

Effects of Species, Water, and Nitrogen on Competition Among Three Prairie Grasses

JERRY L. WEATHERFORD AND RANDALL W. MYSTER¹

Biology Department, Box 89, University of Central Oklahoma, Edmond, OK, 73034,
USA (JLW, RWM)

ABSTRACT We conducted an experiment to investigate effects of species, water (W), and nitrogen (N) on competition among little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), and indiagrass (*Sorghastrum nutans*). All biomass parameters and the root:shoot ratio of little bluestem were reduced by the presence of ≥ 1 of 2 other species, and its shoot biomass and total biomass were both increased by addition of N. Root and shoot biomass of sideoats grama were reduced by the presence of indiagrass and its total biomass was reduced by the presence of itself, whereas its shoot biomass was increased by addition of W at the highest level. Root biomass and total biomass of indiagrass were increased by N and that response pattern was preserved for root biomass but lost for total biomass when W was added. We conclude that grass seedlings were affected by species more than by levels of W and N, interspecific competition was more important than intraspecific competition, and both N and W effects occurred only in the highest levels of addition with some interaction.

KEY WORDS biomass, *Bouteloua curtipendula*, competition, nitrogen, *Schizachyrium scoparium*, *Sorghastrum nutans*, water

Vast areas of the world are characterized by annual precipitation too low to support woody vegetation but higher than precipitation levels characteristic of desert ecosystems (e.g., grasslands; Walter 1979, Cheplick 1998). Within the continental United States, grasslands are one of the most-studied ecosystems and serve as flagship Long-Term Ecological Research sites of the National Science Foundation (Knapp et al. 1998). A major research focus in these grasslands has been the study of temporal and spatial changes of grasses (Collins and Uno 1985, Glenn and Collins 1993, Haught and Myster 2008, Myster 2009, 2011).

Evidence suggests that these changes are produced by individual plant-plant replacements in grasslands where competition is a major mechanism (Grace and Tilman 1990, Glenn and Collins 1993, Myster 2007). Most grasses have the majority of their biomass below-ground in roots and data from both permanent plots (Myster and Pickett 1992, Myster 2007) and greenhouse experiments (Kelley and Clay 1987, Marks et al. 1991, Clay et al. 1993, Weatherford and Myster 2011) have shown that grasses are good competitors for below-ground resources. Indeed competitive outcome among grasses may conform to Resource Ratio theory, where competitive superiority depends on which species has the lowest R^* (requirement for soil nitrate in monoculture; Dybzinski and Tilman 2007) for present soil Nitrogen [N] levels, and depend on the interaction between the properties of root systems (e.g., size, uptake rates, scaling properties) and soil nutrient availability (supply rate, spatial distribution; Biondini 2001, 2007).

However, too often past studies have focused on only two species of grasses or have not included direct manipulation of the below-ground resources thought to

influence competitive outcome (e.g., water [W] and N; Wallace 1981, Kelley and Clay 1987, Grace and Tilman 1990). In addition, experimental study designs have not included interactive effects of species and resource supply on competitive outcome. Thus, our objective was to evaluate the effects of multiple species, interactive effects, and below-ground resources on competitive outcome of warm season grasses in Oklahoma.

METHODS

We conducted our study at the United States Department of Agriculture Agricultural Research Service (USDA-ARS), Southern Plains Range Research Station in Woodward, Woodward County., Oklahoma (36°25'N, 99°25'W), where a heated greenhouse was maintained by the USDA-ARS at an average temperature of 21°C. In August 2002, we locally purchased seeds of three common, native grass species (Johnston's Seed Co., Enid, Oklahoma, USA). We hand-sorted and floated seeds to remove nonviable seeds and litter. We weighed and germinated seeds in trays in a University of Central Oklahoma environmental growth chamber (made by Rheem Environmental of Asheville, North Carolina, USA; Myster 2006) using standard potting mix (Berger BM1 growing mix; ISO 9001 Canadian code).

Our test species were little bluestem (*Schizachyrium scoparium*: 1.4 g per 1,000 seeds fresh mass), sideoats grama (*Bouteloua curtipendula*: 2.26 g per 1,000 seeds fresh mass), and indiagrass (*Sorghastrum nutans*: 1.9 g per 1,000 seeds fresh mass); all three species are C₄, "warm-season" grasses (Kindscher and Wells 1995). We obtained seed fresh mass from the Royal Botanic Gardens Kew, seed information database (<http://www.kew.org/data/sid>). After

¹ Corresponding author email address: rwmyster@gmail.com

3 weeks in the growth chamber, we transported seedlings (12–15 cm tall) into 3.78-L pots in the USDA-ARS greenhouse in standard potting mix. We maintained the greenhouse under natural conditions of full sunlight and light-dark cycles, and a temperature range of 15.4 to 29.2°C.

We used a complete randomized design with a DeWitt-type replacement series (Harper 1977, Clay et al. 1993), in which four seedlings were planted in each pot. We ensured that pots differed by composition of species, having either four seedlings of all one species or two seedlings of the response species and two seedlings of the effect species. Our W treatments consisted of low (W added on day 1 of a 7-day cycle), medium (W added on days 1 and 5 of a 7-day cycle), and high (W added on days 1, 3, and 5 of a 7-day cycle). For the first two months, we added 267 mL of water per pot at each watering. During the third month, we decreased the amount of water added at each watering to 200 mL due to decreased day lengths and reduced evaporation losses. Our N treatment also consisted of low (N added at start of experiment only) medium (N added twice, at the start and after 2 months), and high (N added 3 times, at the start of the experiment, after 1 month, and after 2 months). For each treatment, we added 0.07 g of N per pot using 46-0-0 fertilizer (Agri-nutrients, Port of Catoosa, Oklahoma, USA). Our levels of W and N treatments reflected normal ranges at the study site (R. Gillen, pers. comm. USDA, Woodward, Oklahoma, USA). After 2 months, we randomly re-arranged pots and subsequently kept them separated by 25 cm on greenhouse tables so that plants in adjacent pots would not influence each other. We did not observe any constraining effects of pots on growth of roots during our study.

After 3 months, we harvested, cleaned, dried and weighed to the nearest 0.1 g all seedlings. We used mean root and shoot biomass of the two seedlings of each species in a pot for the response parameters. We divided root biomass by shoot biomass to compute root:shoot ratio, and added root biomass to shoot biomass to calculate total biomass. We conducted separate statistical analyses for each species with the identity of the other species in the pot as the species factor. We used 3-way analyses of variance (ANOVAs) at an α -level of 0.05 and conducted means separation tests using the Tukey procedure (SAS Institute, Inc. 1985) with species, W level, and N level as main effects. With five replicates of each treatment combination, we also were able to examine all possible interactions among each main effect. Prior to conducting statistical analyses, we used box plots to evaluate assumptions of normality.

RESULTS

Root biomass of little bluestem was significantly reduced ($F_2 = 3.46$, $P = 0.041$) by the presence of sideoats grama ($\bar{x} = 1.12 \pm 0.21$ SE) or indiangrass ($\bar{x} = 0.89 \pm 0.14$; Fig. 1A) and shoot biomass was significantly reduced ($F_2 = 7.34$,

$P < 0.001$) by the presence of indiangrass ($\bar{x} = 0.4 \pm 0.16$; Fig. 1B). Similarly, total biomass was significantly reduced ($F_2 = 4.62$, $P = 0.032$) by the presence of either sideoats grama ($\bar{x} = 2.01 \pm 0.18$) or indiangrass ($\bar{x} = 1.51 \pm 0.23$; Fig. 2A), and root:shoot ratio was reduced significantly ($F_2 = 5.78$, $P = 0.007$) by the presence of sideoats grama ($\bar{x} = 1.99 \pm 0.21$; Fig. 2B). Moreover, addition of the highest level of N significantly increased both shoot ($F_2 = 5.91$, $P = 0.005$) biomass ($\bar{x} = 0.66 \pm 0.11$; Fig. 2C) and total ($F_2 = 3.44$, $P = 0.004$) biomass ($\bar{x} = 2.20 \pm 0.17$; Fig. 2D).

Both root ($F_2 = 3.55$, $P = 0.034$) biomass and shoot ($F_2 = 6.27$, $P < 0.001$) biomass of sideoats grama increased significantly in the presence of indiangrass ($\bar{x} = 1.99 \pm 0.22$; Fig. 3A, $\bar{x} = 0.78 \pm 0.19$; Fig. 3B), while sideoats total biomass decreased significantly ($F_2 = 5.02$, $P = 0.009$) in the presence of itself ($\bar{x} = 0.89 \pm 0.10$; Fig. 3C). Also, shoot biomass increased significantly ($F_2 = 5.78$, $P = 0.007$) under the highest W addition ($\bar{x} = 2.58 \pm 0.30$; Fig. 3D). Both root ($F_2 = 5.33$, $P = 0.009$) biomass and total ($F_2 = 5.51$, $P = 0.008$) biomass of indiangrass were increased by addition of the highest level of N ($\bar{x} = 1.98 \pm 0.35$; Fig. 4A, $\bar{x} = 2.51 \pm 0.22$; Fig. 4B).

DISCUSSION

Our findings are consistent with previous studies documenting species-specific responses of plants to the presence of competitors (Myster and McCarthy 1989, Myster and Pickett 1992). During our study, species parameters were affected more by the presence of other species compared to presence of individuals of their own species. Interestingly, all possible directions of species effects were detected. For instance, little bluestem was negatively affected by sideoats grama and indiangrass, whereas sideoats grama was positively affected by little bluestem and indiangrass, and indiangrass was unaffected by little bluestem and sideoats grama. In addition, little bluestem was affected equally by indiangrass and sideoats grama while sideoats grama was most affected by indiangrass, suggesting that indiangrass was the competitive dominant and little bluestem was least dominant.

Nitrogen effects were present in the highest level addition only, increasing total biomass in little bluestem, and increasing both root and total biomass in indiangrass. The addition of W increased shoot biomass of sideoats grama under the highest level and W interacted with N to preserve and destroy previous N effects. Lack of multiple W effects may reflect the ability of many grasses to resume normal growth (e.g. acclimate) quickly after addition of water, even if previously dehydrated (Cheplick 1998). Also, root:shoot ratios were approximately 50% of those observed in other grasslands (Marks et al. 1991), but specific root length (length of longest root/total biomass) may be more meaningful, because uptake rates are proportional to root length (Garnier 1998). Intraspecific effects of sideoats

grama also were reported by Risser (1978). Our findings suggest that species identity and characteristics were more

important in determining competitive outcome than nutrient supply and availability (also seen in Briguglio et al. 2000).

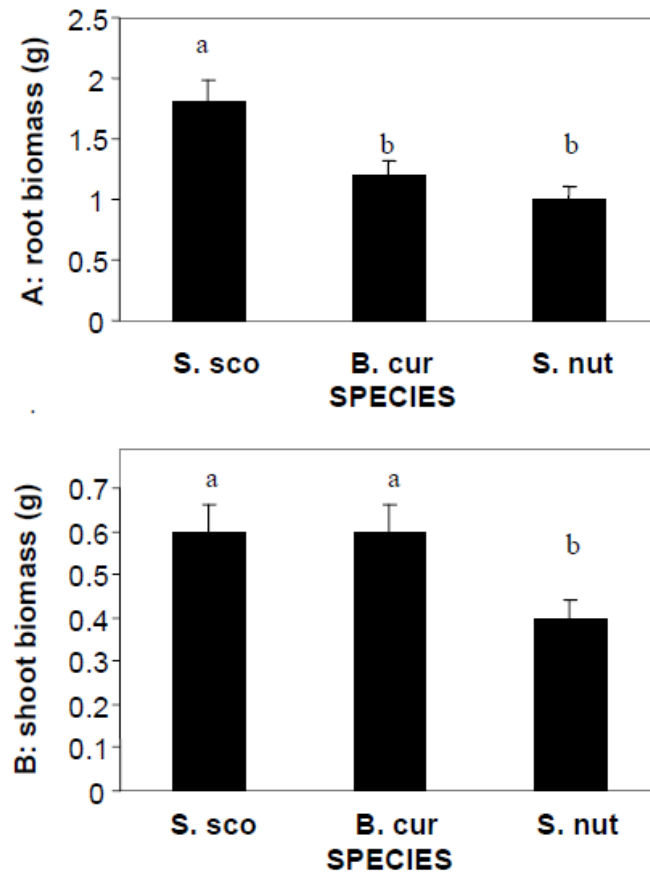


Figure 1. Effects of competition on (A) root biomass and (B) shoot biomass of little bluestem given as means + one SE. Species are abbreviated as “S. sco” for *Schizachyrium scoparium*, “B. cur” for *Bouteloua curtipendula* and “S. nut” for *Sorghastrum nutans*. Different letters were used to label means that were significantly different.

Alternatively, Gibson and Skeel (1996) found that increased density of grasses (though not manipulated during our study) lead to greater competition effects on indiangrass. Further, little bluestem and *Paspalum plicatulum* were competitively equal with growth largely determined by soil resources levels rather than presence of neighbors (Auken and Bush 1997) as found during our study. Another *B.* species (*B. gracilis*) was competitively inferior to *Agropyron cristatum* (for N or P; Bakker and Wilson 2001) and more negatively affected by intraspecific competition rather than competition with *Bromus tectorum* (Lowe et al. 2003) especially as N availability increased. However *B. gracilis* was competitively superior to *Buchloe dactyloides*,

especially at high levels of P and N, elsewhere (Richard and Redente 1995). Test species may well conform to Resource Ratio theory, as other grasses did, by being a superior competitor whenever it's R^* was lowest (requirement for soil nitrate in monoculture; Tilman and Wedin 1991, Dybzinski and Tilman 2007) with faster rates of exclusion on low N soils. Although this study used only species in pair-wise experiments, competition in nature involves multiple species. Biondini (2001) found in species mixtures involving our test species that properties of root systems (e.g., size, uptake rates, scaling properties) and soil nutrients (supply rate, spatial distribution) influenced interspecific competition.

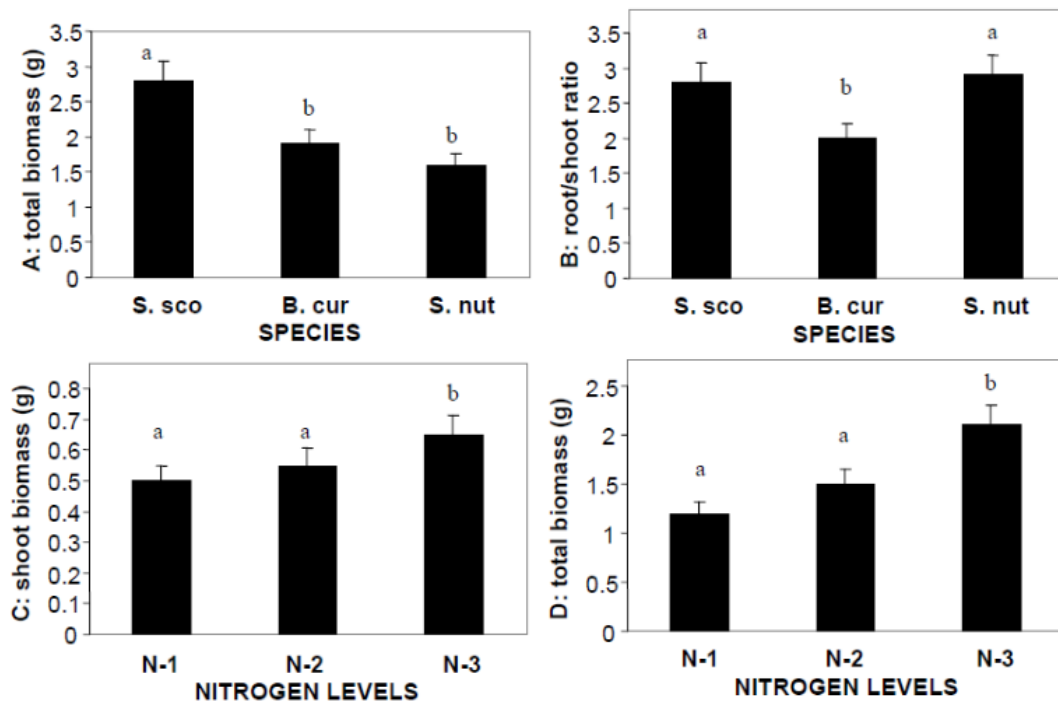


Figure 2. Effects of competition on (A) total biomass and (B) root/shoot ratio of little bluestem. Effects of nitrogen addition on (C) shoot biomass and (D) total biomass of little bluestem. Addition of nitrogen is indicated as N-1 (added one time), N-2 (added two times) and N-3 (added three times). The figure is otherwise labeled as in Figure 1.

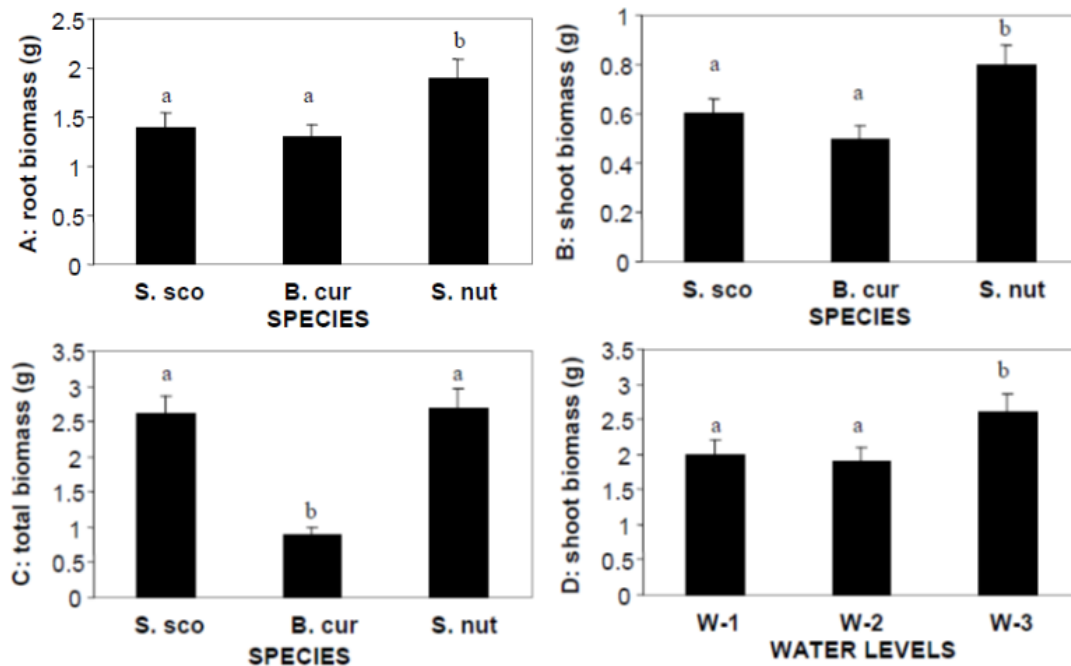


Figure 3. Effects of competition on (A) root biomass and (B) shoot biomass of sideoats grama. Effects of (C) competition on total biomass and (D) water addition on shoot biomass of sideoats grama. Addition of water (W) is indicated as W-1 (added once a week), W-2 (added twice a week) and W-3 (added three times a week). The figure is otherwise labeled as in Figure 1.

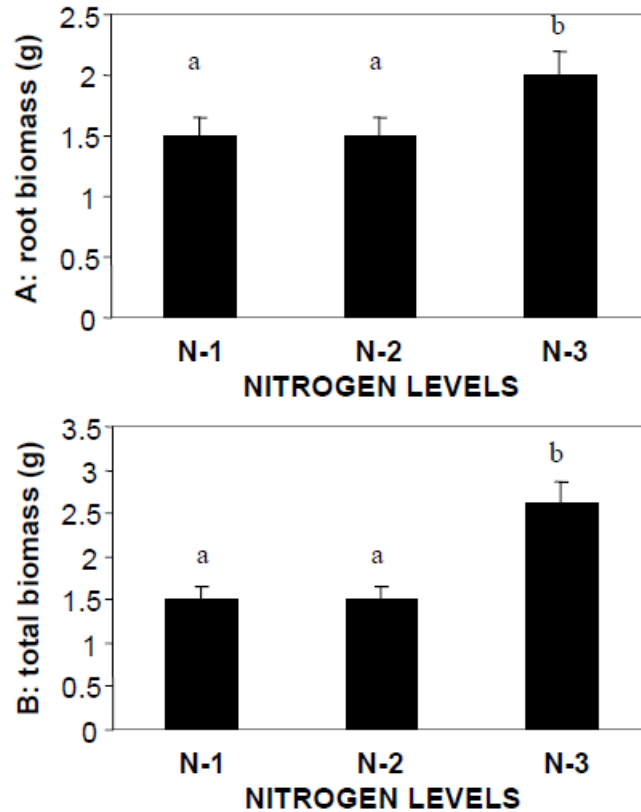


Figure 4. Effects of N addition on (A) root biomass and (B) total biomass of indiagrass. The figure is otherwise labeled as in Figure 1.

All three species tested during our study were warm-season grasses. However, small differences in length of root, density of root hair, mycorrhizal strategy, root:shoot ratio, flow of carbohydrates to the roots, and the “nutrient economy” of species (Berendse and Elberse 1990) could have been important in determining the differences we observed. Physiological traits related to N and P use efficiency (Biondini 2007) and morphological/architectural differences might be critical, such as having a caespitose (tussock, bunchgrass, phalanx) rather than a sodgrass (creeping, spreading, guerrilla) growth form (Briske and Derner 1998). Particular genotypes of grasses within populations (Kelley and Clay 1987) and grass seedlings interactions with litter mat (Myster 2006) also may influence competitive outcome. Our findings suggest that grass seedlings were affected more by other species than by levels of W and N, that interspecific effects dominated intraspecific effects, and that both N and W effects occurred only in the highest levels of addition with some interaction.

MANAGEMENT IMPLICATIONS

Results suggest how managers could decrease or increase grass competition in general, or in specific biomass parameters, among the three test species. Such management

strategies could include species removals, species additions, and addition of both water and nitrogen. Although there may be a competitive hierarchy with these grasses as they grow in a prairie, results show that by careful application of below ground resources such as water and nitrogen, such community structures may be altered.

ACKNOWLEDGMENTS

We thank R. Gillen and the staff at the USDA-ARS station in Woodward, Oklahoma for allowing us to work there and for help in setting up the experiments. We thank the University of Central Oklahoma for a research grant to JLW and for use of laboratory and computer facilities. We thank G. Cheplick, R. Gillen and O. Mironova for providing helpful comments on a previous draft of our manuscript.

LITERATURE CITED

- Bakker, J. and S. Wilson. 2001. Competitive abilities of introduced and native grasses. *Plant Ecology* 157:119–127.
- Berendse, F., and W. T. Elberse. 1990. Competition and nutrient availability. Pages 93–116 in J. B. Grace and D. Tilman, editors. *Perspectives on Plant*

- Competition Academic Press, San Diego, California, USA.
- Biondini, M. 2001. A three dimensional spatial model for plant competition in an heterogeneous soil environment. *Ecological Modeling* 142:189–225.
- Biondini, M. 2007. Plant diversity, production, stability and susceptibility to invasion in restored northern tall grass prairies (United States). *Restoration Ecology* 15:77–87.
- Briguglio, L., P. Janson and L. Oswald. 2000. Competition has a greater effect than supplemental nutrients on the growth of *Sorghastrum nutans* and *Bromus kalmi*. *Tillers* 2:17–21.
- Briske, D. D., and J. D. Derner. 1998. Clonal biology of caespitose grasses. Pages 106–135 in G. P. Cheplick, editor. *Population Biology of Grasses*. Cambridge University Press, Cambridge, UK.
- Cheplick, G. P. 1998. *Population Biology of Grasses*. Cambridge University Press, Cambridge, UK.
- Clay, K., S. Marks and G. P. Cheplick. 1993. Effects of insect herbivory and fungal endophyte infection on competition interactions among grasses. *Ecology* 74:1767–1777.
- Collins, S. L., and G. E. Uno. 1985. Seed predation, seed dispersal and disturbance in grasslands: a comment. *American Naturalist* 125:866–872.
- Dybzinski, R. and D. Tilman. 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *American Naturalist* 170:305–318.
- Garnier, E. 1998. Interspecific variation in plasticity of grasses in response to nitrogen supply. Pages 155–182 in G. P. Cheplick, editor. *Population Biology of Grasses*. Cambridge University Press, Cambridge, UK.
- Gibson, D. J. and V. A. Skeel. 1996. Effects of competition on photosynthetic rate and stomatal conductance of *Sorghastrum nutans*. *Photosynthetica* (Prague) 32: 503–512.
- Glenn, S. M., and S. L. Collins. 1993. Experimental analysis of patch dynamics in tall-grass prairie plant communities. *Journal of Vegetation Science* 4:157–162.
- Grace, J. B., and D. Tilman. 1990. *Perspectives on Plant Competition*. Academic Press, San Diego, California, USA.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press, New York, New York, USA.
- Haight, J. A., and R. W. Myster. 2008. Effects of species, density, season and prairie-type on seed predation in Oklahoma. *American Midland Naturalist* 159: 482–488.
- Kindscher, K., and P. V. Wells. 1995. Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. *Vegetation* 117:29–50.
- Kelley, S. E., and K. Clay. 1987. Interspecific competitive interactions and the maintenance of genotypic variation within the populations of two perennial grasses. *Evolution* 41:92–103.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, D. C., and S. L. Collins. 1998. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, Oxford, UK.
- Lowe, P. N., Lauenroth, W. K. and I. C. Burke. 2003. Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology* 167:247–254.
- Marks, S., K. Clay and G. P. Cheplick. 1991. Effects of fungal endophytes on interspecific and intraspecific competition in the grasses *Festuca arundinacea* and *Lolium perenne*. *Journal of Applied Ecology* 28:194–204.
- Myster, R. W. 2006. Species-specific effects of grass litter mass and type on emergence of three tall-grass prairie species. *Ecoscience* 13:95–99.
- Myster, R. W. 2007. *Post-Agricultural Succession in the Neotropics*. Springer-Verlag, New York, New York, USA.
- Myster, R. W. 2009. Controls on Shumard Oak (*Quercus shumardii*) establishment into the Cross Timbers ecotone of Oklahoma: implications for restoration. *Restoration Ecology* 17:893–899.
- Myster, R. W. 2011. Above-ground vs. below-ground interactive effects of mammalian herbivory on tallgrass prairie plant and soil parameters. *Journal of Plant Interactions* 8:1–8.
- Myster, R. W. and B. C. McCarthy. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56:145–148.
- Myster, R. W. and S. T.A. Pickett. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *Journal of Ecology* 80:291–302.
- Richard, C. E. and E. F. Redente. 1995. Nitrogen and Phosphorus effects on blue grama and buffalograss interactions. *Journal of Range Management* 48:417–422.
- Risser, P. G. 1970. Competitive responses of *Bouteloua curtipendula* (Michx.) Torr. *American Midland Naturalist* 84:259–262.
- SAS Institute, Inc. 1985. *Users Guide: Statistics, Version 5 Edition*. SAS Institute Inc., Cary, North Carolina, USA.
- Silletti, A. M., A. K. Knapp and J. M. Blair. 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. *Canadian Journal of Botany* 82:450–460.

- Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* 72:1038–1049.
- Van Auken, O. W. and J. K. Bush. 1997. The importance of neighbors, soil pH, phosphorus, and nitrogen for the growth of two C₄ grasses. *International Journal of Plant Sciences* 158:325–331.
- Wallace, L. L. 1981. Growth, morphology and gas exchange of mycorrhizal and nonmycorrhizal *Panicum coloratum* L., a C₄ grass species, under different clipping and fertilization regimes. *Oecologia* 49:272–278.
- Walter, H. 1979. *Vegetation of the Earth and Ecological systems of the Geo-biosphere*. Springer-Verlag, New York, New York, USA.
- Weatherford, J. A. and R. W. Myster. 2011. Interactive effects of simulated grazing, species and below-ground resources water on competitive outcome among three prairie grasses. *Journal of the Torrey Botanical Society* 138: 107–119.

Submitted 10 July 2008. Accepted 29 April 2011. Associate Editor was David Mushet.