Weed Science, 50:466–472. 2002

Utilizing *Sorghum* as a functional model of crop–weed competition. I. Establishing a competitive hierarchy

Melinda L. Hoffman
Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824

Douglas D. Buhler
Corresponding author. Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824; buhler@msu.edu

Application of nitrogen (N) fertilizer to sorghum at planting is a common practice that could confound competitive relationships of the crop with weeds. We studied the competitiveness of grain sorghum (Pioneer Brand 8333) relative to that of the annual weed shattercane and the perennial weed johnsongrass. The taxa are closely related, so survival requirements should be similar thus increasing the likelihood of finding differences associated with traits of the crop vs. weediness. Objectives of this research were to establish a competitive hierarchy for this crop–weed complex and to determine if relative competitiveness was affected by added N. A replacement design experiment was used in which plants were grown for 31 d in soil-filled pots placed outdoors. Taxa were planted in monocultures and 50:50 mixtures, representing all possible combinations of taxa, at a total density of 16 plants pot^{-1}. Soil moisture was maintained at field capacity by daily additions of water or 30 μg ml^{-1} N in the form of an inorganic salt solution (KNO_3). There was no response to the solution containing exogenous N likely because the amount of N in soil was greater than demand. Actual shoot and root dry weights in mixtures were compared with the expected dry weights, which were calculated as 50% of the root and shoot dry weights in monoculture. For grain sorghum, actual dry weights in mixture were often better than expected. Replacement series indices calculated from dry weight data described grain sorghum as competitively superior to its weedy relatives. These results indicate that further research on N management for cultivated sorghum, as a means of increasing crop competitiveness relative to that of weeds, may be unwarranted. However, a better understanding of other competition mechanisms inherent in grain sorghum might suggest management alternatives to enhance crop competitiveness with weeds.

Nomenclature: Sorghum, *Sorghum bicolor* (L.) Moench 'Pioneer Brand 8333'; shattercane, *Sorghum bicolor* (L.) Moench SORVU; johnsongrass, *Sorghum halepense* (L.) Pers. SORHA.

Key words: Crop competitiveness, exogenous nitrogen, integrated weed management, KNO_3, replacement design experiment.

Sorghum is grown in the United States as a grain or forage crop on 5 million ha, mainly in Kansas, Texas, and Nebraska. Among the numerous weed species naturalized throughout the area, shattercane and johnsongrass are unique because of their familial ties to the species under cultivation. Shattercane is so biologically similar to cultivated sorghum that the two taxa respond in a similar manner to management practices, making it nearly impossible to selectively control shattercane growing in sorghum (Carlson and Burnside 1981). Johnsongrass is a related noxious weed (Holm et al. 1977) in temperate areas where it spreads by seeds as well as by rhizomes that survive over mild winters (Dowler 1994).

Taxonomists place these three taxa in the same section (*Sorghum*) by way of classification systems ranging from definitive ones splitting the group into as many as 52 species (Snowden 1936, 1955) to more parsimonious treatments. The classification proposed by de Wet (1978) was based on numerous studies in sorghum (de Wet and Harlan 1971; de Wet and Huckabay 1967; de Wet et al. 1970, 1976; Harlan and de Wet 1972). It was developed as a tool for field workers without specialized training (Harlan and de Wet 1972); so it is one of the more intuitive sorghum classification systems and the one we followed.

Annual sorghums are separated by way of seed dispersal mechanisms into three subspecies (de Wet 1978). It is usual to base taxonomic groupings on plants found in their native range, so for *Sorghum*, relatedness is implied from plants found in Africa. In wild African races making up *S. bicolor* subsp. *arundinaceum*, callus forms below the seed (de Wet et al. 1976; Quinby and Martin 1954), lack of callus and seed-shattering mechanisms are traits of cultivated races placed in *S. bicolor* subsp. *bicolor*, and callus formation is suppressed but fragile inflorescence branches break below the spikelet in shattercane assigned to *S. bicolor* subsp. *drummondii*. Because shattercane in North America does not form a callus and its seeds shatter, it is commonly assigned to the same subspecies as the African shattercanes. However, there is considerable evidence that North American shattercane originated in the United States as a feral descendant of cultivated sorghum (Burnside 1965, 1968; Harlan and deWet, 1974). Such a scenario, in which shattercane is a wild type of cultivated sorghum, implies that gene flow between these taxa might still be occurring. In either case shattercane and cultivated sorghum are interbreeding members of the same species.

Also included in this study was *Sorghum halepense*, which was introduced less than 200 yr ago into North America as a perennial forage (de Wet 1978), and it quickly became a weed. The common form in North America is johnsongrass, which likely resulted from introgression of *S. halepense* with cultivated sorghum (Celarier 1958; Warwick et al. 1984). Although tetraploid ($2n$ = 40), it can cross with annual ($2n$ = 20) sorghums (Arriola and Ellstrand 1996; Baker 1972; Hadley 1953, 1958; Karper and Chisholm 1936).

The locations in which these taxa most likely co-occur are cultivated fields characterized by intensive management practices. In spring, vegetation is controlled to create optimum conditions for crop establishment. Fertilizer, herbicides, and cultivation are used during the growing season to optimize crop growth. In temperate agroecosystems it is generally assumed that the amount of available nitrogen (N) will limit plant growth (Tilman 1985). Additionally, the N requirement of sorghum is high compared with that of the other crops (Maranville et al. 1980; Onken et al. 1985). Cultivated sorghums respond to added N with large accumulations of dry weight of grain and fodder (Zweifel et al. 1987). Also, some variation in the N-use efficiency among sorghum cultivars is expected (Gardner et al. 1994). Therefore, to maximize yield, between 50 and 150 kg N ha^{-1} is applied to cultivated sorghum at the time of planting (Lamond et al. 1991; Roy and Wright 1973).

The objectives of this research were to establish a competitive hierarchy for this crop–weed complex and to determine if exogenous N influenced relative competitiveness among the taxa. The taxa used interbreed indicating genetic similarities, but as the result of divergence, crop traits were created in one and weediness in the others. Studies using crops other than sorghum found that added N could affect crop–weed competition (Angonin et al. 1996; Ball et al. 1996; Carlson and Hill 1985; Rasmussen et al. 1996; Tollenaar et al. 1994). We hypothesized that competitive relationships among these closely related *Sorghum* taxa would be influenced by added N because of differences in N-use efficiency between crop and weeds. Because we used related taxa, we assumed that there would be fewer genotypic differences and that requirements for survival would be similar, thus increasing the likelihood of observing traits of the crop that differed and could be compared with those associated with weediness. Therefore, this research could have specific implications regarding the methods of N fertilizer application for cultivated sorghum that might increase competitiveness of the crop over that of the weeds. It could also serve as a functional model to demonstrate the likelihood that added N would affect relative competitiveness among crops and weeds. In Part II of the study, immediately after this paper, this crop–weed complex was again used as a model, but the objective was to uncover traits resulting in competitiveness of the crop for resources shared with weeds.

Materials and Methods

To determine the effects of exogenous N on competition among *Sorghum* taxa, grain sorghum, shattercane, and johnsongrass seedlings were grown in monoculture and two-species mixtures with and without KNO_3 fertilizer. Among the many cultivated sorghums available, we used a grain sorghum (Pioneer Brand 8333) that is frequently grown on the Great Plains in the United States. Shattercane seeds were collected in 1994 from several individuals in a single population in Boone County, IA. Johnsongrass seeds were purchased in 1992 from a company[1] located in southern Illinois. Seeds were stored dry at 7 C until they were used in the experiments.

The experiment was conducted in June through July 1997, at Ames, IA. Pots were placed in a greenhouse during the first week. Thereafter, they were placed outdoors on a bench and brought into the greenhouse each day to be watered. The experiment was designed as a randomized complete block, so pots were removed by blocks to be watered, and the position of the pots was randomized within blocks when they were returned to the bench. Over night, pots were covered with a plastic net to deter herbivores. We left the pots in the greenhouse over three nights during the course of the experiment because heavy rain was predicted.

In replacement design experiments total plant density remains constant but species proportion varies (De Wit 1960). To make sure that planting density would be sufficient to result in interference, preliminary studies were conducted before deciding to set total plant density in monocultures at 16 plants pot^{-1}. Also included were mixtures consisting of two taxa combined in a 50:50 ratio. Pairs of taxa making up the mixtures were grain sorghum with shattercane, grain sorghum with johnsongrass, and shattercane with johnsongrass. Therefore, the experiment consisted of a 3 (taxa) by 3 (mixtures) by 2 (N fertilizer) factorial arrangement of treatments replicated six times.

Seeds were planted in 15-cm-diam by 18-cm-deep pots filled 15.5 cm deep with 2,000 g of Webster silty clay loam (fine-loamy, mixed, mesic, Typic Haplaquoll). This soil is found throughout central Iowa, where it is commonly represented as a Clarion–Nicollet–Webster soil association having 6.5% organic matter, pH of 7, very low phosphorous (less than 8 μg ml^{-1}), very low potassium (K) (less than 60 μg ml^{-1}), and N values described as low even when amended with differing types of fertilizer (Karlen and Colvin 1992; Soil Conservation Service 1981). Soil was sieved through an 8-mm screen to remove clods and was placed in pots. Then, seeds were planted in a grid pattern such that they were equally distant from each other. A template was used so that seed placement would not vary among pots. In mixtures, positions of the two species alternated. Three seeds were planted at each position and extra seedlings removed 7 d after planting, resulting in a pattern of 16 plants spaced 2.8 cm apart. Planting depth was 2 mm, which approximately equaled the diameter of a sorghum seed. After determining, by weight, that moisture content of the soil at field capacity was 35%, 600 g deionized water or KNO_3 solution containing 30 μg ml^{-1} N was added to each pot. Moisture content was maintained by weighing pots daily and adding water or KNO_3 solution as required.

Among the possible forms of N available, KNO_3 was used because it is readily available, easy to apply, relatively nontoxic to plants, and often used as a source for N in laboratory studies. Because we fertilized with KNO_3, K was added at 85 μg ml^{-1} each time the fertilizer solution was applied. Potassium is a plant nutrient that, when supplied in excess, leads to luxury accumulation rather than toxicity. It is also likely that much of the K applied was trapped between clay particles in the soil. Therefore, we considered it relatively innocuous compared with other cations associated with nitrate. Concentrations used in this experiment included those that occur in fertilized fields. For example, Iowa soil test results for K are considered low if less than 44 μg ml^{-1}, medium if 85 to 125 μg ml^{-1}, high if 126 to 188 μg ml^{-1}, and very high if greater than 188 μg ml^{-1} (Voss et al. 1996). Concentrations of exogenous N added were within the range of concentrations used previously in studies of its effect on germination (Sardi and Beres 1996) and seedling growth (Alfoldi and Pinter 1992) of crop and weed species. Nitrogen at 100 μg ml^{-1} is approximately equal to 34 kg ha^{-1} KNO_3 applied to the top 2.5 cm of the soil (Fawcett and Slife 1978).

Plant density, number of leaves, length of the longest extended leaf, and shoot dry weight were measured after 31 d. Length of the longest leaf was measured from the soil surface, so it was also a measure of plant height. After removing plants from the pots and carefully washing the roots in a stream of water to remove the soil, root dry weight was determined. Dry weights are reported on a per pot basis. Root–shoot ratios were calculated from dry weights. Data were subjected to analysis of variance (ANOVA), and Duncan's multiple-range tests ($P = 0.05$) were used to separate means of effects determined to be significant at the 0.05 level. Replacement series indices from Cousens and O'Neill (1993) were calculated using mean shoot or root dry weight for an individual plant from each taxon in monoculture and mixtures. Taxa in each mixture were designated as either taxon A or taxon B, and relative yield (R) was calculated for each taxon as:

$$R_A = (p)(A_{mix}/A_{mon}) \quad [1]$$

$$R_B = (1 - p)(B_{mix}/B_{mon}) \quad [2]$$

where p = proportion of taxa in mixture, A_{mix} = dry weight of taxon A in mixture, A_{mon} = dry weight of taxon A in monoculture, B_{mix} = dry weight of taxon B in mixture, and B_{mon} = dry weight of taxon B in monoculture. This index was used to calculate other indices, including the relative yield total (RYT)

$$RYT = R_A + R_B, \quad [3]$$

which was subjected to the Student's *t* test ($P = 0.05$) to determine if it differed from 1.0, as well as the competitive ratio (CR)

$$CR = ((1 - p)/p)(R_A/R_B), \quad [4]$$

relative crowding coefficient (k)

$$k_A = ((1 - p)/p)(R_A/(1 - R_A)) \quad [5]$$

$$k_B = ((1 - p)/p)(R_B/(1 - R_B)) \quad [6]$$

$$k_{AB} = (R_A/(1 - R_A))(R_B/(1 - R_B)), \quad [7]$$

and aggressivity (A)

$$A = (R_A/2p) - (R_B/(2(1 - p))). \quad [8]$$

Results and Discussion

The reputation of johnsongrass as a rapidly spreading, noxious weed is largely because of its ability to generate new plants from both seeds and rhizomes. Because of this reproduction strategy, resource allocation of this perennial species differs from that of the annual taxa with which it was compared in this study. However, rhizome development in johnsongrass was not observed during the course of this 31-d experiment. Studies have shown that johnsongrass rhizomes begin to form between 42 and 50 d after sowing (Monaghan 1979; Oyer et al. 1959). Nonetheless, it should be noted that conclusions reached as a result of our findings involving johnsongrass apply to seedlings and not to plants arising from rhizomes.

There were no main or interactive effects caused by the addition of KNO_3 solution containing 30 μg ml^{-1} N, so data presented are averaged over treatments with and without exogenous N. Final plant density per pot did not differ among treatments (data not shown), so expected shoot and root dry weights per pot in 50:50 mixtures were calculated as 50% of the dry weights in monoculture. Measures of variability in the form of confidence intervals (0.95) were included to test the hypothesis that shoot and root dry weights for each taxon in the mixture did not differ from the expected dry weights.

Shoot dry weight obtained from grain sorghum grown in mixture with johnsongrass seedlings was greater than expected when compared with shoot dry weight calculated from grain sorghum grown in monoculture; a similar comparison of shoot dry weight of johnsongrass seedlings determined that their shoot dry weight was less than expected when grown in mixture with grain sorghum (Figure 1b). Shoot dry weight did not differ from that expected for the shattercane–sorghum (Figure 1a) or johnsongrass–shattercane (Figure 1c) comparisons. There were two instances when actual root dry weight and expected root dry weight calculated from root dry weight in monoculture differed: root dry weight of grain sorghum grown in mixture with shattercane was greater than expected when compared with root dry weight calculated from grain sorghum grown in monoculture (Figure 2a); and for grain sorghum grown in mixture with johnsongrass seedlings, root dry weight was greater than expected (Figure 2b).

Replacement series indices calculated from shoot or root dry weight for an individual plant in monoculture and in mixture (Cousens and O'Neill 1993) were used to characterize competitiveness among the taxa in this study. RYT was included to describe the demand made by pairs of taxa on the resource or resources in limited supply (Harper 1977). If taxa shared and competed fully for the same limiting resource(s), then the value of RYT was expected to be 1.0; if the value of RYT was greater than 1.0, then it was likely that competition was avoided because supply was greater than demand or the taxa made different demands on resources. Also included were CR, k, and A to indicate which taxon in each mixture was more competitive. If CR > 1.0, $k_A > k_B$, and $A > 0$, then taxon A was more competitive than B; however, taxon B was the more competitive taxon if CR < 1.0, $k_A < k_B$, and $A < 0$.

Replacement series indices showed that these related taxa competed with differing abilities, although data were insufficient to identify the limiting resource(s). We determined, after constructing confidence intervals (0.95), that 1.0 was within the range of each RYT implying that the RYT for every mixture did not differ from 1.0 (Table 1). We concluded that grain sorghum, shattercane, and johnsongrass seedlings shared and competed fully for the same limiting resource(s) thereby supporting our assumption that these

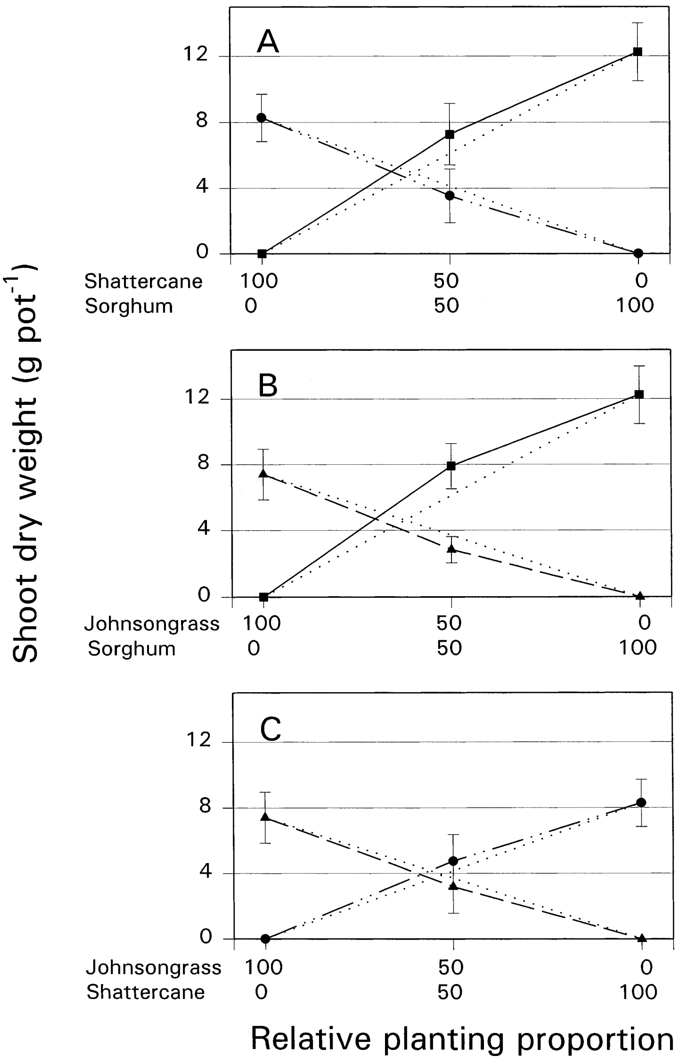

FIGURE 1. Effect of relative planting proportion on shoot dry weight of plants grown in mixtures consisting of (a) shattercane (●) and grain sorghum (■), (b) johnsongrass (▲) and grain sorghum (■), and (c) johnsongrass (▲) and shattercane (●).

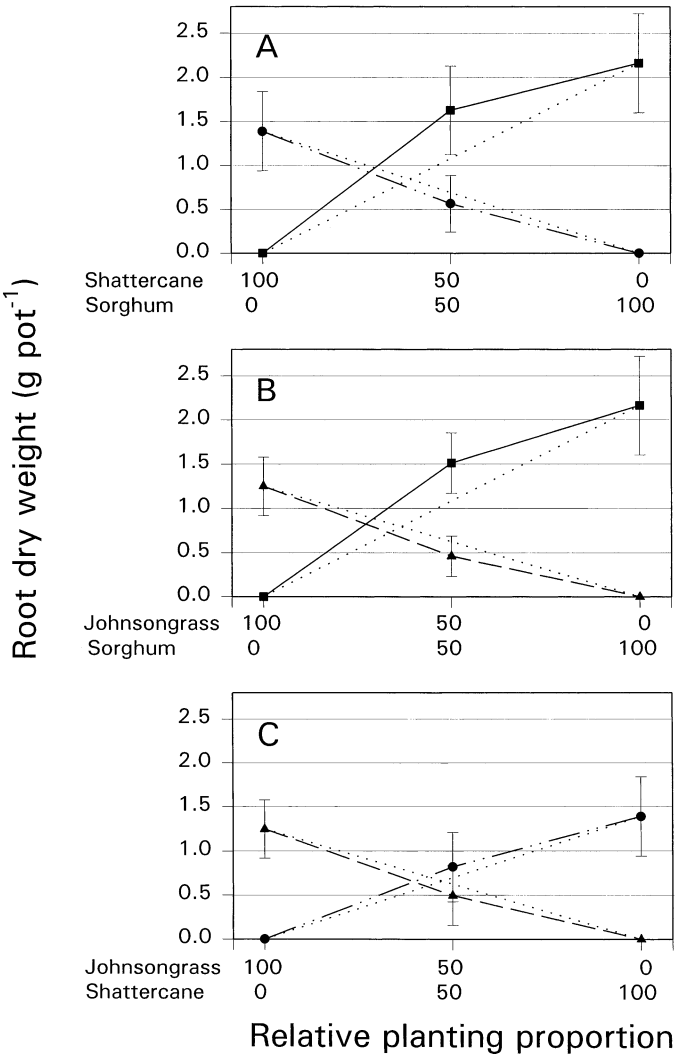

FIGURE 2. Effect of relative planting proportion on root dry weight of plants grown in mixtures consisting of (a) shattercane (●) and grain sorghum (■), (b) johnsongrass (▲) and grain sorghum (■), and (c) johnsongrass (▲) and shattercane (●).

TABLE 1. Replacement series indices calculated for two-species mixtures of grain sorghum [*Sorghum bicolor* (L.) Moench], shattercane [*Sorghum bicolor* (L.) Moench], and johnsongrass [*Sorghum halepense* (L.) Pers.]. Taxa in each mixture were designed as taxon A or B.

	Shoot dry weight			Root dry weight		
Index[a]	A = shattercane, B = grain sorghum	A = johnsongrass, B = grain sorghum	A = johnsongrass, B = shattercane	A = shattercane, B = grain sorghum	A = johnsongrass, B = grain sorghum	A = johnsongrass, B = shattercane
R_A	0.45	0.38	0.45	0.43	0.33	0.43
R_B	0.60	0.66	0.62	0.78	0.75	0.66
RYT	1.06	1.04	1.07	1.21	1.08	1.09
CR	0.75	0.57	0.73	0.55	0.44	0.64
k_A	0.83	0.61	0.83	0.75	0.49	0.74
k_B	1.53	1.98	1.61	3.54	3.04	1.98
k_{AB}	1.27	1.21	1.35	2.67	1.48	1.46
A	−0.15	−0.28	−0.16	−0.35	−0.42	−0.24

[a] R_A is the relative yield of taxon A; R_B is the relative yield of taxon B; RYT is the relative yield total; CR is the competitive ratio; k_A is the relative crowding coefficient of taxon A; k_B is the relative crowding coefficient of taxon B; k_{AB} is the relative crowding coefficient for the mixture of taxa A and B; and A is the aggressivity, according to Cousens and O'Neill (1993).

taxa have similar requirements for survival because they are close relatives. A competitive hierarchy for the three taxa was suggested by the calculated values of CR, k, and A. CR was less than 1.0 for all pairs implying that taxon B was more competitive than taxon A; between the taxa in each pair in this experiment, a larger k value identified taxon B as the more aggressive taxon; A was greater than 0 for all mixtures in this experiment implying that taxon B was more competitive than taxon A. These three indices describe grain sorghum as the most competitive taxon, and between the weedy taxa, shattercane was more competitive than seedlings of johnsongrass.

Taxa were the only main or interactive effects for which it was shown by ANOVA that number of leaves, plant height, and root–shoot ratio differed. Averaged over mixtures and regardless of N fertilizer application, number of leaves differed among taxa ($P = 0.0001$) such that grain sorghum had the greatest number of leaves, shattercane leaf number was intermediate, and johnsongrass seedlings had the fewest number of leaves (data not shown). Height of an average grain sorghum plant did not differ from that of shattercane and was approximately 58 cm, whereas johnsongrass seedlings were shorter with an average height of only 53 cm ($P = 0.0008$). Root–shoot ratio of grain sorghum was 0.20, which was larger than root–shoot ratios of shattercane and johnsongrass seedlings. Root–shoot ratios of shattercane and johnsongrass seedlings did not differ and were approximately equal to 0.16 ($P = 0.0012$).

The general conclusion of the replacement design experiment was that at the end of this 31-d-long trial, grain sorghum was competitively superior to its weedy relatives. For *Sorghum*, growth during this period was primarily vegetative with inflorescences just beginning to differentiate toward the end. Therefore, this was a time of rapid growth when it was most likely that competitive hierarchies were formed. During this period, the crop was more competitive than either weed species. Data from experiments included in this paper were insufficient to describe the mechanisms involved. However, as previously alluded to, this paper is followed by Part II of the series (Hoffman et al. 2002), the objective of which was to describe traits that could bring about greater competitiveness in grain sorghum for the resources shared with its weedy relatives. Results of the replacement design experiment also showed that grain sorghum, shattercane, and seedlings of johnsongrass shared and competed fully for the same limiting resource(s), although it was not possible to identify the resources involved. Because these closely related taxa differ in competitive ability and compete for similar resources, they could be useful subjects for future studies. For example, theories involved in the present debate over traits that determine competitive success (Grace 1991) predict that competitive superiority will result from the ability to either grow quickly and capture resources rapidly (Grime 1979, 1987) or draw resources down to a low level and still prosper (Tilman 1977, 1988). We propose that these *Sorghum* taxa might be of use to differentiate these two theories experimentally.

Although many find fault with replacement series experiments (Connolly 1986; Firbank and Watkinson 1985; Inouye and Schaffer 1981; Mead 1979), we found this design effective as a means of establishing a competitive hierarchy and testing the effects of exogenous N. Results of preliminary studies lead us to conclude that added N could have measurable effects on *Sorghum*. One such study was a petri dish bioassay in which seeds were incubated for 7 d in the presence of water or various levels of N. In each petri dish, an equal number of grain sorghum or shattercane seeds were placed on a filter paper moistened with water or inorganic N salt solution (KNO_3), containing 10, 30, 50, 300, or 3,000 $\mu g\ ml^{-1}$ N. Moisture was maintained by daily additions of the appropriate solution to each petri dish. No effect on germination of either taxon was detected, and shoot dry weight of grain sorghum and shattercane seedlings was similar whether grown in the presence of water or solution containing 10, 30, 50, or 300 $\mu g\ ml^{-1}$ N (data not shown). The highest rate of N stunted shoot growth of both grain sorghum and shattercane.

To gain a clearer understanding of how shattercane might respond to exogenous N, another preliminary experiment was conducted. This experiment was a 14-d greenhouse study in which shattercane was grown in pots filled with soil moistened with water or inorganic N salt solution (KNO_3), containing N at 10, 30, or 50 $\mu g\ ml^{-1}$. To maintain soil at field capacity, the appropriate solution was added as required by subsurface irrigation. As an additional treatment, half of the pots contained a single shattercane plant, whereas shattercane was planted with intraspecific competitors in the others. When grown without competitors, shattercane shoot dry weight did not differ between treatments moistened with water compared with those moistened with various levels of the N-containing solution (data not shown). Therefore, resources in soil were such that adding the fertilizer solution did not increase shoot growth of shattercane grown without competition. Also, there were no deleterious effects on shattercane grown in soil kept moist by repeated applications of solutions containing 10, 30, or 50 $\mu g\ ml^{-1}$ N. When grown with competitors in the presence of the solution containing N at 30 $\mu g\ ml^{-1}$, shattercane shoot dry weight increased when compared with shoot dry weight of shattercane grown in soil moistened with water. In treatments receiving solution containing 10 or 50 $\mu g\ ml^{-1}$ N, shoot dry weight of shattercane did not differ from that of shattercane grown in soil moistened with water. This study was repeated, so it is likely that the response by shattercane to an interactive effect of the solution with 30 $\mu g\ ml^{-1}$ N and intraspecific competition was real. Our intention was to further examine this effect on shattercane grown with competition from other *Sorghum* taxa including a crop and another weedy species.

Based on investigations by other researchers studying timing of N application in which competitive interactions between crops and weeds were confounded (Davidson 1984; Wicks 1984), our expectation was that competitive relationships among *Sorghum* taxa would be affected by added N. Exley and Snaydon (1992), for example, reported that fertilization with N lessened some of the effects of root competition between wheat (*Triticum aestivum* L.) and blackgrass (*Alopecurus myosuroides* Huds.). In addition, to maximize the chance of detecting the effects of N on competitive relationships among *Sorghum* taxa, the fertilizer was supplied in a continuous low dose over the course of our studies. Finally, the replacement design experiment was conducted for 31 d to coincide with the time when *Sorghum* growth was vegetative, active, and most likely responsive to exogenous N. However, neither crop nor weeds responded to added N likely because the amount of the nutrient naturally occurring in the soil was greater than demand. Therefore, on the basis of these data, we cannot suggest further research on N management for cultivated sorghum as a means of increasing crop competitiveness relative to that of weeds. Furthermore, in soil similar to Webster silty clay loam, the common practice of applying N fertilizer at planting (Lamond et al. 1991; Roy and Wright 1973) might not coincide with the crop's demand for N and could promote leaching or other undesirable effects.

Sources of Materials

[1] V & J Seed Farms, P.O. Box 82, Woodstock, IL 60098.

Acknowledgments

Contribution from the U.S. Department of Agriculture Research Service, National Soil Tilth Laboratory, Ames, IA. The authors thank Dr. T. Kaspar and Dr. M. Liebman for reading early versions of the manuscript and providing helpful comments.

Literature Cited

Alfoldi, Z. and L. Pinter. 1992. Accumulation and partitioning of biomass and soluble carbohydrates in maize seedlings as affected by source of nitrogen, nitrogen concentration, and cultivar. J. Plant Nutr. 15:2567–2583.

Angonin, C., J. P. Caussanel, and J. M. Meynard. 1996. Competition between winter wheat and *Veronica hederifolia*: influence of weed density and the amount and timing of nitrogen application. Weed Res. 36: 175–187.

Arriola, P. E. and N. C. Ellstrand. 1996. Crop-to-weed gene flow in the genus *Sorghum* (Poaceae): spontaneous interspecific hybridization between johnsongrass, *Sorghum halepense*, and crop sorghum, *S. bicolor*. Am. J. Bot. 83:1153–1160.

Baker, H. G. 1972. Migration of weeds. Pages 327–347 *in* D. H. Valentine, ed. Taxonomy, Phytogeography and Evolution. London: Academic Press.

Ball, D. A., D. J. Wysocki, and T. G. Chastain. 1996. Nitrogen application timing effects on downy brome (*Bromus tectorum*) and winter wheat (*Triticum aestivum*) growth and yield. Weed Technol. 10:305–310.

Burnside, O. C. 1965. Seed and Phenological Studies with Shattercane. Lincoln, NE: Nebraska Agricultural Experiment Station Research Bulletin 220. 37 p.

Burnside, O. C. 1968. Control of wild cane in soybean. Weed Sci. 16:18–22.

Carlson, D. R. and O. C. Burnside. 1981. Use of the recirculating sprayer to control tall weed escapes in crops. Weed Sci. 29:174–179.

Carlson, H. L. and J. E. Hill. 1985. Wild oat (*Avena fatua*) competition with spring wheat: effects of nitrogen fertilization. Weed Sci. 34:29–33.

Celarier, R. P. 1958. Cytotaxonomic notes on the subsection Halepensia of the genus *Sorghum*. Bull. Torrey Bot. Club 85:49–62.

Connolly, J. 1986. On difficulties with replacement-series methodology in mixture experiments. J. Appl. Ecol. 23:125–137.

Cousens, R. and M. O'Neill. 1993. Density dependence of replacement series experiments. Oikos 66:347–352.

Davidson, S. 1984. Wheat and ryegrass competition for nitrogen. Rural Res. 122:4–6.

de Wet, J.M.J. 1978. Systematics and evolution of *Sorghum* sect. *Sorghum* (Gramineae). Am. J. Bot. 65:477–484.

de Wet, J.M.J. and J. R. Harlan. 1971. The origin and domestication of *Sorghum bicolor*. Econ. Bot. 25:128–135.

de Wet, J.M.J., J. R. Harlan, and E. G. Price. 1970. Origin of variability in the spontanea complex of *Sorghum bicolor*. Am. J. Bot. 57:704–707.

de Wet, J.M.J., J. R. Harlan, and E. G. Price. 1976. Variability in *Sorghum bicolor*. Pages 453–463 *in* J. R. Harlan, J.M.J. de Wet, and A.B.L. Stemler, eds. Origins of African Plant Domestication. The Hague: Mouton Press.

de Wet, J.M.J. and J. P. Huckabay. 1967. The origin of *Sorghum bicolor*. II. Distribution and domestication. Evolution 21:787–802.

De Wit, C. T. 1960. On competition. Versl. Landbouwkd. Onderz. 66:8–82.

Dowler, C. C. 1994. Weed survey—southern states. Proc. South. Weed Sci. Soc. 47:279–299.

Exley, D. M. and R. W. Snaydon. 1992. Effects of nitrogen fertilizer and emergence date on root and shoot competition between wheat and blackgrass. Weed Res. 32:175–182.

Fawcett, R. S. and F. W. Slife. 1978. Effects of field applications of nitrate on weed seed germination and dormancy. Weed Sci. 26:594–596.

Firbank, L. G. and A. R. Watkinson. 1985. On the analysis of competition within two-species mixtures of plants. J. Appl. Ecol. 22:503–517.

Gardner, J. C., J. W. Maranville, and E. T. Paparozzi. 1994. Nitrogen use efficiency among diverse sorghum cultivars. Crop Sci. 34:728–733.

Grace, J. B. 1991. A clarification of the debate between Grime and Tilman. Funct. Ecol. 5:583–587.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. London: J. Wiley. 222 p.

Grime, J. P. 1987. Dominant and subordinate components of plant communities: implications for succession, stability and diversity. Pages 413–428 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, eds. Colonization, Succession and Diversity. Oxford: Blackwell.

Hadley, H. H. 1953. Cytological relationships between *Sorghum vulgare* and *S. halepense*. Agron. J. 45:139–143.

Hadley, H. H. 1958. Chromosome numbers, fertility and rhizome expression of hybrids between grain sorghum and johnsongrass. Agron. J. 50:278–282.

Harlan, J. R. and J.M.J. de Wet. 1974. Sympatric evolution in sorghum. Genetics 78:473–474.

Harlan, J. R. and J.M.J. de Wet. 1972. A simplified classification of cultivated sorghum. Crop Sci. 12:172–176.

Harper, J. L. 1977. The Population Biology of Plants. London: Academic Press. pp. 255–380.

Hoffman, M. L., D. D. Buhler, and E. E. Regnier. 2002. Utilizing *Sorghum* as a functional model of crop–weed competition. II. Effects of manipulating emergence time or rate. Weed Sci. 50:473–478.

Holm, L. G., D. L. Plucknett, J. V. Pancho, and J. P. Herberger. 1977. The World's Worst Weeds: Distribution and Biology. Honolulu, HI: University Press of Hawaii. pp. 54–61.

Inouye, R. S. and W. M. Schaffer. 1981. On the ecological meaning of ratio (deWit) diagrams in plant ecology. Ecology 62:1679–1681.

Karlen, D. L. and T. S. Colvin. 1992. Alternative farming system effects on profile nitrogen concentrations on two Iowa farms. Soil Sci. Am. J. 56:1249–1256.

Karper, R. E. and A. T. Chisholm. 1936. Chromosome numbers in *Sorghum*. Am. J. Bot. 23:369–374.

Lamond, R. E., D. A. Whitney, J. S. Hickman, and L. C. Bonczkowski. 1991. Nitrogen rate and placement for grain sorghum production in no-tillage systems. J. Prod. Agric. 4:531–535.

Maranville, J. W., R. B. Clark, and W. M. Ross. 1980. Nitrogen efficiency in grain sorghum. J. Plant Nutr. 2:577–589.

Mead, R. 1979. Competition experiments. Biometrics 35:41–54.

Monaghan, N. 1979. The biology of johnson grass (*Sorghum halepense*). Weed Res. 14:261–267.

Onken, A. B., M. J. Lavelle, and G. C. Peterson. 1985. Improving nutrient use efficiency in sorghums. Pages 15–27 *in* D. Wilkinson, ed. Proceedings of the 41st Annual Corn and Sorghum Industry Research Conference. Washington, DC: American Seed Trade Association.

Oyer, E. B., G. A. Gries, and B. J. Rogers. 1959. The seasonal development of johnson grass plants. Weeds 7:13–19.

Quinby, J. R. and J. H. Martin. 1954. Sorghum improvement. Adv. Agron. 6:305–359.

Rasmussen, K., J. Rasmussen, and J. Petersen. 1996. Effects of fertilizer placement on weeds in weed harrowed spring barley. Acta Agric. Scand. 46:192–196.

Roy, R. N. and B. D. Wright. 1973. Sorghum growth and nutrient uptake in relation to soil fertility: I. Dry matter accumulation patterns, yield, and N content of grain. Agron. J. 65:709–711.

Sardi, K. and I. Beres. 1996. Effects of fertilizer salts on the germination of corn, winter wheat, and their common weed species. Commun. Soil Plant Anal. 27:1227–1235.

Snowden, J. D. 1936. The Cultivated Races of *Sorghum*. London: Allard and Son. 272 p.

Snowden, J. D. 1955. The wild fodder sorghums of the section *Eusorghum*. J. Linn. Soc. 5:191–260.

Soil Conservation Service. 1981. Soil Survey of Boone County, Iowa. Washington, DC: U.S. Government Printing Office. 149 p.
Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348.
Tilman, D. 1985. The resource ratio hypothesis of succession. Am. Nat. 125:827–852.
Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton: Princeton Monographs. 296 p.
Tollenaar, M., S. P. Nissanka, A. Aguilera, S. F. Weise, and C. J. Swanton. 1994. Effect of weed interference and soil nitrogen on four maize hybrids. Agron. J. 86:596–601.
Voss, R. D., A. P. Mallarino, and R. Killorn. 1996. General Guide for Crop Nutrient Recommendations in Iowa. Ames, IA: Iowa State University Extension Service Publication Pm-1688. 22 p.
Warwick, S. I., B. K. Thompson, and L. D. Black. 1984. Population variation in *Sorghum halepense*, johnson grass, at the northern limits of its range. Can. J. Bot. 62:1781–1790.
Wicks, G. A. 1984. Integrated systems for control and management of downy brome (*Bromus tectorum*) in cropland. Weed Sci. 32(Suppl. 1): 26–31.
Zweifel, T. R., J. W. Maranville, W. M. Ross, and R. B. Clark. 1987. Nitrogen fertility and irrigation influence on grain sorghum nitrogen efficiency. Agron. J. 79:419–422.

Received January 18, 2001, and approved December 8, 2001.