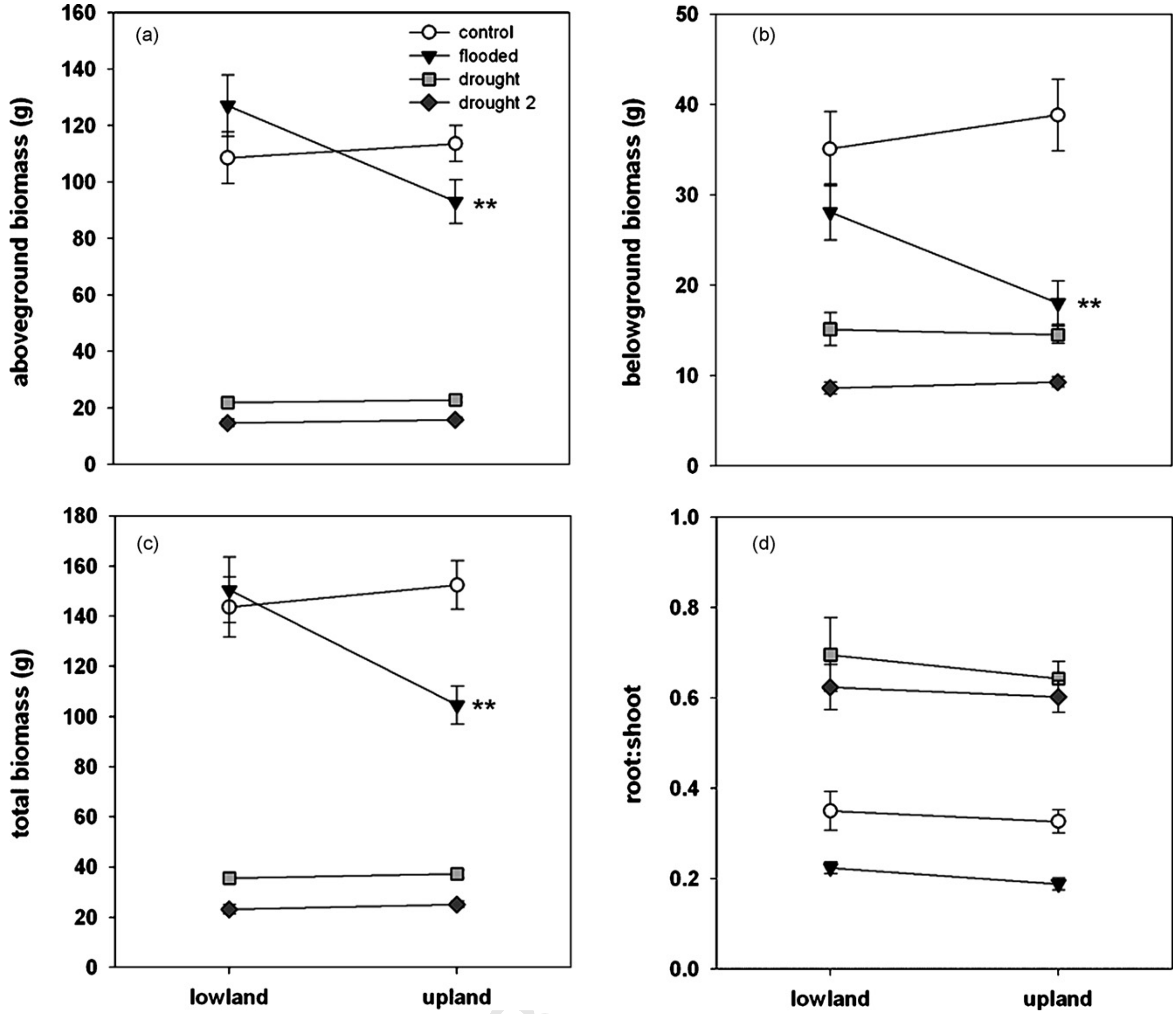

Fig. 3. Aboveground biomass (a), belowground biomass (b), total biomass (c), and root-to-shoot ratio (d) for lowland (Alamo, Kanlow) and upland (Blackwell, Cave-In-Rock) switchgrass under flooded, control, drought (5–10% soil moisture = drought), and extreme drought (<5% soil moisture = drought 2) soil moisture treatments. Reaction norms followed by an asterisk (*) and probability are ecotypically different ($P < 0.017$) within a treatment. Contrasts were performed for flood, moderate drought, and extreme Q3 drought (drought 2) treatments only ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$).

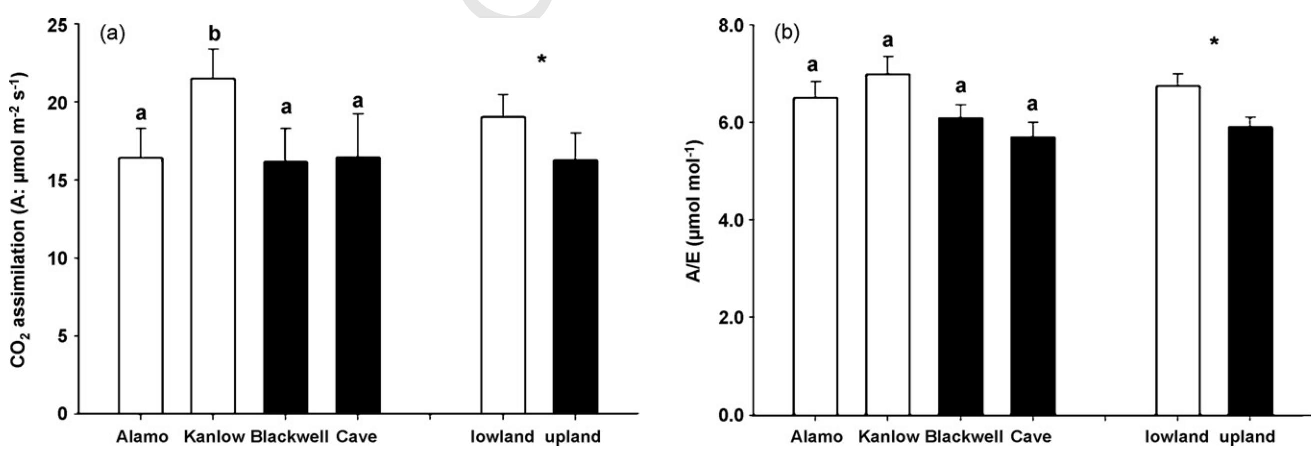

Fig. 4. Cultivar and ecotype means for (a) photosynthetic rate and (b) photosynthetic water-use-efficiency. White bars indicate lowland ecotypes, and black bars represent upland ecotypes. Cultivars with different letters are significantly different at $P < 0.05$, and an asterisk represents ecotypic differences ($^{*}P < 0.05$).

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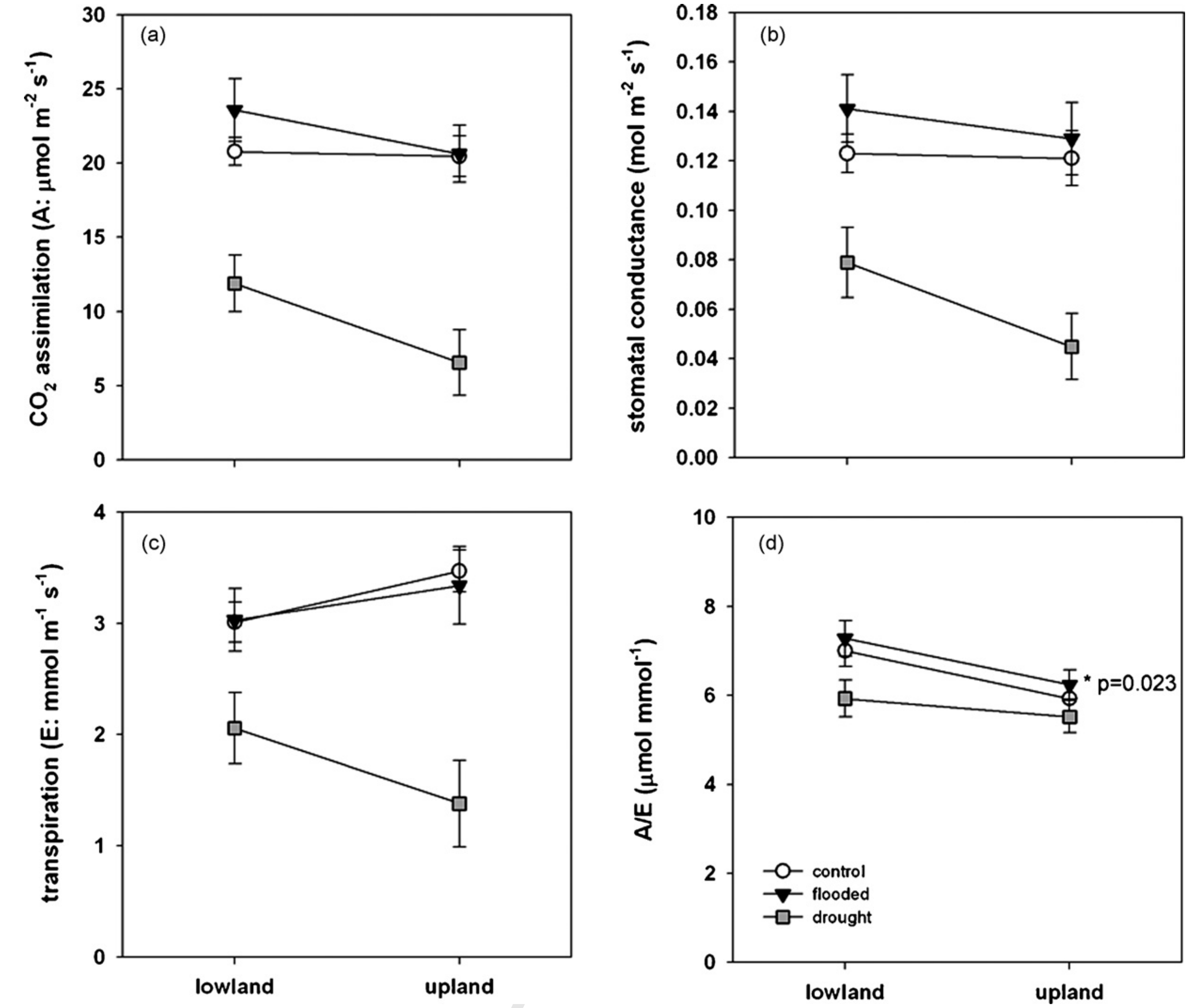

Fig. 5. Net photosynthesis (a), stomatal conductance (b), transpiration (c), and photosynthetic water-use-efficiency (d) for lowland (Alamo, Kanlow) and upland (Blackwell, Cave-In-Rock) switchgrass under flooded, control, and drought (5–10% soil moisture = drought) soil moisture treatments. Data was collected before the extreme drought (drought 2) treatment was imposed. Reaction norms followed by an asterisk (*) and probability are ecotypically different ($P < 0.025$) within a treatment. Contrasts were performed for flood and drought treatments only.

under broad soil moisture conditions, may be productive under a wide range of moisture conditions, and should be candidates for future genetic and agronomic improvement.

Among the abiotic variables regulating habitat suitability for a species, soil moisture availability is critical. Precipitation amount and seasonality will partially determine the regions in which biofuel crops can be profitably cultivated [9]. Soil moisture availability is low during the summer growing season in much of the arid West and Great Plains, which tend to select for more drought tolerant crops. However, our data suggests that ecosystems with high moisture availability throughout the year (e.g., irrigated fields) may be particularly productive.

In addition to being tolerant of dry soils, we found switchgrass to be well adapted to flooded soils, and may actually favor standing water conditions. In a reciprocal transplant experiment, Porter [12] found that lowland ecotypes outperformed upland types under both high and low soil moisture conditions for 14 ecological and morphological traits. In our study, lowland ecotypes produced more aboveground biomass under flooded conditions than under control conditions, while upland ecotypes yielded less aboveground (20%), belowground (55%), and total (30%) biomass (Fig. 3(a)–(c)). In a greenhouse study with switchgrass clones, Porter [12] found that lowland ecotypes produced 40% more total biomass and were 40% taller under flooded conditions as compared to a control, while upland ecotypes yielded 60% less biomass and were 44% shorter under flooded conditions. While agronomically less important than drought stress tolerance, the ability to thrive in flooded soils expands cultivatable lands to those that experience periodic flooding.

In our study, both lowland and upland switchgrass ecotypes had significantly reduced performance, but survived and achieved flowering, at soil water potentials below −4 MPa. Both ecotypes continued producing new tillers and biomass at soil water potentials below −2 MPa (data not shown). Net photosynthetic rate was reduced 50% across switchgrass ecotypes when soil water potentials were −1.5 MPa (soil water potential of drought treatments when measurements were taken). Photosynthetic rates did not differ between flooded and control treatments and were within the range recorded in greenhouse and field trials [17]. Knapp [15] found that when water stress was most severe, switchgrass photosynthesis decreased to near zero but recovered to 30% of maximum following precipitation. A possible survival mechanism for switchgrass in drought conditions may be reallocation of nitrogen from shoot tissue to roots and rhizomes in response to drought stress, which is typical of mesic species of the tallgrass prairie [16]. Contrary to previous findings [17], the

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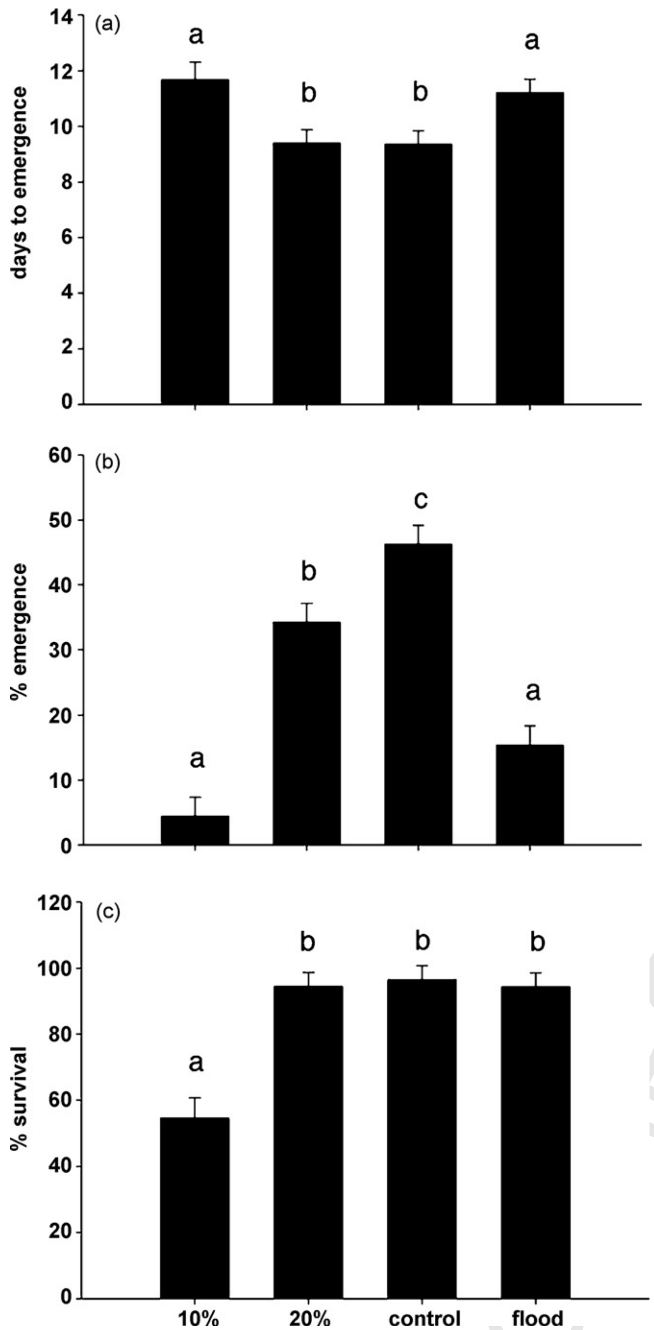

Fig. 6. Days to emergence (a), percent emergence (b), and percent survival of emerged individuals (c) of switchgrass in four soil moisture environments from the germination and establishment study. Means are shown for all four cultivars pooled, and treatments with a different letter are significantly different at $P < 0.05$.

two upland ecotypes tested in our study did not maintain higher photosynthetic rates under drought conditions.

We recorded a photosynthetic water-use-efficiency (A/E) of $\sim$6 μmol mmol^{-1} under moisture stress, which is within the range found *in situ* (5.8–6.8 μmol mmol^{-1}) following a stress period that reduced soil moisture to a 20% deficit [18]. In our study, photosynthetic water-use-efficiency differed little among soil moisture treatments (Fig. 4(b)). Under moisture deficit conditions, switchgrass lowered transpiration rates and stomatal conductance (Fig. 5(b) and (c)). Switchgrass leaves may adjust osmotically to deal with low soil moisture potentials [15,19]. In our study, no ecotypic differences were found for stomatal conductance within any treatment despite inherent soil moisture preferences. Both ecotypes experienced reduced aboveground (5.5-fold) and belowground (2.5-fold) biomass production under drought stress compared to those in control treatments, though drought individuals had root-to-shoot ratios 2–3-fold higher (Fig. 3(d)). Our results suggest that despite a dramatic decrease in biomass and tiller production, currently available switchgrass cultivars can survive in environments with very low soil moisture availability once established. However, these reductions will likely preclude a sustainable biomass crop in arid regions (e.g., California) without supplemental irrigation. Further breeding and genetic modification may be viable options for future cultivation in arid regions.

Surprisingly, some switchgrass seeds germinated and emerged under all moisture conditions imposed in our study, from −0.3 MPa (10% moisture) to under water (flooded). In our study, 55% of the emerged seedlings survived at −0.3 MPa, which is 2.5% of all seeds and 5% of germinable seeds (55% were dormant or dead). Switchgrass seed production in biofuel crop field trials has been estimated between 300 and 900 kg ha^{-1}, with a mean seed weight of 100 mg per 100 seeds [20–22], resulting in 300–900 million seeds ha^{-1}. A conservative estimate of 300 million seeds ha^{-1} and 60% dormancy results in 3 million seeds ha^{-1} able to germinate in mesic soils (≥ -0.3 MPa), and 18 million seeds ha^{-1} able to establish in flooded soils. However, demographic studies of perennial tallgrass prairie species suggest that seedling recruitment comprises <1% of annual extant shoots [23], with the remaining seed crop entering the seed bank.

5. Conclusions

Switchgrass demonstrates broad tolerance to soil moisture availability by germinating, establishing, and reproducing under both moisture deficit and flooded conditions. Environmental variability throughout its vast native range has likely led to this adaptive tolerance, which appears greater in current cultivars than in wild-types of a few generations ago [12]. However, there may be a fitness trade-off for broad environmental tolerance (e.g., reduced competitive ability), as switchgrass is often difficult to establish in weedy agronomic fields [10]. The current experiments do not directly address competition in field environments, which will influence the ability to establish in minimally managed environments regardless of soil moisture stress tolerance, as well as influencing the economics of production fields (i.e., increased competitive ability would decrease herbicide use). More studies are necessary to evaluate tolerance to other environmental variables (e.g., disturbance) and their interactions with competitive ability.

Acknowledgements

We would like to thank Charlie Campbell, Nicholas Eattock, Carlos Figuero, Jacinta Gimeno, and Salil Saxena for help with planting, collecting data, and harvesting. This work was supported by University of California Discovery grant GCP06-10233.

References

[1] United States Congress, Energy Independence and Security Act. Publ. 110–140, 2007.
[2] G.P. Robertson, et al., Sustainable biofuels redux, Science 322 (2008) 49–50.
[3] R.D. Perlack, et al., Biomass as Feedstock for a Bioenergy and Bioproducts Industry: The Technical Feasibility of a Billion-Ton Annual Supply, Oak Ridge National Laboratory, Oak Ridge, TN, 2005, p. 78.
[4] C.B. Field, J.E. Campbell, D.B. Lobell, Biomass energy: the scale of the potential resource, Trends Ecol. Evol. 23 (2008) 65–72.
[5] S.M. Chapotin, J.D. Wolt, Genetically modified crops for the bioeconomy: meeting public and regulatory expectations, Transgenic Res. 16 (2007) 675–688.
[6] I. Lewandowski, et al., The development and current status of perennial rhizomatous grasses as energy crops in the US and Europe, Biomass Bioenergy 25 (2003) 335–361.

Please cite this article in press as: J.N. Barney, et al., Tolerance of switchgrass to extreme soil moisture stress: Ecological implications, Plant Sci. (2009), doi:10.1016/j.plantsci.2009.09.003

[7] J.N. Barney, J.M. DiTomaso, Nonnative species and bioenergy: are we cultivating the next invader? BioScience 58 (2008) 64–70.
[8] The Royal Society, Sustainable Biofuels: Prospects and Challenges, London, 2008, p. 90.
[9] J.L. Schnoor, et al., Water Implications of Biofuels Production in the United States, The National Academies Press, Washington, DC, 2008, p. 86.
[10] D.J. Parrish, J.H. Fike, The biology and agronomy of switchgrass for biofuels, Crit. Rev. Plant Sci. 24 (2005) 423–459.
[11] Flora of North America Editorial Committee, Flora of North America North of Mexico, Flora of North America Editorial Committee, vol. 12+, New York/Oxford, 1993+.
[12] C.L. Porter, An analysis of variance between upland and lowland switchgrass, *Panicum virgatum* L., in central Oklahoma, Ecology 47 (1966) 980–992.
[13] M.D. Casler, A. Boe, Cultivar × environment interactions in switchgrass, Crop Sci. 43 (2003) 2226–2233.
[14] J.A. Stroup, et al., Comparison of growth and performance in upland and lowland switchgrass types to water and nitrogen stress, Bioresour. Technol. 86 (2003) 65–72.
[15] A.K. Knapp, Water relations and growth of three grasses during wet and drought years in a tallgrass prairie, Oecologia 65 (1984) 35–43.
[16] S.A. Heckathorn, E.H. DeLucia, Drought-induced nitrogen retranslocation in perennial C_4 grasses of tallgrass prairie, Ecology 75 (1994) 1877–1886.
[17] S.D. Wullschleger, et al., Photosynthetic rates and ploidy levels among populations of switchgrass, Crop Sci. 36 (1996) 306–312.
[18] A.K. Knapp, Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie, Ecology 66 (1985) 1309–1320.
[19] D.J. Barker, C.Y. Sullivan, L.E. Moser, Water deficit effects on osmotic potential, cell wall elasticity, and proline in five forage grasses, Agron. J. 85 (1993) 270–275.
[20] A. Boe, Variation between two switchgrass cultivars for components of vegetative and seed biomass, Crop Sci. 47 (2007) 636–642.
[21] M.A. Sanderson, et al., Switchgrass and big bluestem hay, biomass, and seed yield response to fire and glyphosate treatment, Agron. J. 96 (2004) 1688–1692.
[22] P.C. Kassel, R.E. Mullen, T.B. Bailey, Seed yield of three switchgrass cultivars for different management practices, Agron. J. 77 (1985) 214–218.
[23] E.J. Bensen, D.C. Hartnett, The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie, Plant Ecol. 187 (2006) 163–177.