The Competitive Response of *Panicum virgatum* Cultivars to Non-Native Invasive Species

Lauren M. Schwartz[1] & David J. Gibson[1]

[1] Department of Plant Biology and Center for Ecology, Southern Illinois University Carbondale, Carbondale, Illinois, USA

Correspondence: Lauren M. Schwartz, Department of Plant Biology and Center for Ecology, Southern Illinois University Carbondale, Carbondale, IL 62901-6509, USA. Tel: 1-618-453-3231. E-mail: lschwartz@siu.edu

Abstract

It is important to use the most appropriate plant cultivar in restoration or biofuel trials especially when plantings are likely to be invaded by undesirable species. In this study, the competitive response of two lowland and three upland cultivars of the dominant C_4 grass *Panicum virgatum* to three invasive species (*Bromus inermis, Schedonorus phoenix,* and *Poa pratensis*) was tested using a simple pair-wise greenhouse experiment. Response variables (height, number of leaves, tiller density, and biomass of *P. virgatum*) and resources (soil moisture and light intensity) were measured over a seven-month period. Performance of the different *P. virgatum* cultivars were differentially reduced by the three invasive species, especially the performance of the Kanlow (lowland) and Blackwell (upland) cultivars. Low soil moisture reduced the performance of *P. virgatum* in the presence of only one invasive (*Bromus inermis*) irrespective of cultivar source. Root, shoot, and total biomass depended on cultivar and did not show an interaction with invasive species identity. The results of this greenhouse study suggest that the *P. virgatum* cultivars differentially responded to the invasive species and that the cultivar used should be considered carefully in planning prairie restorations or biofuel trials in the context of likely invasive species.

Keywords: *Panicum virgatum*, invasive species, competition

1. Introduction

Non-native invasive species in North American tallgrass prairies have large ecological impacts (Nemec, Allen, Helzer, & Wedin, 2013). These invasive species can quickly evolve in areas of disturbance through founder effects and hybridization by responding to selection pressures in the environment (Mealor & Hild, 2006). Tallgrass prairies are vulnerable to invasive species because 90% of invaders are C_3 grasses (A. C. Cully, J. F. Cully, & Hiebert, 2003). This is in contrast with the dominant prairie biomass, which is composed predominantly of C_4 grasses. To help gain this advantage, invasive C_3 species may use available resources before C_4 species establish in assembling communities such as restoration or warm-season grass plantings (Culley et al., 2003). Invasive species in tallgrass prairies can alter soil chemistry, increase soil erosion, reduce forage and biofuel quality and wildlife populations, and fragment plant populations (Melor & Hild, 2006). These species may spread with global climate change and in return this will cause a decrease in native species diversity (Maron & Marler, 2007). Resource availability is also important to the habitat of the invasive species (Seabloom, Harpole, Reichman, & Tilman, 2003). Communities within the tallgrass prairie with high species richness may be more resistant to invasive species than species-poor communities (Culley et al., 2003). Therefore, low-diversity restorations or plantings may be particularly susceptible to invasive species and an understanding of the competitive response of native C_4 species to individual invasive species will help practitioners.

Switchgrass (*Panicum virgatum* L.) is a perennial, warm season C_4 grass occurring as many ecotypes that can dominate mesic tallgrass prairies in the Great Plains of North America (Parrish & Fike, 2005). Ecologically, *P. virgatum* determines the structure and function of the North American tallgrass prairie. *Panicum virgatum* is photoperiod sensitive, and flowering is related to latitude, where northern ecotypes flower earlier than southern ecotypes (Lemus et al., 2002). Soil type has little effect on the development or morphology of *P. virgatum* (Parrish & Fike, 2005; Porter, 1966). There is also considerable genotypic and phenotypic variation within the species. The variability within this species can be attributed to ecotypic adaptation across a large geographical

and environmental range (Hartman, Nippert, Orozco, & Springer, 2011). *Panicum virgatum* has considerable economic value as commercial cultivars have been developed from the native ecotypes and are widely planted for forage and hay, soil stabilization, wildlife habitat, and biofuel. Cultivars are generally divided into upland and lowland categories and within the last few decades, *P. virgatum* has been identified as an important biofuel crop (Vogel, 1996; Berdahl et al., 2005; Wang, Lebauer, & Dietze, 2010). Understanding the response of *P. virgatum* cultivars to invasives is important in these settings.

Typically, upland cultivars of *Panicum virgatum* are associated with higher, mesic sites and lowland cultivars are associated with lower, wetter locations (Porter, 1966). Morphologically, upland cultivars are typically shorter, rhizomatous and have finer, thinner stems than lowland cultivars (Lemus et al., 2002). Upland cultivars tend to favor drier soils and are more susceptible to disease than lowland cultivars (Lemus et al., 2002). Lowland cultivars are vigorous, thick-stemmed, coarser, and can grow up to one meter taller than upland cultivars (Lemus et al., 2002). Compared with upland cultivars, lowland cultivars tend to grow better in wetter and denser soil (Porter, 1966). Upland cultivars grew best in more moderate moisture conditions (Porter, 1966). Upland and lowland cultivars vary in their nitrogen requirements. The lowland cultivars require less nitrogen than the upland cultivars (Porter, 1966). There are multiple ploidy levels among *P. virgatum* cultivars and ecotypes. Upland cultivars are hexaploids or octoploids and lowland cultivars are tetraploids (Parrish & Fike, 2005; Porter, 1966).

The study aimed to determine whether native *P. virgatum* cultivars would grow and establish differently in the presence of non-native invasive species and to compare their ecological habitats. Specifically, the objective was to determine the competitive response of *P. virgatum* cultivars to non-native invasive species and to describe their responses in relation to non-native invasive species.

2. Methods

2.1 Study Species

The competitive response to invasive grasses of three upland cultivars (Blackwell, Cave in Rock and Trailblazer) and two lowland cultivars (Alamo and Kanlow) of *Panicum virgatum* were tested. The three upland cultivars are octoploid and the two lowland cultivars are tetraploid (Elbersen et al., 2001). Blackwell originated from Northern Oklahoma and is a disease resistant variety that produces vigorous stems and roots (Elbersen et al., 2001). Cave in Rock, originally from Southern Illinois, is palatable and disease resistant. This cultivar grows best in years of average rainfall and temperature and can reach an average of 3 m in height. Trailblazer is an upland cultivar from Nebraska (Elbersen et al., 2001) that is winter hardy, late maturing and has a high seed production (Elbersen et al., 2001). Alamo was developed in Texas and is a coarse-grained cultivar that matures late allowing for production into early fall (Parrish & Fike, 2005). Kanlow, originally from Kansas, is suitable for growth in the southern 2/3rds of the United States and is especially well suited for poorly drained soils (Elbersen et al., 2001). Alamo and Kanlow produced more biomass than Blackwell, Cave in Rock, and Trailblazer in a 2000-2001 study by Lemus et al. (2002).

Three invasive species were tested, i.e., *Poa pratensis* L., *Bromus inermis* L., *Schedonorus phoenix* (Scop.) Holub (syn. *S. arundinaceus* (Schreb.) Dumort.), *Festuca arundinaceae* (Schreb.). These three species are all on a top ten list of prairie invaders (Culley et al., 2003) and are all cool season, C_3 perennial, rhizomatous grasses (Kaufman & Kaufman, 2007). *Poa pratensis* is native to Europe and northern Asia (Duble, 2000) and is used for erosion control, forage, recreation, wildlife cover, and as an ornamental (Huff, 2001; Shortell, Meyer, & Bonos, 2009). *Poa pratensis* is found throughout North America except in the southwest (Duble, 2000). *Bromus inermis* is native to Europe and Asia and was introduced to North America in 1884 (Peeters, 2004; Roberts & Kallenbackh, 2000). It is used for erosion control, wildlife cover, hay, silage and forage (Fink & Wilson, 2011). *Bromus inermis* can be grown on a variety of soils and is found all over the United States and southern Canada (Kaufman & Kaufman, 2007). This species is also drought resistant (Davis, Grime, & Thompson, 2000). *Schedonorus phoenix* is native to Europe and North Africa and was introduced to North America in the late 1800s (Burns, Fisher, & Pond, 2011). It is well adapted to humid, temperate areas (Burns et al., 2011) and can be found in all of the United States, except Florida, Georgia and Alabama, as well as Canada and Europe (Kaufman & Kaufman, 2007; U.S. Department of Agriculture, 1948). *Schedonorus phoenix* is especially well adapted to rough ground and a variety of soil types (Gibson & Newman, 2001). The preferred habitat is along open riverbanks, roadsides, edges of fields, prairies, and pastures (Kaufman & Kaufman, 2007). *Schedonorus phoenix* is used primarily for forage, silage and hay (Gibson & Newman, 2001).

2.2 Experimental Design and Growth Conditions

A greenhouse experiment was established using a simple pairwise competion design (Gibson et al., 1999) with a randomized complete block design with repeated measures. The treatment design was a fully factorial

combination of five *P. virgatum* cultivars and a cultivar mixture (Alamo, Kanlow, Blackwell, Cave in Rock, Trailblazer, and a mixture of the cultivars), three invasive species (control [no invasives], *Poa pratensis* [local variety unknown, Belville Seed House, Inc.], *Bromus inermis* 'Lincoln', and *Schedonorus phoenix* 'KY 31'), and a moisture treatment (high and low), were established in three blocks. There were three replicates of each treatment combination for a total of $6 \times 4 \times 2 \times 3 = 144$ pots.

Plants were grown from seed in the Horticulture Research Center greenhouse (HRC) at Southern Illinois University Carbondale (SIUC) beginning in the summer of 2010. Seeds were planted in 15.2 cm diameter by 15.2 cm deep plastic pots filled with a 1:1 ratio of sand and silt-clay loam soil that was collected from the Southern Illinois University Carbondale Agronomy Center. The soil was sieved before use to remove rocks and other debris. Twenty seeds of a cultivar and twenty seeds of one of the invasive species were sown together in a grid system for a total of forty seeds per pot (seeding rates were adjusted as needed based on preliminary germination data). The pots were sterilized before use. After sowing, the pots were placed under a mister for two weeks. The pots were misted for 8-10 seconds every 12 minutes for 13 hours a day. Once seedlings had established, the pots were moved to a different wing of the same greenhouse. Upon emergence the twenty seedlings was thinned down to ten cultivar seedlings and ten invasive species seedlings per pot. Each of the five cultivars and a mixture of the five cultivars (n = 6 for cultivar treatment) were either planted as a monoculture (control) or with one of the three invasive species individually (n = 4 for invasive species treatment). The cultivar mixture was planted in a grid so that each cultivar could be tracked. Control pots were sown with twenty seeds of a *P. virgatum* cultivar that were thinned down to ten seedlings following emergence with no invasive species seeded.

The experiment also tested the competiveness between the five cultivars under differing resource conditions: i.e., high moisture and low moisture. These conditions were chosen because the sites of origin of the *P. virgatum* cultivars vary in precipitation. The low moisture treatment was watered to field capacity twice every week and the high moisture treatment was watered to field capacity every five days using potable greenhouse water. Water treatments began August 3, 2010. Pots were fertilized twice (July 20, 2010 at 400 mg g^{-1} N and February 2, 2011 at 200 mg g^{-1} N) with a 20-10-20 (NPK) Peters Water Soluble Fertilizer (JR Peters Inc., Allentown, Pennsylvania).

2.3 Data Collection

Number of vegetative tillers, number of leaves, and height of the *P. virgatum* cultivars was recorded on the plants in each pot. Measurements were recorded on three separate occasions (days 39, 166 and 213 of the experiment). The number of leaves and height of the *P. virgatum* cultivars were only analyzed for the first two dates of collection. Soil moisture was recorded for each pot eleven times with an ECH$_2$0 Decagon Soil Moisture meter (Decagon Devices, Inc., Pullman, Washington), which were collected on days 3, 19, 30, 43, 58, 70, 84, 98, 118, 136 and 157 of the experiment. Light intensity at the soil surface was recorded using a LI-COR Light Meter (Model LI-250, LiCOR, Lincoln, Nebraska) eleven times (days 3, 19, 30, 43, 58, 70, 84, 98, 118, 136 and 157 of the experiment). Biomass of both the cultivars and of the non-native invasive species was measured at the end of the experiment after 213 days (collected March 4-5, 2011; days 214-215 of the experiment). The roots and shoots were harvested separately, dried for at least 48 hr at 55 °C and weighed.

The soil in the pots at the time of biomass harvest was tested for soil pH and conductivity on April 28-29, 2011. A 1:2 (15 grams of soil: 30 mL of deionized water) ratio of soil to deionized water was placed into 125 mL Pyrex Erlenmeyer flasks. The flasks were hand shaken and allowed to stand for 30 minutes. After 30 minutes, the flasks were covered with one square of Parafilm and placed on a New Brunswick Scientific Innova 2000 platform shaker for 30 minutes at 250 rpms (Robertson, Coleman, Bledsoe, & Sollins, 1999). Once a slurry was attained, conductivity was tested with an EcoSense, EC 300 conductivity meter. Soil pH was tested on the same samples after conductivity was tested with a Fisher Scientific Accument, AP62 pH meter. The pH meter was calibrated before use with three Fisher Scientific buffer solutions (pH 4.00, pH 7.00 and pH 10.00). In between each test, the conductivity or pH meter probe was dipped into deionized water and wiped with a Kimberly Clark Professional kimwipe. Samples were not allowed to settle.

2.4 Data Analysis

Data were analyzed using a repeated measures mixed model in SAS (PROC MIXED, SAS Institute, 2003) to determine if there were significant differences in the performance (mean tiller density, leaf number, plant height per pot) of *P. virgatum*, soil moisture and light intensity between cultivar (6 treatment levels), invasive species (4 treatment levels) and soil moisture (2 treatment levels) treatments or their interaction. The repeated measure was the number of days from the start of the experiment that a measurement was taken. The three groups in which the

pots were placed on the greenhouse bench were included as random effects (blocks) in the model. Biomass, soil pH and soil electrical conductivity was analyzed using a three-way mixed model. Significance was assessed at $P < 0.05$. A *post-hoc* Tukey's test was used to determine significant differences among means.

3. Results

Vegetative tiller number per plant of *P. virgatum* cultivars was related to the interaction between cultivar and day (Table 1, Figure 1). After an initial period of growth, tiller number decreased in both the lowland cultivars and the upland cultivars from day 166 to day 213. The highest tiller number was found in Cave in Rock on day 39. The mixture of cultivars had the highest number of tillers per plant on day 213. There was a marginally significant interaction between invasive species and day (Figure 2). The number of tillers per plant of *P. virgatum* was lowest when planted with *B. inermis* on day 39 and 166; but by day 213, differences in the number of tillers per plant of *P. virgatum* did not differ in response to the invasive species. On day 39, there were fewer tillers of *P. virgatum* associated with *B. inermis* than compared with in the monoculture controls, or with *S. phoenix* and with *P. pratensis* on day 166. All *P. virgatum* plants had died in the pots planted with *B. inermis* by day 213 of the experiment. There were no data for reproductive tiller number because *P. virgatum* did not flower over the course of the experiment. There was a significant difference in root biomass, belowground biomass of *P. virgatum* cultivars, and the total belowground biomass only among *P. virgatum* cultivars. The highest belowground biomass of *P. virgatum* was in the cultivar mixture (Table 2, Figure 3). The highest aboveground biomass was found in Blackwell, Trailblazer, and the cultivar mixture (Figure 4). Cave in Rock had the lowest aboveground biomass out of the five cultivars.

Table 1. F statistics from mixed model analysis conducted on height, number of leaves, and tiller number of *Panicum virgatum* plants in response to the effects of *P. virgatum* cultivars (CV), invasive species (INV), and soil moisture (Moist) treatments over time (DAY). Subscripts represent the denominator of the degrees of freedom (DF)

Effect	Num. DF (Ht and No. Lvs)	Num. DF (Tiller)	Height	No. of Leaves	Tiller number per plant
Cultivar (CV)	5	5	$95.41_{83.5}^{***}$	$0.44_{83.2}^{+}$	26.79_{94}^{***}
Moisture (Moist)	1	1	$63.84_{83.5}^{***}$	$1.14_{83.5}^{+}$	14.41_{94}^{**}
CV*Moist	5	5	$7.21_{83.6}^{***}$	$0.32_{83.2}^{+}$	0.77_{94}^{+}
Invasive (INV)	3	3	$1.56_{83.6}^{+}$	$0.49_{83.5}^{+}$	3.99_{94}^{*}
CV*INV	15	15	$1.55_{83.5}^{+}$	$1.01_{83.2}^{+}$	0.48_{94}^{+}
Moist*INV	3	3	$1.99_{83.5}^{+}$	$2.54_{83.5}^{+}$	0.75_{94}^{+}
CV*Moist*INV	15	15	$0.99_{83.4}^{+}$	$1.17_{83.2}^{+}$	0.86_{94}^{+}
DAY	1	2	$10.01_{79.2}^{**}$	$7.24_{79.6}^{**}$	506.24_{192}^{***}
CV*DAY	5	10	16.76_{79}^{***}	$0.98_{79.2}^{+}$	14.61_{192}^{***}
Moist*DAY	1	2	$0.76_{79.2}^{+}$	$7.99_{79.6}^{**}$	8.27_{192}^{**}
CV*Moist*DAY	5	10	6.46_{79}^{***}	$0.57_{79.2}^{+}$	1.35_{192}^{+}
INV*DAY	3	6	$3.41_{79.2}^{*}$	$0.23_{79.5}^{+}$	1.93_{192}^{+}
CV*INV*DAY	15	30	$2.16_{78.9}^{**}$	0.85_{79}^{+}	0.70_{192}^{+}
Moist*INV*DAY	3	6	$0.36_{79.2}^{+}$	$0.63_{79.5}^{+}$	0.42_{192}^{+}
CV*Moist*INV*DAY	15	30	$0.88_{78.9}^{+}$	0.73_{79}^{+}	0.79_{192}^{+}

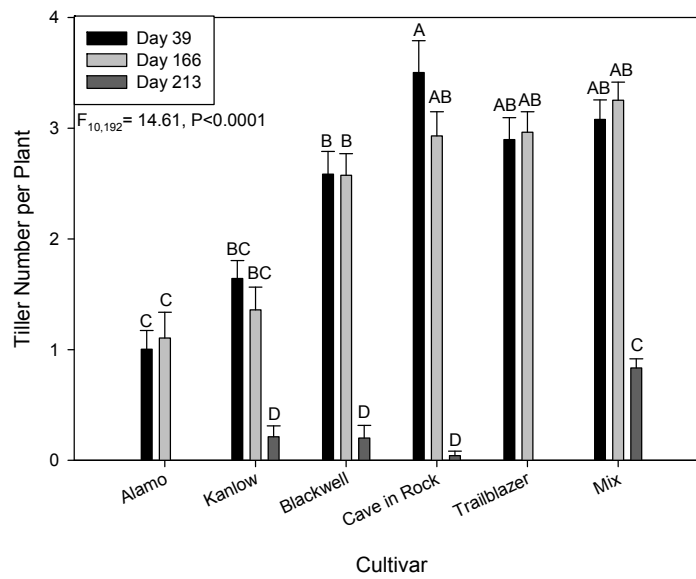* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; Marginal significance: $^{+}P < 0.1$.

Figure 1. Mean (± se) total tiller number per plant of *P. virgatum* cultivars and a mix of *P. virgatum* cultivars over three sampling dates. Mean values with the same letters are not significantly different at $\alpha = 0.05$

Table 2. F statistics from mixed model analysis conducted on aboveground, belowground, and total aboveground biomass of *Panicum virgatum* plants in response to the effects of *P. virgatum* cultivars (CV), invasive species (INV), and soil moisture (Moist) treatments. Subscripts represent the denominator of the degrees of freedom (DF)

Effect	Num. DF	Aboveground Biomass	Belowground Biomass	Total Aboveground Biomass
Cultivar (CV)	5	$3.05_{94.1}{}^{*}$	$3.39_{94}{}^{**}$	$2.65_{96}{}^{*}$
Moisture (Moist)	1	$0.25_{94.1}{}^{+}$	$0.11_{94}{}^{+}$	$0.04_{96}{}^{+}$
CV*Moist	5	$0.93_{94.1}{}^{+}$	$0.97_{94}{}^{+}$	$0.88_{96}{}^{+}$
Invasive (INV)	3	$0.14_{94.1}{}^{+}$	$1.34_{94}{}^{+}$	$16.18_{96}{}^{***}$
CV*INV	15	$1.24_{94.1}{}^{+}$	$1.33_{94}{}^{+}$	$1.04_{96}{}^{+}$
Moist*INV	3	$0.29_{94.1}{}^{+}$	$1.42_{94}{}^{+}$	$0.08_{96}{}^{+}$
CV*Moist*INV	15	$1.19_{94.1}{}^{+}$	$1.06_{94}{}^{+}$	$1.46_{96}{}^{+}$

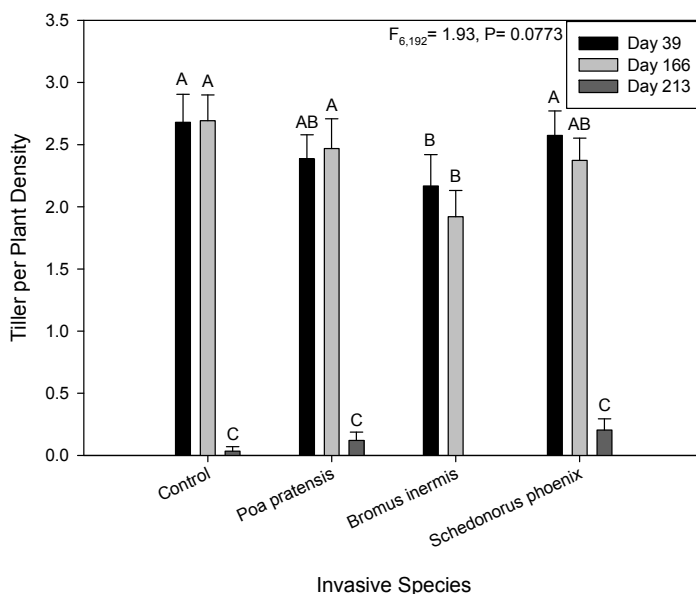* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; Marginal significance: $^{+}P < 0.1$.

Figure 2. Mean (± se) total tiller number per plant of the *P. virgatum* cultivars in response to the three invasive species or no invasive species (control) over three sampling dates. Mean values with the same letters are not significantly different at $\alpha = 0.05$
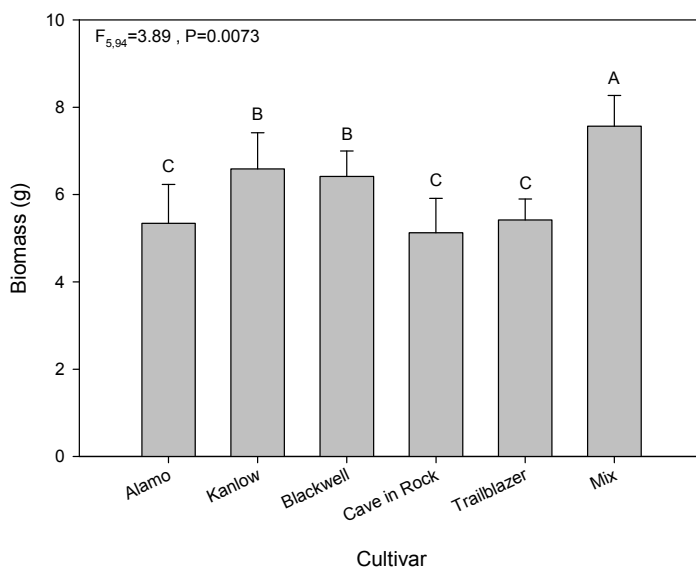

Figure 3. Mean (± se) total belowground biomass of *P. virgatum* and invasive species in response to planted cultivar. Mean values with the same letters are not significantly different at $\alpha = 0.05$
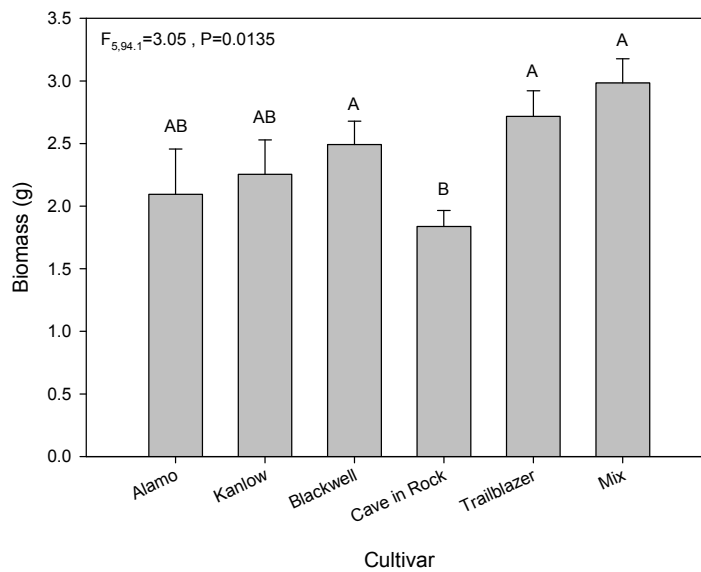
Figure 4. Mean (± se) aboveground biomass of *P. virgatum* cultivars. Mean values with the same letters are not significantly different at $\alpha = 0.05$

There was a highly significant difference in height (P < 0.0001) among cultivars, especially Kanlow, Cave in Rock, Trailblazer, and the cultivar mixture over days 39 and 166 (Table 1). There was also a three-way interaction between day, cultivar, and invasive species affecting the mean height of *P. virgatum* between cultivars and invasive species that showed two main patterns. Kanlow on day 39 was shorter than the upland cultivars in the presence of invasive species, but was taller with the presence of *P. pratensis* on day 166. Blackwell, however, showed the opposite pattern to Kanlow; on day 39, the cultivar grew taller with *S. phoenix* than with the other two invasive species, but by day 166 this difference was lost. Cave in Rock, on day 39, was tallest with *S. phoenix* and remained the same on day 166. The cultivar mix showed similar results as Kanlow, i.e., there was a reduced height in the presence of an invasive species. Leaf number of *P. pratensis* and *S. phoenix* were individually affected by the moisture treatment (Table 1). *Schendonorus phoenix* showed a significant difference in performance among moisture treatments; whereas *P. pratensis* did not. The height of *P. pratensis* was not significantly different among *P. virgatum* cultivars; however, the height of *S. phoenix* was shorter in the presence of a cultivar compared with when grown in the cultivar mix.

There was a significant interaction between cultivar and soil moisture treatment affecting soil moisture (Figure 5). In both low and high moisture treatment levels, the soil in the pots with the lowland cultivars (Alamo and Kanlow) had low soil moisture levels; whereas, the soil in the pots with the upland cultivars (Blackwell, Cave in Rock, and Trailblazer) and the cultivar mixture had significantly higher levels of soil moisture.
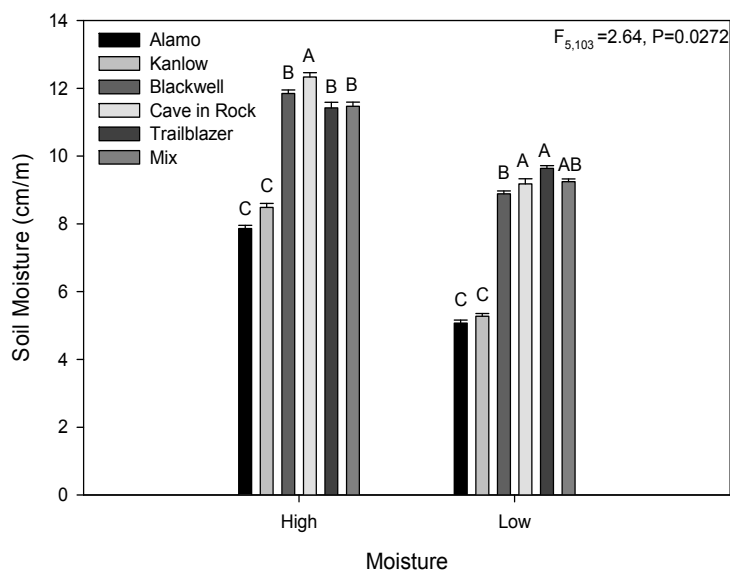
Figure 5. Mean (± se) soil moisture in response to cultivar under high and low moisture treatments. Mean values with the same letters are not significantly different at α = 0.05 within a soil moisture treatment

Soil electrical conductivity (EC) showed no interaction among treatments, but did show highly significant separate effects of both the *P. virgatum* cultivars and invasive species (Table 3). Among the *P. virgatum* cultivars, Trailblazer (upland) had the highest mean EC (83.83 ± 0.35 mS/m); whereas, both lowland species (Alamo = 80.60 ± 0.57 mS/m and Kanlow = 81.05 ± 0.37 mS/m) had the lowest mean EC. *Schedonorus phoenix* had the highest mean EC for the invasive species (83.93 ± 0.27 mS/m); with *B. inermis* having the lowest mean EC (82.25 ± 0.31 mS/m), but in neither case was EC under an invasive species significantly different to it in the control pots. Soil pH showed a highly significant interaction between *P. virgatum* cultivars and invasive species (P = 0.0013, Table 3). Among the lowland cultivars, the controls had a lower mean pH (5.97 ± 0.03) than the invasive species (6.43 ± 0.03). The soil in the pots with *Poa pratensis* had the highest mean pH for both lowland cultivars (6.51 ± 0.33). The upland cultivars and the cultivar mixture consistently had the highest mean soil pH when growing in the presence of *S. phoenix* (6.89 ± 0.17).

Table 3. F statistics from mixed model analysis conducted on soil electrical conductivity (EC) and soil pH of *Panicum virgatum* plants in response to *P. virgatum* cultivars (CV), invasive species (INV), and soil moisture (Moist) treatments. Subscripts represent the denominator of the degrees of freedom (DF)

Effect	Num. DF	Soil EC	Soil pH
Cultivar (CV)	5	$9.02_{94}{}^{***}$	$8.03_{96}{}^{***}$
Moisture (Moist)	1	$5.31_{94}{}^{+}$	$0.36_{96}{}^{+}$
CV*Moist	5	$1.12_{94}{}^{+}$	$0.66_{96}{}^{+}$
Invasive (INV)	3	$16.39_{94}{}^{***}$	$11.99_{96}{}^{***}$
CV*INV	15	$1.63_{94}{}^{+}$	$2.78_{96}{}^{**}$
Moist*INV	3	$0.93_{94}{}^{+}$	$0.96_{96}{}^{+}$
CV*Moist*INV	15	$1.50_{94}{}^{+}$	$0.62_{96}{}^{+}$

[*] $P < 0.05$, [**] $P < 0.01$, [***] $P < 0.001$; Marginal significance: [+] $P < 0.1$.

4. Discussion

Previous studies have suggested that competition among plants is relatively unimportant in unproductive, or stressful, environments because resource levels are low (Goldberg & Novoplansky, 1997; Grime, 1979).

Consequently, it has been suggested (Newman, 1973; Tilman, 1987) that unproductive environments are dominated by species that are poor competitors but are highly stress tolerant because they survive better than other species during periods of severe resource shortage. Therefore, it was predicted that cultivars from the least productive environments (i.e. upland cultivars) would minimize their competitive response at the expense of stress tolerance in the presence of neighboring non-native invasive species compared with lowland cultivars from more productive environments.

The greenhouse experiment showed that the height, number of leaves, and tiller density of the lowland cultivars were affected by the presence of the invasive species (Schwartz, 2011). The lowland cultivars had fewer tillers than the upland cultivars, in contrast to findings reported in a study by Porter (1966). However, lowland cultivars tend to grow more slowly than upland cultivars in the first year (Hartman et al., 2011) and grow better under the highest moisture conditions (Berdahl et al., 2005; Lemus et al., 2002). The response of *P. virgatum* and the measurements of environmental resources (light, soil moisture, soil pH and EC) indicated that the cultivar mixture was less affected by the invasive species than the cultivar monocultures were. The cultivar mixture appeared to be more adaptable and had more resources available than the lowland cultivars. The cultivar mixture had the highest available soil pH and EC, with the exception of the Cave in Rock cultivar, which had the highest mean soil moisture in the high moisture level treatment. The intraspecific interaction could be a factor because the cultivars have similar resource requirements (Mangla et al., 2011). Initially the cultivar mixture responded best to the invasive species (Wassmuth et al., 2009); however, the resources in the cultivar mixture became depleted in this study (Brown et al., 2008). The resource depletion could be due to the germination, emergence and initial root and shoot development, which may be very sensitive to competition for resources (Foster, 1999).

Total biomass and biomass of the individual plant parts showed no interactions between *P. virgatum* cultivar and the invasive species. This lack of relationship could be a real effect or be due to the length of time that the experiments were conducted (i.e. a Type II experimental error falsely interpreting a lack of an effect as a real effect) if the experiment ran too long for an interaction to be present. However, the lowland cultivars had higher aboveground biomass compared to the upland cultivars (consistent with Lemus et al., 2002). A limitation of interpreting these biomass measurements could have been that the plants may have become root-bound by the end of the experiment, which had run for 213 days. A greater investment in belowground biomass, compared to aboveground biomass, may reflect the importance of over wintering in perennial plants, and the survival through unproductive environments as dormant underground roots (Raven, Evert, & Eichhorn, 1999). The performance measurements (i.e. plant height, number of vegetative tillers, and leaf number), however, help alleviate these limitations by assessing the temporal responses to competition exhibited by the *P. virgatum* plants.

Bennett et al. (2011) showed that invasive species strongly affects soil microbial communities, thus altering the native species around them. This effect of the soil microbial community could be an explanation for the response of the *P. virgatum* cultivars to the non-native invasive species. In this greenhouse experiment, *B. inermis* grew taller and had more leaves than the other two invasive species. An explanation for this could be that these plants did not become root bound. The upland cultivars had the highest soil moisture when grown with *P. pratensis*; whereas the lowland cultivars had the highest soil moisture when grown with *S. phoenix*. Competition is partially driven by the available resources in the community. Non-native invasive species have been shown to decline in abundance as resource levels decrease (Barney & DiTomaso, 2010; Maron & Marler, 2007). The amount of available resources and the fact that the invasive species grew faster and larger in this experiment could be a reason why they competed so well with the *P. virgatum* cultivars.

5. Conclusions

This study indicates that competition with non-native invasive species can affect the performance of cultivars of *Panicum virgatum*, a dominant prairie species, in terms of its response and resource allocation. Cultivars showed early signs of allocating their resources to growth and not to competition. However, once the cultivars were established resource allocation shifted towards competition. The non-native invasive species, especially *B. inermis*, differentially affected the growth of *P. virgatum* cultivars. There was a positive relationship between response variables and the resources showing that the upland and lowland cultivars respond differently to soil moisture level not just alone as expected, but in a competitive environment. There was little competitive advantage of the cultivar mixture when compared to the *P. virgatum* monocultures. Therefore, cultivar selection may act as a potential filter on community and ecosystem assembly if intraspecific variation in the dominant species affects how they are able to compete with interspecific neighbors (Gibson et al., 2012).

The implications for ecosystem restoration are particularly relevant for the tallgrass prairie due to the extreme loss and degradation this system has experienced (Samson & Knopf, 1994). Only about 10-15% of the original

extent of the tallgrass prairie remains (Camill et al., 2004; Samson, Knopf, & Ostlie, 2004), and in some areas such as Illinois less than 0.01% of the tallgrass prairie remains (Illinois Department of Energy and Natural Resources, 1994). Prairie restoration projects are imperative to restore this highly degraded ecosystem and their success may depend on factors such as cultivar source. Therefore, cultivar selection and knowledge of the dominant grasses should be considered as a potential filter in tallgrass prairie restorations and in warm-season grass plantings (e.g. for biofuels) in response to invasive species invasions.

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