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Research

The Effect of Biochar on Native and Invasive Prairie Plant Species

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Biochar, a carbon-rich product formed by the incomplete combustion of biomass, has been shown to improve soil quality and increase crop growth but has not been evaluated in prairie ecosystems. We assessed the response of a native perennial grass, big bluestem, and an invasive herbaceous perennial, sericea, to biochar amendments in two greenhouse experiments in 2010 and 2011. In the first experiment, big bluestem and sericea were grown in monoculture; the main treatments were soil type (silt, sand), percent biochar (0%, 1%, 2%, and 4%) and nitrogen (0 and 10 g N m^{-2}). Big bluestem growth was increased by the addition of biochar, particularly in the sand soil. In contrast, sericea growth was either not affected or decreased when biochar was added to the soil, particularly at the higher biochar rates. Adding N to the soil appeared to increase sericea growth in the presence of biochar and the silt soil, which suggests that biochar may have reduced N availability. A replacement series was used in the second experiment to evaluate the effect of biochar on competition between the two species. Main treatments were biochar rates (0% and 2%), nitrogen rates (0 and 10 g N m^{-2}) and the following big bluestem to sericea ratios: 6 : 0, 4 : 2, 3 : 3, 2 : 4, and 0 : 6. After 180 d, big bluestem height and biomass were significantly greater in biochar-amended soils than in unamended soils. However, sericea height and biomass were unaffected by biochar amendments and the addition of biochar did not alter competitive outcomes. Competition between big bluestem and sericea was asymmetrical; sericea reduced the growth of big bluestem but big bluestem had relatively little effect on the growth of sericea. Our research suggests that biochar has the potential to increase the growth of big bluestem and may be a useful tool for prairie restoration.

Nomenclature: Big bluestem, *Andropogon gerardii* Vitman; sericea, *Lespedeza cuneata* (Dumont) G. Don.

Key words: Black carbon, carbon sequestration, competition, prairie restoration. replacement series.

By the start of the twentieth century, most North American prairie had been converted to cropland (Cully et al. 2003; Samson and Knopf 1994). More recently, attempts have been made to re-establish prairie species on abandoned agricultural fields as part of the Conservation Reserve Program and by land managers interested in increasing prairie acreage (Mlot 1990; Skold 1989). However, the restoration of prairie habitat continues to be problematic and it is not uncommon for efforts to fail or to take decades before ecosystem function and species diversity goals are achieved (Foster and Gross 1998; Packard and Mutel 1997). For example, the conversion of prairie to agricultural use has resulted in a substantial loss of soil carbon (Mann 1986); restoring soil carbon (C) to levels typically found in prairies may take as long as 200 yr (Knops and Tilman 2000). Weeds can also pose a substantial challenge to the restoration of native grassland communities, particularly during early establishment (Foster et al. 2002; Gross and Werner 1982) and on abandoned agricultural fields with high levels of soil nitrogen (N) and large weed seed banks (Averett et al. 2004). Many plant communities, including tall-grass prairie (Foster and Gross 1998; Wedin and Tilman 1993), were historically limited by N availability and plant invasions in these systems have been linked with increased nitrogen availability (Chapin 1980; Davis et al. 2000, Rashid and Reshi 2010).

The addition of organic C to soils can provide a substrate for heterotrophic microbes, leading to greater

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Management Implications

Sericea is an important weed in prairie and grassland systems in North America. The use of biochar as a soil amendment has the potential to improve the growth of big bluestem and may limit sericea growth in some soils. However, our research suggests that sericea is much more competitive than big bluestem and that biochar amendments alone may not be sufficient to alter competitive outcomes between these two species.

microbial uptake and immobilization of N (Averett et al. 2004; Paschke et al 2000; Perry et al. 2004). Blumenthal et al. (2003) added sawdust (39% C and 0.21% N) and sucrose (42% C) to soil containing weedy and native tallgrass prairie species at a restoration site in Minnesota. The C additions resulted in a 54% reduction in weed biomass, and a sevenfold increase in prairie biomass, which the authors attributed to a large reduction in available nitrate. The authors noted that C additions might also affect the growth of native and invasive prairie plants through direct chemical inhibition (i.e. sorption of allelopathic compounds), or immobilization of other nutrients. Although several researchers have reported reduced weed growth and/or greater growth of desired species following the addition of labile carbon to the soil (Blumenthal et al. 2003; Grygiel et al. 2010; Perry et al. 2004; Prober et al. 2005; Rashid and Reshi 2010), others have found no effect of C addition on the growth of weeds or desired species (Corbin and D'Antonio 2004; Kardol et al. 2008; Mangold and Sheley 2008; Morghan et al. 1999) or that C additions reduced the growth of desired species more than that of weed species (Averett et al. 2004).

Soil black carbon consists of highly condensed aromatic polymers (Kramer et al. 2004) formed primarily from the pyrolysis of organic matter during fires (Fernandes et al. 2003; Simpson and Hatcher 2004). Black carbon is highly stable in soils with mean residence times in excess of 1000 yr (Glaser 2007); significant amounts of black carbon have recently been identified in soils worldwide (Glaser and Amelung 2003; Masiello 2004). Fire is an important ecosystem driver in North American prairies that structures plant communities and regulates N availability. Repeated fires can limit N availability by volatizing plant N tissue and by favoring species that compete strongly for N and/or produce large amounts of high C : N litter (Dijkstra et al. 2006; Ojima et al. 1994; Turner et al. 1997). However, this may not occur in all systems and invasive plants can increase in some plant communities following fire (DiTomaso et al. 2006). Fire can also result in the deposition of black carbon in the form of charred plant material into prairie soils. Glaser and Amelung (2003) examined soils in North American prairies and concluded that black carbon was an important C pool in this ecosystem, comprising between 4 and 18% of the soil organic carbon.

Biochar is a form of black carbon obtained from the pyrolysis of plant biomass in a process similar to charcoal production that has been proposed as a means to sequester C and to increase plant growth (Chan et al. 2008; Graber et al. 2010, Lehmann 2007; Van Zwieten et al. 2010; Yamato et al. 2006). Interest in biochar has been driven by the discovery of black carbon in Terra Preta soils (Portuguese for 'dark earth') that were developed by indigenous tribes of the Brazilian Amazon. These 'biochar' soils appear to be hundreds to thousands of years old but remain more fertile than nearby unamended soils (Glaser 2007). Biochar has been shown to improve soil cation exchange capacity (CEC), pH, water holding capacity, and the availability of several nutrients including phosphorus (P) (Chan et al. 2007; Glaser et al. 2001; Major et al. 2005; Novak et al. 2009; Solaiman et al. 2011). Mechanisms proposed to explain increased P availability include changes to soil pH, increased microbial biomass and activity, greater mycorrhizal–plant associations, and through the mineralization of P from biochar itself (Amonette and Joseph 2009; DeLuca et al. 2006, 2009; Gundale and DeLuca 2007; Warnick et al. 2007). The effect of biochar on N availability, immobilization, N-fixation, and denitrification is less clear (DeLuca et al. 2009). N fertilizer is commonly applied with biochar to increase crop growth and there is evidence that combining biochar with nitrogen can increase crop growth to a greater extent than biochar alone (Atkinson et al. 2010; Major et al. 2005; Steiner et al. 2008). Thus, the addition of biochar to soils is likely to result in more complex changes to soils than the addition of more labile C sources such as sucrose and sawdust. We are not aware of published studies in which biochar has been added to soil to assess its effect on the growth of native and invasive prairie plant species.

Andropogon gerardii Vitman (big bluestem) is a tall, native, warm-season, perennial grass responsible for a large fraction of primary production in tallgrass prairie (Barnes et al. 2005; Hartnett and Fay 1998; Kakani and Reddy 2010; Knapp 1985; Silletti and Knapp 2004). *Lespedeza cuneata* (Dumont) G. Don (sericea) is a warm-season, herbaceous, perennial legume that is native to eastern Asia but now widespread in the United States where it displaces big bluestem and other prairie species (Cummings et al. 2007; Fechter and Jones 2001; Kalburtji and Mosjidis 1992). Potential mechanisms contributing to its ability to invade grasslands include the loss of natural enemies (Schutzenhofer and Knight 2007), allelopathic properties (Kalburtji et al. 2001), high reproductive capacity (Sanders et al. 2007), and relatively high total and specific leaf area that enable it to outcompete native species for light (Brandon et al. 2004; Allred et al. 2010).

The goal of our research was to assess the response of sericea and big bluestem to biochar when grown individually and in competition. We hypothesized that biochar would reduce sericea growth and increase the ability of big bluestem to compete with sericea. We also

Table 1. Characteristics of soil types and biochar used in the experiments. Both soils were used in the biochar rate experiment but only the sand soil was used in the replacement series experiment. Values are least square means; parentheses enclosed are standard errors of the means.

	Silt[a]	Sand[b]	Biochar[c]
pH	7.3 (0.01)	5.5 (0.1)	7.8 (0.1)
Organic Matter (%)	4.5 (0.2)	2.6 (0.1)	82.2 (0.9)
CEC (meq/100 g)	14.6 (0.2)	8.9 (0.4)	13.3 (0.1)
Magnesium (ppm)	505.0 (8.9)	193.8 (5.2)	293.0 (4.3)
Calcium (ppm)	1975.0 (32.3)	725.0 (14.4)	550.0 (0.0)
Potassium (ppm)	212.3 (3.4)	143.5 (3.8)	3167.0 (31.7)
Phosphorus (ppm)	75.5 (0.5)	22.8 (0.1)	221.0 (2.9)
Total Nitrogen (%)	0.24 (0.1)	0.17 (0.1)	1.8 (0.01)

[a] Sawabash series (fine silt clay loam, mixed superactive calcareous mesic Cumulic Endoaquolls) consisting of approximately 10% sand, 49% silt and 41% clay.

[b] Mahalasville series (sandy loam, mixed, superactive, mesic Typic Argiaquolls) consisting of approximately 60% sand, 28% silt and 12% clay.

[c] Biochar was produced under slow pyrolysis from loblolly pine and switchgrass.

hypothesized that big bluestem grown with biochar would have greater biomass than big bluestem grown without biochar.

Materials and Methods

Two experiments, referred to as the ''biochar rate'' and the ''replacement series'' experiments, were conducted under greenhouse conditions in 2010 and 2011. Soil used for both experiments was collected from the top 10 cm (3.9 in) of a 2-yr-old prairie restoration site at Prophetstown State Park located near Battleground, IN (40°30′N, 86°50′W). Biochar used in both experiments was produced under slow-pyrolysis from loblolly pine (*Pinus taeda* L.) and switchgrass (*Panicum virgatum* L. var. *virgatum*) by a commercial vendor (Eprida, Inc., 3020 Canton Road Suite 105 Marietta, GA 30066). The field soil and biochar were passed through a 4-mm (0.2 in) mesh sieve for both experiments to achieve uniform particle size and mixed in a 50-L (13.2 gal) electric concrete mixer for 2 h. Prior to mixing, four 500 g (1.1 lbs) samples of each soil type and biochar were sent to a commercial laboratory (A&L Great Lakes Laboratories, 3505 Conestoga Drive Fort Wayne, IN 46808) for analyses of pH, CEC, percent organic matter, and extractable Bray 2-phosphorus, potassium, calcium, and magnesium (Table 1). Organic matter content was measured by loss-on-ignition of the dry mass at 360 C (680 F) (Nelson and Sommers 1996). Soil pH was determined using a 1 : 1 ratio of soil : water and CEC was measured by a modified ammonium-acetate compulsory displacement (Sumner and Miller 1996). Plant available nutrients (magnesium, calcium and potassium) were extracted using the Mehlich 3 method and analyzed by inductively coupled plasma-atomic emission spectroscopy (Mehlich 1984). Total N was estimated using the Dumas combustion method.

A complete randomized block design with three treatments and four blocks was used in the biochar rate experiment. The main treatments were soil type, biochar incorporated into the soil at rates equivalent to 0%, 1%, 2%, and 4% of the soil dry weight (DW), and nitrogen incorporated into the soil in the form of ammonium nitrate (0 and 10 g N m^{-2}). The biochar rates reflect rates used in agricultural experiments and the nitrogen rate was chosen to reflect rates used in prairie restoration (Major et al. 2005; Seastedt et al. 1991). The ''sand'' and ''silt'' soils were a Mahalasville series (sandy loam, mixed, superactive, mesic Typic Argiaquolls) and a Sawabash series (fine silt clay loam, mixed, superactive, calcareous mesic Cumulic Endoaquolls), respectively (Table 1). The experiment was initiated on September 25, 2010 and repeated starting on June 28, 2011. Plants were grown under grown under natural and supplemental light (14 hr day length) to simulate Indiana summer day length. Minimum and maximum air temperatures were recorded daily. Average minimum and maximum temperatures were 20.8 C (± 0.80 SE) and 33.5 C (± 0.72 SE) in 2010 and 22.4 C (± 0.34 SE) and 35.6 C (± 0.56 SE) in 2011.

Preliminary germination trials suggested differences between the species in the proportion of seed that germinated and in the length of time to germination. To insure a uniform initial ht and reduce variability because of differences in germination and emergence between the species, big bluestem (average ht 4.09 cm ± 0.10 SE) and sericea (average ht 3.10 cm ± 0.07 SE) seedlings were transplanted from trays containing unamended soil to pots (10 cm diam by 8.5 cm). All pots were watered daily to maintain water content near field capacity throughout the duration of the experiment. Plants were harvested in both years when big bluestem first produced flowers, approximately 90 d after transplanting (DAT). Our ability to assess the effect of the treatments on plant growth is therefore limited to vegetative growth for the biochar rate experiment. Plants were separated by species into roots, shoots, leaves, and inflorescences if present (sericea was harvested before inflorescences were produced), dried at 60 C for 7 d and weighed.

In the replacement series experiment, the effect of biochar and N on competition between big bluestem and sericea was assessed using a complete randomized block design with three treatments and four blocks. The main treatments were plant ratio, percent biochar (0% and 2% of the soil) and nitrogen added in the form of ammonium nitrate (0 and 10 g N m^{-2}). The experiment was initiated on September 23, 2010 and repeated starting on December 12, 2010. Plants were grown under natural and supplemental light as in the biochar rate experiment. Minimum and maximum air temperatures were 19.5 C ± 0.33 SE and 28.4 C ± 0.26 SE in 2010 and 22.0 C ± 0.22 SE and 32.0 C ± 0.37 SE in 2011, respectively. Big bluestem (6.8 cm tall ± 0.12 SE) and sericea (5.2 cm tall ± 0.08 SE) seedlings were transplanted from trays containing unamended soil to pots (25 cm diam by 31 cm) containing the "sand" soil described above at the following big bluestem to sericea proportions: 6 : 0, 4 : 2, 3 : 3, 2 : 4, and 0 : 6. The seedlings were arranged in rows within each pot with an inter-plant spacing of 4 cm. All pots were watered daily. Plants were harvested at first sign of leaf senescence in big bluestem, approximately 180 DAT in both years. Plants were separated by species into roots, stems, leaves, and panicles if present (sericea was harvested before seeds were produced), dried at 60 C for 7 d and weighed. The height of each big bluestem plant (measured from the soil surface to the tip of the longest leaf) and each sericea plant (measured from the soil surface to the tip of the plant) was recorded.

Mixed model ANOVAs were used to evaluate the effects of soil type, biochar and nitrogen on plant variables for the biochar rate experiment and to evaluate the effects of plant ratio, biochar and nitrogen on plant variables for the replacement series experiment. Year and block were treated as random factors in both experiments while the remaining treatments were considered fixed factors. Mixed model ANOVAs were also used to evaluate the effects of biochar and nitrogen on the relative crowding coefficient (see below) at the end of the replacement series experiment. Year and species interacted with each other and with other independent variables to affect most dependent variables in the biochar rate experiment so the data were separated by year and species and reanalyzed. Year also interacted with most independent variables in the replacement series experiment and data were separated by year and reanalyzed. Mean comparisons for all analyses were conducted using the Tukey-Kramer Honestly Significant Difference (HSD) adjusted to maintain a family-wise alpha level of 0.05. Data were tested for normality and heterogeneity of variance and square root or arcsine of the square root transformed as needed to comply with the assumptions of ANOVA. Data were back-transformed for presentation. All statistical analyses were conducted using SAS 9.2 software package (SAS Institute Inc., Cary, NC, USA).

Replacement series diagrams were constructed using the following equations for total DW (Harper 1977):

$$\text{Relative yield(RY)of species} = \text{yield per pot of species in a mixture} / \text{yield per pot of species in a monoculture} \quad [1]$$

$$\text{Relative yield total(RYT)} = \text{relative yield of species A} + \text{relative yield of species B} \quad [2]$$

If neither species had a competitive advantage, then the RY lines for each species should intersect when they were grown at equivalent ratios, i.e. the 3 : 3 ratio (Estorninos et al. 2002; Harper 1977). A shift in the point of intersection from the 3 : 3 ratio suggests that one species was more competitive than the other. RYT values of approximately 1 indicate that the species competed equally for resources. Values greater than 1 indicate that interspecific competition affected the growth of at least one species less than intraspecific competition and may suggest that the species were limited by different resources. RYT values less than 1 suggest there is mutual antagonism between the two species (Harper 1977; Radosevich 1987). The relative crowding coefficient (RCC), which serves as an index of competition when the two species are competing at equal proportions (Gealy et al. 2005), was calculated at the 3 : 3 mixture using the following equation:

$$\text{RCC} = (\text{mixture yield of species A}/\text{mixture yield of species B}) / (\text{monoculture yield of species A} / \text{monoculture yield of species B})$$

or

$$\text{RCC} = (\text{mixture yield of species B}/\text{mixture yield of species A}) / (\text{monoculture yield of species B} / \text{monoculture yield of species A}) \quad [3]$$

RCC values of approximately 1 indicate the two species are equal competitors and values greater or less than 1

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Table 2. The effect of biochar rate on big bluestem growth in a sandy loam soil in 2010 and 2011. Values are means; parentheses enclose standard errors of the means. Treatment means followed by different letters indicate that significant differences were detected ($P \leq 0.05$).

Biochar	Height	Root DW[a]	Shoot DW	Leaf DW	Inflorescence DW[b]	Total DW[a]
	cm	g plant^{-1}				
2010						
0%	29.0 (6.5) c	—	0.15 (0.05) b	0.21 (0.06) b	ND	—
1%	46.0 (8.2) ab	—	0.34 (0.09) a	0.47 (0.12) a	ND	—
2%	50.5 (3.5) a	—	0.38 (0.06) a	0.45 (0.06) a	ND	—
4%	39.0 (7.5) bc	—	0.23 (0.07) ab	0.34 (0.09) ab	ND	—
2011						
0%	99.0 (20.9) c	3.94 (0.56) b	2.60 (0.64) c	1.17 (0.11) d	0.08 (0.05) b	7.78 (1.06) b
1%	154.0 (17.8) b	5.86 (1.02) a	3.89 (0.50) b	1.58 (0.29) c	0.35 (0.09) a	11.67 (1.26) a
2%	183.9 (13.7) a	2.24 (0.37) c	4.85 (0.51) ab	2.28 (0.37) b	0.36 (0.06) a	9.73 (1.08) ab
4%	184.0 (9.3) a	2.64 (0.39) c	5.31 (0.97) a	2.83 (0.64) a	0.47 (0.11) a	11.25 (1.66) a

[a] Interaction was not detected between biochar rate and soil type in 2010 for root and total dry weight. Big bluestem root and total dry weights were not affected by biochar rate in 2010 but big bluestem plants produced more root dry weight in the sand soil than in the silt soil (0.56 g ± 0.08 SE and 0.30 g ± 0.04 SE, respectively) and nearly twice the total dry weight in the sand soil than in the silt soil (1.20 g ± 0.15 SE and 0.62 g ± 0.06 SE, respectively).

[b] Acronym: ND, no data. Plants were harvested before producing inflorescences in 2010.

indicate that one species is more or less competitive than the other species.

Results and Discussion

Biochar rate experiment. The only big bluestem variables in either year that were not affected by interaction between soil type and biochar were root and total DW in 2010. Big bluestem root and total dry weight were not affected by biochar but were affected by soil type in 2010. Big bluestem plants produced more root DW in the sand soil than in the silt soil (0.56 g ± 0.08 SE and 0.30 g ± 0.04 SE, respectively) and nearly twice as much total DW in the sand soil as in the silt soil (1.20 g ± 0.15 SE and 0.62 g ± 0.06 SE, respectively) in 2010. The remaining data were separated by soil type and reanalyzed. In 2010, big bluestem height, shoot DW, and leaf DW were greater in the sand soil when plants were grown with 1% and 2% biochar than without biochar (Table 2). Differences were not detected in ht, shoot DW, or leaf DW between plants grown without biochar or with 4% biochar (Table 2). In 2011, big bluestem plants in the sand soil were taller and had greater shoot, leaf, panicle, and total DW when grown with biochar than when grown without biochar (Table 2). In the sand soil, root dry weight in 2011 was greater for plants grown at 1% biochar than at 0% biochar but plants grown without biochar produced more root DW than plants grown with 2% and 4% biochar (Table 2). No differences in ht or DW were detected between the 2% and 4% treatments in the sand soil (Table 2). Thus big bluestem growth was not increased in either yr by increasing biochar rates from 2% to 4%.

The response of big bluestem to biochar was less consistent in the silt soil (Table 3). In 2010, big bluestem plants grown in the silt soil without biochar were taller and produced more leaf DW than plants grown with 1% biochar but did not differ in height or leaf DW from plants grown with 2% or 4% biochar (Table 3). In 2011, bluestem plants grown in the silt soil at 2% biochar had greater root and total DW than plants grown without biochar or with 1% or 4% biochar (Table 3). However, big bluestem ht and shoot DW in 2011 were not affected by biochar in the silt soil and leaf DW was lower for plants grown with biochar than for plants grown without biochar (Table 3). Inflorescence DW was lower for big bluestem plants grown at 4% biochar than for plants grown in the other treatments (Table 3). The response of big bluestem to biochar depended therefore on soil type.

Nitrogen did not interact with soil type to affect big bluestem ht or DW in 2010. Differences between the 10 g N m^{-2} and 0 g N m^{-2} treatments were only detected in 2010 for root DW (0.50 g ± 0.06 SE and 0.37 g ± 0.07 SE, respectively). In 2011, big bluestem plants grown with N had greater root DW (4.56 g ± 0.46 SE and 2.61 g ± 0.21 SE), shoot DW (4.65 g ± 0.38 SE and 2.72 g ± 0.26 SE), inflorescence DW (0.34 g ± 0.05 SE and 0.19 g ± 0.04 SE), and total DW (11.66 g ± 0.66 SE and 7.05 g ± 0.39 SE) than plants grown without N, respectively. N interacted with soil type to affect plant ht and with biochar to affect leaf DW in 2011. Plants that grew in the silt soil

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Table 3. The effect of biochar rate on big bluestem growth in a silt clay soil in 2010 and 2011. Values are means; parentheses enclose standard errors of the means. Treatment means followed by different letters indicate that significant differences were detected ($P \leq 0.05$).

Biochar	Height	Root DW[a]	Shoot DW	Leaf DW	Inflorescence DW[b]	Total DW[a]
	cm	g plant^{-1}				
2010						
0%	35.0 (4.6) a	—	0.10 (0.02) b	0.25 (0.04) a	ND	—
1%	23.0 (4.3) b	—	0.14 (0.04) ab	0.12 (0.04) b	ND	—
2%	29.7 (6.1) ab	—	0.09 (0.03) b	0.20 (0.06) ab	ND	—
4%	30.0 (5.0) ab	—	0.20 (0.04) a	0.19 (0.04) ab	ND	—
2011						
0%	133.0 (20.6) a	2.28 (0.53) b	2.71 (0.63) a	2.45 (0.41) a	0.32 (0.10) a	7.75 (1.22) b
1%	145.0 (18.2) a	2.56 (0.29) b	3.67 (0.65) a	1.67 (0.23) b	0.23 (0.11) a	8.13 (1.01) b
2%	132.1 (24.3) a	6.17 (0.73) a	3.83 (0.79) a	1.14 (0.16) b	0.26 (0.11) a	11.40 (1.35) a
4%	126.6 (20.8) a	3.01 (0.73) b	2.64 (0.67) a	1.42 (0.23) b	0.06 (0.02) b	7.13 (1.39) b

[a] Interaction was not detected between biochar rate and soil type in 2010 for root and total dry weight. Big bluestem root and total dry weights were not affected by biochar rate in 2010 but big bluestem plants produced more root dry weight in the sand soil than in the silt soil (0.56 g ± 0.08 SE and 0.30 g ± 0.04 SE, respectively) and nearly twice the total dry weight in the sand soil than in the silt soil (1.20 g ± 0.15 SE and 0.62 g ± 0.06 SE, respectively).

[b] Acronym: ND, no data. Plants were harvested before producing inflorescences in 2010.

with nitrogen were taller (169.0 cm ± 6.9 SE) than plants grown in the silt soil without N (99.3 cm ± 14.5 SE). Big bluestem plants that received N produced more leaf DW at 4% biochar (2.78 g ± 0.68 SE) than at 1% biochar (1.33 g ± 0.22 SE).

Interaction was not detected between soil type and the other treatments in either yr for sericea. Biochar did not affect sericea growth in 2010. Sericea plants that received nitrogen produced more root DW than plants that did not receive nitrogen in 2010 (0.10 g ± 0.01 SE and 0.06 g ± 0.01 SE, respectively). Nitrogen did not affect any other sericea variables in 2010. In 2010, sericea plants were taller (14.2 cm ±1.3 SE vs. 19.9 cm ± 1.7 SE) and had greater shoot (0.18 g ± 0.03 SE and 0.11 g ± 0.02 SE), leaf (0.32 g ± 0.04 SE and 0.19 g ± 0.03 SE), and total (0.59 g ± 0.06 SE and 0.37 g ± 0.05 SE) DW in sand than in the silt, respectively. Sericea root DW was not affected by soil type in 2010. In 2011, soil type did not affect sericea growth (data not shown). N and biochar only affected sericea root dry weight in 2011. Root dry weight was greater with than without N (1.40 g ± 0.11 SE and 1.08 g ± 0.09 SE, respectively). Sericea plants grown with 0% and 1% biochar had greater root DW (1.53 g ± 0.15 SE and 1.45 g ± 0.17 SE, respectively) than plants grown with 2% and 4% biochar (1.07 g ± 0.16 SE and 0.91 g ± 0.14 SE, respectively) rates of biochar. Interaction was detected between biochar and N rates for sericea ht, leaf DW, and total DW. In absence of N, sericea plants were shorter (74.9 cm ± 6.3 SE, 70.8 ± 6.8 SE, and 99.2 cm ± 4.8 SE for 2%, 4%, and 0% biochar, respectively) and produced less leaf (1.47 g ± 0.20 SE, 2.44 g ± 0.69 SE, and 4.15 g ± 0.32 SE for 2%, 4%, and 0% biochar, respectively) and total DW (3.26 g ± 0.49 SE, 4.93 g ± 1.31 SE, and 8.92 g ± 0.59 SE for 2%, 4%, and 0% biochar, respectively) when grown with 2% and 4% biochar than without biochar. No differences in plant growth were detected between the 0% and the 2% and 4% biochar treatments in the presence of N.

Replacement series experiment. Biochar generally increased big bluestem, but not sericea, growth in both years. In 2010, big bluestem shoot and total dry weight were greater for plants grown with biochar than for plants grown without biochar (Table 4). Sericea height and biomass were not affected by biochar in 2010 (data not shown). In 2011, bluestem plants grown with biochar were taller and produced more root, shoot, panicle, and total DW than plants grown without biochar (Table 4). Sericea plants grown with biochar in 2011 produced less root dry weight than plants grown without biochar (3.04 g plant^{-1} ± 0.21 SE and 3.71 g plant^{-1} ± 0.29 SE, respectively). Sericea shoot DW was not affected by biochar but biochar interacted with N fertilizer to affect sericea leaf and total DW in 2011. Sericea plants grown with N did not differ in leaf and total DW between biochar rates. However, differences in leaf and total DW were detected between biochar rates when sericea was grown without N fertilizer. Sericea leaf DW for plants grown without N fertilizer was 4.83 g plant^{-1} ± 0.38 SE with biochar and 6.39 g plant^{-1} ± 0.63 SE without biochar. Total DW for sericea grown without N fertilizer was 11.61 g plant^{-1} ± 1.1 SE with

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Table 4. The effect of biochar rate on big bluestem growth in a replacement series experiment in 2010 and 2011. Values are means; parentheses enclose standard errors of the means. Treatment means followed by different letters indicate that significant differences were detected ($P \leq 0.05$).

Biochar	Height	Root DW	Shoot DW	Leaf DW	Panicle DW[a]	Total DW[a]
	cm	g plant^{-1}				
2010						
0%	74.4 (2.7) a	2.64 (0.25) a	0.82 (0.07) b	1.19 (0.07) a	—	5.59 (0.44) b
2%	78.6 (3.2) a	3.09 (0.32) a	1.16 (0.13) a	1.42 (0.11) a	—	7.06 (0.68) a
2011						
0%	92.9 (5.1) b	4.15 (0.47) b	1.90 (0.25) b	1.20 (0.08) a	3.76 (0.70) b	11.01 (1.34) b
2%	107.1 (4.5) a	5.31 (0.44) a	2.57 (0.20) a	1.36 (0.13) a	7.48 (1.09) a	16.72 (1.59) a

[a] Plant ratio interacted with biochar in 2010 to affect panicle dry weight. Big bluestem plants grown with biochar had greater panicle dry weight than plants grown without biochar in the 6 : 0 ratio (2.5 g ± 0.68 SE and 0.58 g ± 0.28 SE, respectively) and in the 3 : 3 ratio (1.42 g ± 0.75 SE and 0.29 g ± 0.12 SE, respectively).

biochar and 15.46 g plant^{-1} ± 1.4 SE without biochar. Thus there is evidence from both experiments that, in the absence of N, higher rates of biochar might reduce the growth of sericea.

Competition between sericea and big bluestem was generally asymmetric; big bluestem growth was more affected by interspecific competition than sericea. In 2010, the average big bluestem plant produced less root, shoot, and total DW when grown at the 3 : 3 and 2 : 4 ratios than in monoculture (Table 5). Big bluestem ht was not affected by plant ratio in 2010. Plant ratio interacted with biochar to affect panicle DW and with N to affect big bluestem leaf DW in 2010. Big bluestem plants grown with biochar had greater panicle dry weight than plants grown without biochar in the 6 : 0 ratio (2.50 g plant^{-1} ± 0.68 SE and 0.58 g plant^{-1} ± 0.28 SE, respectively) and in the 3 : 3 ratio (1.42 g plant^{-1} ± 0.75 SE and 0.29 g plant^{-1} ± 0.12 SE, respectively). Big bluestem plants grown with N had greater leaf dry weight than plants grown without N in the 4 : 2 ratio (0.94 g plant^{-1} ± 0.39 SE and 1.33 g plant^{-1} ± 0.07 SE) and the 2 : 4 ratio (1.13 g plant^{-1} ± 0.49 SE and 1.31 g plant^{-1} ± 0.67 SE)

Table 5. The effect of plant ratio on big bluestem growth in a replacement series in 2010 and 2011. Big bluestem was grown with sericea at the following big bluestem : sericea ratios: 6 : 0, 4 : 2, 3 : 3, and 2 : 4. Values are means; parentheses enclose standard errors of the means. Treatment means followed by different letters indicate that significant differences were detected ($P \leq 0.05$).

Ratio	Height	Root DW	Shoot DW	Leaf DW[a]	Panicle DW[b]	Total DW[a]
	cm	g plant^{-1}				
2010						
6 : 0	83.8 (4.5) a	3.95 (0.57) a	1.34 (0.22) a	—	—	8.53 (1.15) a
4 : 2	74.1 (4.8) a	2.80 (0.41) ab	0.98 (0.13) ab	—	—	6.02 (0.70) ab
3 : 3	73.3 (4.1) a	2.45 (0.17) b	0.74 (0.09) b	—	—	5.17 (0.52) b
2 : 4	75.0 (2.8) a	2.25 (0.22) b	0.89 (0.09) b	—	—	5.58 (0.54) b
2011						
6 : 0	122.3 (4.6) a	7.14 (0.71) a	3.33 (0.28) a	1.42 (0.06) a	8.91 (1.58) a	20.79 (2.22) a
4 : 2	108.9 (6.9) a	5.27 (0.49) a	2.61 (0.31) ab	1.54 (0.14) a	5.39 (1.26) ab	14.81 (2.03) ab
3 : 3	89.0 (5.3) b	3.84 (0.47) b	1.74 (0.29) bc	1.28 (0.23) ab	3.63 (0.87) b	10.48 (1.60) b
2 : 4	80.1 (6.0) b	2.68 (0.32) b	1.28 (0.20) c	0.88 (0.08) b	4.56 (1.40) b	9.40 (1.76) b

[a] Plant ratio interacted with nitrogen to affect big bluestem leaf dry weight in 2010. Big bluestem plants grown with N had greater leaf dry weight than plants grown without N in the 4 : 2 ratio (0.94 g ± 0.39 SE to 1.33g ± 0.07 SE) and in the 2 : 4 ratio (1.13 ± 0.49 SE and 1.31g ± 0.67 SE).

[b] Plant ratio interacted with biochar in 2010 to affect panicle dry weight. Big bluestem plants grown with biochar had greater panicle dry weight than plants grown without biochar in the 6 : 0 ratio (2.5 g ± 0.68 SE and 0.58 g ± 0.28 SE, respectively) and in the 3 : 3 ratio (1.42 g ± 0.75 SE and 0.29 g ± 0.12 SE, respectively).

Table 6. The effect of plant ratio on sericea growth in a replacement series in 2010 and 2011. Sericea was grown with big bluestem at the following sericea : big bluestem ratios: 6 : 0, 4 : 2, 3 : 3, and 2 : 4. Values are means; parentheses enclose standard errors of the means. Treatment means followed by different letters indicate that significant differences were detected ($P \leq 0.05$).

Ratio	Height	Root DW	Shoot DW	Leaf DW[a]	Total DW
	cm	g plant^{-1}			
2010					
6 : 0	67.4 (1.7) b	1.21 (0.06) ab	1.10 (0.07) b	1.56 (0.09) b	3.87 (0.21) b
4 : 2	66.7 (2.9) b	1.07 (0.08) b	1.15 (0.09) b	1.67 (0.13) b	3.88 (0.28) b
3 : 3	66.1 (2.9) b	1.07 (0.10) b	1.18 (0.12) b	1.78 (0.16) b	4.03 (0.37) b
2 : 4	80.2 (5.0) a	1.58 (0.14) a	1.93 (0.26) a	2.64 (0.31) a	6.16 (0.70) a
2011					
6 : 0	81.3 (3.4) b	2.50 (0.25) c	2.90 (0.23) c	—	9.18 (0.75) c
4 : 2	88.2 (4.0) b	3.11 (0.31) bc	3.89 (0.32) bc	—	11.91 (0.94) bc
3 : 3	92.4 (4.9) b	3.55 (0.30) ab	5.16 (0.62) b	—	15.05 (1.45) ab
2 : 4	102.5 (3.4) a	4.33 (0.43) a	7.23 (0.74) a	—	19.63 (1.80) a

[a] Interaction was detected between plant ratio and N in 2011. Differences between N treatments were only detected for sericea leaf dry weight at the 3 : 3 ratio; leaf dry weights for plants grown with and without N were 7.18 g plant^{-1} ± 0.75 SE and 5.49 g plant^{-1} ± 0.78 SE, respectively.

in 2010. In 2011, big bluestem plants grown in the 6 : 0 treatment were taller and had greater root, shoot, panicle and total DW than plants in the 3 : 3 and 2 : 4 treatments in 2011 (Table 5). In contrast, the average sericea plant in the 2 : 4 (sericea : big bluestem) treatment was taller and had greater shoot, and total DW than sericea grown in the 6 :0 ratio in both years (Table 6). Plant ratio interacted with N to affect sericea leaf DW in 2010. Differences between N treatments were only detected for sericea leaf DW at the 3 : 3 ratio; leaf DW for plants grown with and without N were 7.18 g plant^{-1} ± 0.75 SE and 5.49 g plant^{-1} ± 0.78 SE, respectively.

RCC for big bluestem and sericea, calculated for the 3 : 3 mixture, were 0.82 and 1.98 in 2010 and 0.42 and 4.16 in 2011, respectively. RCC values were not affected by biochar or N in either year (data not shown), which suggests that biochar and N did not alter competitive outcomes between big bluestem and sericea. The shape of the replacement curve of the RY for total DW also suggests that sericea outcompeted big bluestem. When the lines for two species intersect at the equal mixture proportion, then neither species is considered to have a competitive advantage (Harper 1977). However, the lines for big bluestem and sericea intersected when at least twice as many big bluestem plants as sericea plants were present in both years (Figure 1). This suggests that big bluestem had a disadvantage capturing resources when grown with sericea. Relative yield totals (RYT) were slightly less than 1 in 2010 but greater than 1.0 for all the mixtures in 2011. Sericea relative yields were greater than 0.8 for all mixtures in 2011 (Figure 1). This suggests that sericea was more affected by intraspecific competition than by interspecific competition in 2011.

Although the behavior of plants under greenhouse conditions may not directly correspond to plant growth under field conditions, greenhouse studies are useful for exploring plant responses (Mangla 2011; Novoplansky and Goldberg 2001). Our study suggests that biochar has the potential to increase the growth of big bluestem and may be a useful tool for prairie restoration. Big bluestem responded to both N fertilizer and to biochar—in the sand soil—with increased growth. Since biochar can contain relatively high quantities of N, the response of big bluestem to biochar could be attributed to increased N availability. However, several studies have suggested that N is tightly bound to biochar and crop responses to biochar may be limited unless N fertilizer is also provided (Gaskin et al. 2010; Lehman et al. 2003). Biochar did not consistently affect big bluestem growth in the silt soil. There is some evidence that the performance of biochar is affected by soil texture and nutrient content (Joseph et al. 2010; Streubel et al. 2011). Novak et al. (2009) reported that biochar increased CEC, pH, and available calcium, phosphorus, and potassium more in sand loam soils in the southern United States than in soils with higher clay content. The silt soil used in our study had a more neutral pH, more organic matter and greater CEC than the sand soil (Table 1). Thus biochar may have increased soil pH, CEC, and macronutrient availability in the sand soil, which led to greater big bluestem growth, while having little effect on soil properties in the silt soil.

The use of C additions to improve native prairie plant growth in mixed cultures typically depends on the immobilization of N, which reduces the growth and competitive ability of invasive plant species (Blumenthal et

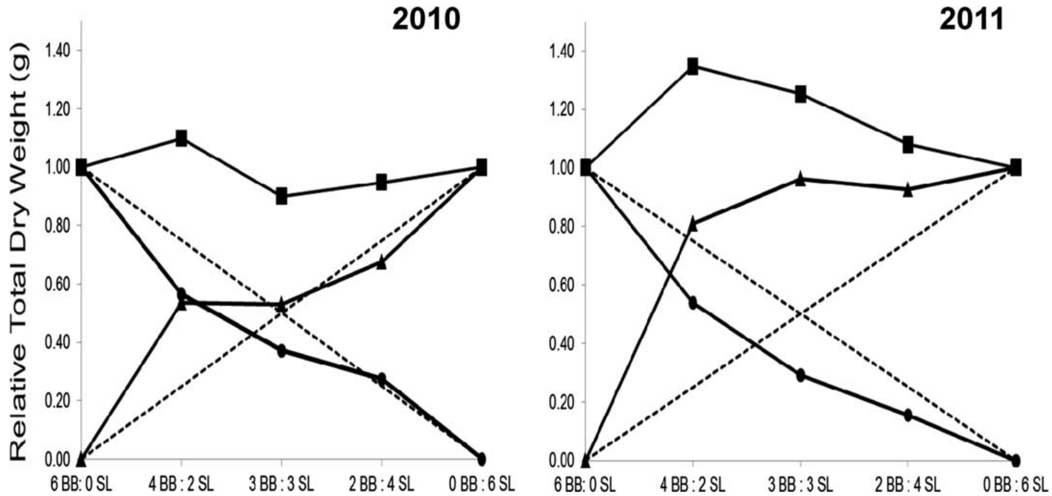

Figure 1. Relative yield and relative yield totals ■ for total dry weight of big bluestem (BB) ● and sericea (SL) ▲ based on their proportions in a replacement series experiment in 2010 and 2011. The dashed lines represent the expected responses of two equally competitive species and intersect at the point of equivalency. Relative competition coefficients (RCC), calculated for each species for the 3 : 3 mixture, for big bluestem and sericea were 0.82 and 1.98 in 2010 and 0.42 and 4.16 in 2011, respectively.

al. 2003). The effect of biochar on sericea varied with N fertilizer; N additions appeared to limit the negative effect of biochar on sericea growth. Although sericea is a legume, root nodules were not detected in either experiment and sericea produced more root dry weight in the biochar rate experiment with N than without N. The ability of sericea to fix N has not been well characterized but several researchers concluded that sericea contributes relatively little N to soils, suggesting that sericea may fix relatively low quantities of N (Brandon et al. 2004; Mays and Bengston 1985; Ritchie and Tilman 1995). The interaction of biochar, inorganic N, and N-fixation in sericea and other legumes is unclear and warrants further research. However, the effect of biochar on big bluestem and sericea growth was clearly not sufficient to alter competitive outcomes between sericea and big bluestem. Big bluestem growth was reduced by sericea but the replacement series data suggest that sericea plants were more affected by intraspecific competition than by competition with big bluestem (Figure 1). Our results support the hypothesis that big bluestem is less competitive than sericea—at least during the first year of growth—and agree with research showing that sericea has the ability to displace native prairie species (Allred et al. 2010).

Prairie soils historically contained substantial amounts of black carbon deposited over long periods of time from fire (Glaser and Amelung 2003). The use of biochar amendments in prairie restoration projects has potential therefore to not only improve the growth of big bluestem, a key prairie species, but also to sequester carbon (Lehman 2007) and accelerate the recovery of an important carbon pool in prairie soils. However, this potential is likely to be affected by soil type, climate, biochar quantity and quality, and time (Major et al. 2010; Novak et al. 2009; Steiner et al. 2007). Further work is needed to (1) assess the long-term effects of biochar amendments on prairie plant and soil dynamics under field conditions and (2) develop a mechanistic understanding of how biochar affects the growth of native and invasive prairie plant species in different soil types. Additional research is also needed to better understand the nature of competition between big bluestem and sericea.

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