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Growth and fitness components of wild × cultivated *Sorghum bicolor* (Poaceae) hybrids in Nebraska[1]

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- *Premise of the study:* Gene flow from crops to wild relatives has received considerable attention since the advent of genetically modified crops. Numerous researchers have found wild–crop hybrids to be nearly as fit as their wild parents, which suggests that crop genes may persist in wild populations. Components of the ecological fitness of cultivated sorghum, its wild relative, shattercane, and their hybrids have not been studied.
- *Methods:* To assess the potential for gene introgression into shattercane, we crossed cultivated sorghum to a single inbred shattercane line to produce F_1 hybrids and measured growth and several components of ecological fitness in relation to both parents in Nebraska, USA.
- *Key results:* Germination of F_1 seeds was similar to that of its shattercane parent except at high temperatures, where it was as sensitive as the sorghum parent. The F_1 grew taller and produced more biomass than either parent, but the F_1 leaf area index was intermediate. Fecundity of the F_1 plant was similar to that of shattercane and much greater than that of cultivated sorghum.
- *Conclusions:* Considering all data, the ecological fitness of shattercane × cultivated sorghum F_1 hybrids may be equivalent to the wild shattercane parent, which suggests that crop genes that are either neutral or beneficial to shattercane would persist in populations within agroecosystems.

Key words: fecundity; fitness; germination; introgression; phenology; wild–crop gene flow.

Gene flow drives evolutionary changes in plant populations (Arnold et al., 1999; Barton, 2001). The ultimate result of gene flow is to introduce new alleles or to change the frequency of alleles within the population (Mercer et al., 2006). Many agricultural crops have weedy relatives, and crop-to-weed gene flow is common if both the crop and the weed are sexually compatible, share a common pollinator, and have synchronous flowering times (Baker, 1972; Doggett, 1988; Arriola and Ellstrand, 1997; Ellstrand et al., 1999). Although many studies have reported on the existence of gene flow and hybridization between crop and wild populations, little is known about the rate of hybridization, the importance of crop alleles on weediness, and the persistence of crop traits in wild populations (Arriola and Ellstrand, 1997; Spencer and Snow, 2001). With the global interest to commercialize transgenic crops to express traits for herbicide resistance, insect resistance, and improved nutritional quality, additional crop–wild hybridization and ecological fitness studies are essential to assess potential risks associated with transgene escape to the wild population (Goodman and Newell, 1985; Tiedje et al., 1989; Ellstrand and Hoffman, 1990; Raybould and Gray, 1994). Understanding the components of the ecological fitness of wild–crop hybrids will provide baseline information to predict the success of such hybrids and the potential for introgression of the transgene into the wild population (Ellstrand et al., 1999).

Sorghum (*Sorghum bicolor* subsp. *bicolor* [L.] Moench) is the fifth most important cereal crop worldwide (Doggett, 1988) and is consumed as a staple food in many countries in Africa and Asia. In the United States, it is a major economic crop grown for animal feed and ethanol production (Paterson, 2008). The sorghum genus includes a wide variety of feral populations, many of which are regarded as agricultural weeds. Shattercane (*S. bicolor* subsp. *drummondii* Nees ex Steud de Wet & Harlan) closely resembles cultivated sorghum (Defelice, 2006), primarily differing from it by three traits: (1) seed shattering, which enables the weed to disperse its seeds prior to crop harvest; (2) seed dormancy and longevity; and (3) height, for which cultivated sorghum varieties contain a dwarf trait that is controlled by four recessive genes (Quinby and Karper, 1954; Burnside, 1965; Fellows and Roeth, 1992). Being a close weedy relative of cultivated sorghum, shattercane is considered the most troublesome weed in sorghum fields and a major economic problem in row crops in the United States (Kegode and Pearce, 1998; Hans and Johnson, 2002; International Crops Research Institute for the Semi-Arid Tropics, 2002).

Grain sorghum and shattercane are both diploid (2n = 20) and sexually compatible. Grain sorghum has been shown to outcross at a rate of 10–15%, and pollination can occur at a frequency of 0.06% at a distance of 158 m from the pollen source (Ellstrand and Foster, 1983; Schmidt and Bothma, 2006). Sudangrass, a cultivated form of *S. bicolor* subsp. *drummondii*, is a related (2n = 20) species that outcrosses at a much higher rate (20–61%) than grain sorghum, presumably because sudangrass

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has a more open panicle than grain sorghum (Pedersen et al., 1998). Shattercane panicles are morphologically more similar to those of sudangrass than to those of grain sorghum, and shattercane may outcross at a greater rate than grain sorghum. If this is the case, the opportunity for natural shattercane × sorghum hybridization in the field may be greater than the rate of sorghum outcrossing.

Arriola and Ellstrand (1996, 1997) showed that hybridization between grain sorghum and johnsongrass (*S. halepense* L.), a tetraploid (4n = 40) relative, produced mostly sterile hybrids. Nevertheless, sorghum × johnsongrass hybrids were fertile at a hybridization rate of 2% at a distance of 100 m from the crop. Arriola and Ellstrand (1997) also studied several ecological fitness characteristics of johnsongrass, sorghum, and their hybrids and found no increase in fitness with respect to time of flowering, panicle production, pollen viability, and seed production. There was apparently no barrier to prevent the transfer of any beneficial or neutral traits from the crop to the wild *S. halepense* population (Arriola and Ellstrand, 1997). However, there are no reports of similar studies on the ecological fitness of shattercane, sorghum, and their hybrids.

Traits that contribute to the ecological fitness of a wild population include seed dormancy and viability, germinability, vegetative growth and competitive ability, mode of reproduction, male–female fertility, and fecundity (Jenczewski et al., 2003). Many field crops are annuals and derived from weedy progenitors (Simmonds, 1976; Linder, 1998). Most crops were bred to remove seed dormancy, so seed germination occurs at uniform rates soon after sowing. However, dormancy is an important weedy characteristic among wild relatives of the crop because it allows the species a mechanism for dispersal over time. Time of emergence and early seedling growth can determine the relative fitness of individual species under competition (Schmitt and Ehrhardt, 1990; Miller et al., 1994). If a newly inherited allele affects germination, dormancy, or seed longevity in soil, fitness and population persistence could be affected by that trait (Linder and Schmitt, 1995). Therefore, the dormancy and germination characteristics of wild–crop hybrids will influence the persistence of hybrids and the opportunities for introgression of crop genes into the wild population (Linder and Schmitt, 1995). Biomass accumulation, leaf area, and height characteristics of a species contribute to its competitive success in a mixed canopy (Lindquist et al., 1998), thus contributing to the overall life-cycle fitness of the species (Song et al., 2004). Although the fitness components of F_1 hybrids do not determine the ultimate introgression of all crop genes, they affect the initial course of introgression, altering the genetic frequencies of crop alleles over generations and subjecting them to further selection or drift (Mercer et al., 2006).

Our objectives in this study were to determine growth and several components of the ecological fitness of shattercane × sorghum F_1 hybrids in comparison with their parents, in germination chambers and in the field. Measured components of ecological fitness of shattercane, sorghum, and their F_1 hybrid included early emergence and seedling survival, phenological development, plant height, tiller production, leaf area, aboveground biomass, panicle production, and fecundity. Understanding the relative ecological fitness of shattercane, sorghum, and their hybrids will be useful for predicting the fate of potential transgene escapes from cultivated sorghum to its weedy relative, shattercane, in the United States.

MATERIALS AND METHODS

Plant material—The parental line of cultivated sorghum we used, RTx430 (Miller, 1984), is an elite inbred line of commercial importance. The shattercane line we used was selected by single-seed descent from a single shattercane population of unknown origin collected near Lincoln, Nebraska, USA. That selection was self pollinated for six generations to ensure homozygosity. A cytoplasmic male sterile version of this shattercane line was concurrently created by first crossing the shattercane selection to a source of A_3 cytoplasm (A_3N243 sudangrass [*Sorghum bicolor* subsp. *drummondii* Nees ex Steud de Wet & Harlan]; Pedersen and Toy, 1998), then backcrossing each of six backcross generations to the shattercane line as it was being advanced through its six selfing generations. The result was the development of an A_3/B pair shattercane line, with the A_3-line being cytoplasmic male sterile and the B-line being fully fertile. The two lines are nearly identical phenotypically, with ~97% of the nuclear genes of the A_3-line being from the B-line. The B-line is commonly referred to as the "maintainer" line of the pair because it is necessarily used as a source of pollen to produce seed of successive generations of the A_3 line. This A_3/B pair is stable and provided a repeatable and stable source of male-fertile and male-sterile shattercane seed for this study and facilitated the production of large numbers of F1 shattercane × sorghum (RTx430) seed. Sorghum (RTx430), shattercane, A_3 shattercane, and A_3 shattercane × RTx430 hybrid seeds used in this study were produced in individual greenhouse isolations in winter 2007. Seeds of each genotype were harvested at maturity and threshed. An aliquot of seeds were kept at room temperature for use within 4 d. All remaining seeds were stored at 4°C until further use.

Laboratory germination experiment—Germination of fresh seeds of each genotype was tested within 4–30 d of collection from mature plants. An experiment was conducted in germination chambers to determine the effect of temperature on seed germination over time. Each experimental unit consisted of an 11-cm-diameter Petri dish with 25 seeds evenly spaced on wet blotter paper. Deionized water was sprayed as required to keep the blotter paper moist. Petri dishes were incubated in temperature-controlled germination chambers (LT 36VL seed chamber, Geneva Scientific, Fontana, Wisconsin, USA) at the Nebraska Crop Improvement Association laboratory at the University of Nebraska–Lincoln. Temperature treatments included four constant temperatures (20, 25, 30, and 35°C) and three variable temperatures: standard germination test for sorghum (varying diurnally from 20 to 30°C, used as the control group for comparison), cold germination (prechill at 10°C for 5 d followed by standard germination), and accelerated-aging germination (accelerated aging at 43°C for 3 d at high humidity followed by standard germination). The accelerated-aging treatment allows for an assessment of seed response to temperatures in excess of 40°C, which may occur within the top 1–2 cm of an agricultural soil in the middle and southern latitudes, where sorghum species are common. Special (9 cm diameter) Petri dishes were used in the accelerated-aging treatment, in which seeds were suspended on a metallic screen 2–3 cm above 40 mL water during the 3 d at 43°C. Four replicates of 25 seeds of each type were incubated in each temperature treatment. The photoperiod maintained during the experiment was 14:10 h day:night for all germination chambers. Standard 2006 Association of Official Seed Analysts (AOSA) procedures were followed to conduct germination tests, and the entire experiment was conducted twice. Germination counts were made daily for a maximum of 27 d. Seeds with protruded radicles were considered germinated. Final germination was converted to percentage germinated out of 25 seeds. At the end of the experiment, tetrazolium (TZ) tests were conducted to evaluate the viability of nongerminated seed. The nongerminated seeds were stripped vertically in the middle of the seed coat under a microscope. One-half portion of the seed embryo was embedded into 30–40 mL of 1% 2, 3, 5-triphenyl-tetrazolium chloride solution for 12 h at room temperature. Seeds that turned red were considered viable, whereas dead seeds remained colorless.

Field experiment—A field experiment was conducted at two locations in 2008 to measure components of ecological fitness of the F_1 hybrids and their parents. Locations included the horticultural research farm on the University of Nebraska campus in Lincoln and the Agricultural Research and Development Center near Ithaca, Nebraska. Soil at Lincoln was an eroded Wymore silty clay loam (fine, smectitic, mesic, Aquic Argiudoll) with 3–7% slope, pH 6.5–7.2, and 3.0% soil organic carbon (based on soil test). Soil at Ithaca was a Sharpsburg silty clay loam (fine, smectitic, mesic, Typic Argiudoll) with <1% slope, pH 5.6–6.4, and 3.5% soil organic carbon. Prior to establishing the experiment, fields were tilled with a tandem disk. The field at Ithaca was fertilized with

150 kg N ha^{-1} applied as anhydrous ammonia, whereas the Lincoln location was not fertilized because of adverse weather conditions prior to planting.

Two seed treatments were included in the field experiment because shattercane seeds display various degrees of dormancy (Burnside, 1965; Kegode and Pearce, 1998). Seeds in their natural state were considered potentially dormant and are hereafter labeled as the dormant (D) treatment. A preliminary experiment with a dormant line of shattercane showed that the accelerated aging treatment described above was effective at breaking shattercane dormancy but was partially deleterious to sorghum. Therefore, to overcome possible dormancy in our seeds, we placed the shattercane, A_3 shattercane, and F_1 hybrid seeds in the accelerated-aging treatment (as described above) immediately prior to planting them in the field. These seeds are hereafter labeled as the nondormant (ND) treatment. Sorghum seeds of the ND treatment were placed in similar dishes and kept under high humidity but were exposed to room temperature rather than 43°C.

Seeds of all four genotypes and both seed treatments were sown at both locations on 2 June 2008 (day 154). Fifty seeds of each type were sown in a uniform spacing (~6 cm apart) by hand to a depth of 2 cm in a single 3-m-long row. Four adjacent rows, one for each genotype, were spaced 0.76 m apart to make up a complete block. Temperature and relative humidity at planting were 27°C and 89% at Lincoln and 31°C and 75% at Ithaca, respectively.

An experimental unit consisted of a single row of each genotype arranged in four complete replicate blocks. Blocks were separated by a 0.6-m alley. Seed treatments were established in separate but adjacent blocks. The experiment at Ithaca was irrigated three times during the growing season with a linear-move irrigation system to ensure sufficient water supply to surrounding corn and sorghum experiments. The experiment at Lincoln was not irrigated. Weeds that emerged during the season were removed as needed by hand or with a hoe.

Data on emergence and mortality were collected every other day or as required for the first 20 d. Field emergence over time was tracked by marking all newly emerged plants with colored plastic pot stakes; the color of the stake signified the date of emergence. Stakes were removed and their color recorded as plants died to follow plant mortality over time. Five plants were randomly selected and permanently marked within the first week of emergence to obtain nondestructive measures of plant height, vegetative growth stage, tiller height, and number of tillers on a weekly basis throughout the growing season. Vegetative growth stage was assessed weekly from emergence through emergence of the flag leaf on the main culm by counting the number of fully emerged leaf collars (the junction between the lamina and sheath). Total plant biomass and leaf area were measured by clipping five randomly selected plants per experimental unit at the soil surface at panicle emergence on days 217 and 225 at Lincoln and Ithaca, respectively. Destructively harvested plants were different from those used to assess development over time and were separated from those plants by at least three plants to minimize border effects after their harvest. The five harvested plants from each experimental unit were then separated into leaves and stems, the pooled leaf area was determined with an area meter (LI-3000, Li-Cor, Lincoln, Nebraska, USA), tissues within an organ group (e.g., leaves, stems, and reproductive tissue) were pooled and dried at 60°C to constant weight. Panicles of the five plants used for measuring development over time were bagged after pollination and tied to a stake to ensure no loss of seed and panicles harvested when seeds were fully mature. Seeds of each panicle were threshed by hand and counted with a seed counter (Old Mill Seed Counter, International Marketing and Design, San Antonio, Texas, USA) and 100 seed mass determined on at least four samples of 100 seeds from each panicle. Fecundity was determined as the total number of seeds produced per plant and averaged across the five plants within an experimental unit.

Statistical analysis—The experimental design in the germination chambers was completely randomized; seven temperature treatments were randomly treated to the four levels of genotype. Total percent germination was compared among treatments with analysis of variance (ANOVA) using the mixed procedure in SAS (SAS Institute, Cary, North Carolina, USA), in which experimental run, genotype, and temperature treatment were treated as fixed effects and replicate block and block interactions were random effects. Data were pooled over experimental runs because run × treatment interactions were not significant ($P = 0.12$). Germination of the shattercane and the A_3 shattercane within temperature treatments were compared using orthogonal contrasts and were pooled into a common shattercane population because they did not differ in any temperature treatment ($P > 0.27$ for all temperature treatments). Germination of the F_1 hybrid was compared with that of its parents (sorghum and shattercane) within a temperature treatment using orthogonal contrasts.

To assess differences in the pattern of seed germination over time among genotypes, a two-parameter logistic model $Y = 1/[1 + \exp(\alpha - \beta x)]$ was fit to proportional seed germination within each experimental unit using nonlinear regression analysis (SAS PROC NLIN), where Y is cumulative emergence expressed as a fraction of the maximum emergence for that experimental unit, x is time (days), and α and β are shape coefficients. The ratio α/β provides an estimate of the time (d) to reach 50% maximum emergence and was calculated for each experimental unit, then subjected to ANOVA as described above to determine whether the time to reach 50% germination differed between the F_1 and its parents within a temperature treatment. Parameter estimates averaged across genotype were compared with that in the control-group temperature treatment (20–30°C) using orthogonal contrasts.

The field experimental design was a randomized complete block. Data were analyzed with ANOVA using the mixed procedure in SAS, in which location, seed treatment, and genotype were treated as fixed effects. Block nested in location was the random effect in the overall ANOVA (Table 1), and block and its interactions were random effects for within-location analyses. Our first aim was to test whether the genotype treatment effects differed among seed treatments. If there was no seed treatment × genotype interaction within a location, seed treatments were pooled for subsequent analysis (analyses not shown). Our second aim was to test the hypothesis that genotype treatment effects do not differ between locations. If there was no location × genotype interaction effect, locations were pooled for further analysis. Our third aim was to test, using an orthogonal contrast, the hypothesis that the wild-type shattercane and the A_3 shattercane do not differ (Table 2). If the shattercane and A_3 shattercane did not differ for a response variable, these treatments were pooled to create a common shattercane type. If $n = 4$ or 8 at each site, only very large differences between wild and A_3 shattercane are likely to be statistically significant, depending on how variable the data are. Our final aim was to test the hypothesis that the F_1 hybrid did not differ from their shattercane or sorghum parents, also using orthogonal contrasts. When discussing results, least-squares means are reported ± SE.

RESULTS

Laboratory germination—The three genotypes responded differently in all temperature treatments except the standard (20–30°C) and cold (10 + 20–30°C) germination treatments (Fig. 1). Total germination of the F_1 hybrids at 20°C (69 ± 3.5%) did not differ from that of the shattercane parents (76 ± 2.5%) but was lower than that of the sorghum parents (87 ± 1.7%). Tetrazolium tests indicated that the nongerminated seeds of shattercane and the F_1 were 86% and 78% viable; thus, their lack of germination was probably due to the cold temperature. By contrast, all the nongerminated sorghum seeds were dead. Total germination of all three genotypes was greater at 25°C than at 20°C. Germination of the F_1 hybrid was 87 ± 3.2% at 25°C, lower than either shattercane (95.3 ± 2.2%) or sorghum (97.5 ± 3.2%). Germination of the F_1 hybrid was equal to that of shattercane and greater than that of sorghum at 30°C and 35°C. In the accelerated-aging treatment, shattercane had greater germination (91 ± 2.4%) than the F_1 hybrid (80 ± 3.3%), which did not differ from sorghum (72 ± 3.3%). All nongerminated sorghum and F_1 seeds in the accelerated-aging treatment were dead.

The 20–30°C treatment was used as the control group for comparison of temperature treatments because it is considered the standard germination treatment of the *Sorghum* species based on AOSA rules. Average time to 50% maximum germination of all genotypes differed from the control in all but the constant 25°C and 30°C treatments (Table 3). Time to 50% germination was greater (6.9 ± 0.15 d) in the constant 20°C treatment than in the control (4.6 ± 0.15 d), smaller in the constant 35°C treatment (3.7 d), and smallest in the accelerated-aging treatment (2.0 ± 0.15 d). Time to 50% germination was greater for the F_1 hybrid than for sorghum or shattercane in the 20°C treatment and greater for the F_1 hybrid than for sorghum in the 25°C, 35°C, standard germination, and prechill. However, sorghum had the longest time to 50% germination in the accelerated-aging treatment.

TABLE 1. Effect of location, seed treatment, and genotype on components of the ecological fitness of sorghum growing at Lincoln and Ithaca, Nebraska. Seed treatment included dormant (nontreated seed) and nondormant (treated to break dormancy). Genotypes include grain sorghum, wild-type shattercane, male sterile shattercane, and the male sterile shattercane × sorghum F_1 hybrid. *F* values are given, with *P* values in parentheses; $n = 64$ for all variables.

Effect	df	Total emergence	Time to 50% emergence	Mortality	Leaf area index	Biomass	Final plant height	Seed mass	Spikelets panicle^{-1}	Seeds plant^{-1}
Location	1	2.25 (0.18)	269.34 (<0.001)	10.67 (0.02)	0.18 (0.68)	0.16 (0.70)	4.74 (0.07)	0.14 (0.72)	0.53 (0.49)	2.53 (0.16)
Seed treatment	1	6.43 (0.02)	129.57 (<0.001)	2.23 (0.14)	3.53 (0.07)	0.36 (0.55)	0.31 (0.58)	0.42 (0.52)	0.12 (0.73)	0.06 (0.81)
Location × seed treatment	1	17.02 (<0.001)	33.82 (<0.001)	3.37 (0.07)	4.33 (0.04)	0.00 (0.98)	0.06 (0.80)	1.56 (0.22)	8.95 (0.005)	5.89 (0.02)
Genotype	3	4.14 (0.01)	16.69 (<0.001)	5.28 (0.004)	41.01 (<0.001)	18.69 (<0.001)	167.51 (<0.001)	283.38 (<0.001)	72.11 (<0.001)	49.68 (<0.001)
Location × genotype	3	1.72 (0.18)	0.67 (0.57)	1.43 (0.25)	0.75 (0.53)	0.79 (0.50)	2.01 (0.13)	5.66 (0.002)	3.23 (0.03)	3.76 (0.02)
Seed treatment × genotype	3	2.60 (0.07)	4.56 (0.007)	0.57 (0.63)	1.37 (0.26)	0.90 (0.45)	1.18 (0.33)	0.67 (0.57)	1.60 (0.20)	2.14 (0.11)
Location × seed treatment × genotype	3	7.23 (<0.001)	2.91 (0.05)	1.00 (0.40)	4.52 (0.008)	0.52 (0.67)	0.70 (0.56)	0.43 (0.73)	0.29 (0.83)	0.15 (0.93)

Field emergence and seedling mortality—Total emergence of the three genotypes in the field did not differ among seed treatments at Lincoln (84 ± 1.2%). Total emergence of nontreated seeds (92 ± 1.0%) did not differ at Ithaca, but emergence was lower (64 ± 4.4%) for sorghum seeds exposed to the high humidity prior to planting than for shattercane (88 ± 3.9%) and the F_1 hybrid (86 ± 4.4%) at that location, probably as a result of dehydration during storage from when they were removed from high humidity until they were planted (about 5 h).

Time to 50% emergence was 2 d later at Ithaca (DOY 161) than at Lincoln (DOY 159). Seeds treated to break dormancy emerged almost two full days earlier than nontreated seeds at Lincoln and 1 d earlier at Ithaca. This effect was greater for sorghum, A_3 shattercane, and the hybrid at Lincoln (i.e., the wild-type shattercane emerged only 1 d earlier in Lincoln). Sorghum emergence generally occurred 1 d earlier than that of shattercane or the F_1 population (results not shown). Seedling mortality of all genotypes was minimal but was greater overall at Lincoln (2.1 ± 0.44%) than at Ithaca (0.47 ± 0.44%), and seedling mortality of cultivated sorghum was greater (2.7 ± 0.57%) than that of shattercane (1.1 ± 0.40%) or the F_1 hybrid (0.3 ± 0.57%).

Vegetative growth—Although height growth progressed differently between locations, the general trend in height growth was similar among genotypes (Fig. 2). Shattercane and the F_1 hybrid began to exceed the height of sorghum at the 11th leaf (V11) stage of development (day of year = 196), and the F_1 hybrids exceeded the shattercane height at days 217 and 227 in Lincoln and Ithaca, respectively. The final heights of the shattercane and F_1 plants were 223 cm and 259 cm at Lincoln and 248 and 274 cm at Ithaca, respectively, whereas sorghum plants were only 114 and 108 cm (Tables 1 and 4). The heights of the F_1 and shattercane plants were comparable to those of wild shattercane populations growing in agricultural fields in the United States (Beckett et al., 1988; Defelice, 2006).

Vegetative-stage phenology differed among genotypes and between locations. Leaf appearance was generally more rapid at Lincoln than at Ithaca, especially during early growth (data not shown). The number of shattercane leaf collars that emerged was slightly smaller than in sorghum and the F_1, especially during early development (e.g., 5.5 ± 0.14 vs. 6.0 ± 0.17 collars at DOY 175 in Lincoln) at both locations. Therefore, shattercane development was slightly delayed compared with that of sorghum and the hybrid during early stages of development. Both parents and the hybrid showed their first tillers at the sixth leaf (V6) stage of sorghum (Fig. 3), and sorghum produced more tillers than either shattercane or the hybrid. Most tillers were lost to senescence, but sorghum maintained more tillers throughout the growing season. Few tillers produced a panicle, especially at Lincoln.

The first panicles appeared in the shattercane and A_3 shattercane plants on day 210 in Lincoln, whereas the F_1 and sorghum plants showed their first panicles on days 213 and 219, respectively. At Ithaca, the shattercane and A_3 shattercane plants showed their first panicles on day 217, whereas the F_1 and sorghum plants showed their first panicles on days 220 and 227, respectively. All plants reached anthesis (the central florets of the head having shed their pollen) 5–8 d after the panicle was visible. Secondary shattercane and F_1 panicles continued flowering until harvest, so the flowering period of shattercane and cultivated sorghum plants overlapped in both locations. Cultivated sorghum had the greatest leaf area index (LAI),

TABLE 2. *F* statistic and *P* value (in parentheses) of differences between wild-type shattercane and A_3 male sterile shattercane genotypes for several components of their ecological fitness (n = 16 for all comparisons within the two locations in Nebraska and seed treatment; D = dormant and ND = nondormant).

Location	Seed treatment	Total emergence	Time to 50% emergence	Mortality	Leaf area index	Biomass	Final plant height	Seed mass	Spikelets panicle^{-1}	Seeds plant^{-1}
Lincoln	D	1.88 (0.20)	0.54 (0.48)	4.02 (0.08)	0.04 (0.84)	1.73 (0.22)	3.59 (0.09)	0.01 (0.91)	1.12 (0.32)	1.18 (0.30)
	ND	0.92 (0.36)	26.17 (<0.001)	0.15 (0.71)	0.90 (0.37)	1.73 (0.22)	3.59 (0.09)	0.01 (0.91)	0.06 (0.81)	0.00 (0.97)
Ithaca	D	0.12 (0.74)	2.56 (0.14)	1.68 (0.23)	2.92 (0.12)	1.73 (0.22)	0.36 (0.56)	0.20 (0.67)	1.39 (0.27)	1.11 (0.32)
	ND	1.04 (0.33)	0.06 (0.0.82)	2.00 (0.19)	0.72 (0.42)	1.73 (0.22)	0.36 (0.56)	0.20 (0.67)	0.30 (0.60)	0.76 (0.41)

followed by the F_1 hybrid and shattercane (Table 4). However, the hybrid had the greatest aboveground biomass, whereas cultivated sorghum and shattercane biomass did not differ (Tables 1 and 4).

Seed production—The mass of 100 seeds was greatest in sorghum, followed by the hybrid and shattercane (Table 4). Shattercane seed mass did not differ between locations, whereas sorghum seeds had greater mass at Lincoln than at Ithaca, and the hybrid had greater seed mass at Ithaca than at Lincoln. The number of seeds per primary (main culm) panicle was lowest in sorghum at both locations. Shattercane had the greatest number of seeds per panicle at Lincoln, whereas the F_1 had an intermediate number of seeds. However, at Ithaca, shattercane and the hybrid produced equal numbers of seeds per panicle. Similarly, fecundity (total seeds per plant) was greatest in shattercane and intermediate in the hybrid at Lincoln, but was similar for shattercane and the F_1 hybrid at Ithaca.

DISCUSSION

We evaluated several components of the ecological fitness of inbred lines of wild *Sorghum bicolor* subsp. *drummondii* (shattercane), cultivated *S. bicolor* subsp. *bicolor* (cultivated sorghum), and their hybrid progeny to obtain a preliminary assessment of the potential for successful gene flow from cultivated sorghum to shattercane. These fitness components may contribute to the overall success of the hybrids. For example, temperature influences the total proportion of seeds that germinate, the rate of germination, and the dormancy level of weed seeds in temperate regions (Forcella, 1998). Plant breeders have eliminated dormancy from cultivated sorghum, whereas shattercane displays varying degrees of dormancy (Kegode and Pearce, 1998) and tends to germinate over an extended

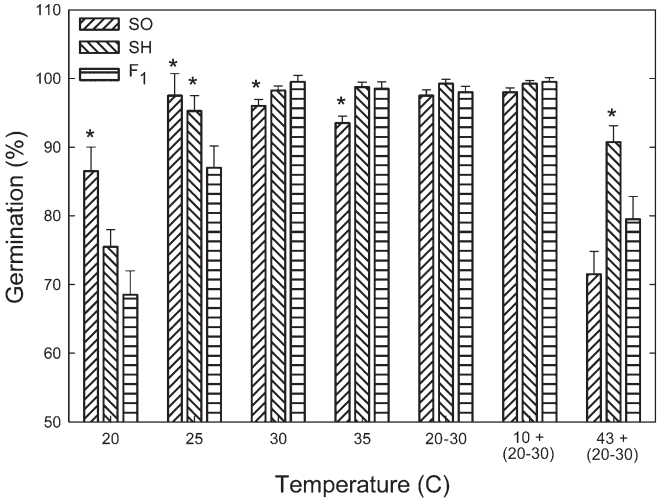

Fig. 1. Least-squares mean total percent germination of grain sorghum (SO, n = 8), shattercane (SH, n = 16), and their F_1 hybrid (n = 8) within seven temperature treatments. Bars represent the standard error of the mean. An asterisk above a bar indicates that total germination of that genotype differs from that of the F_1 hybrid in that temperature treatment at $P < 0.05$.

TABLE 3. Parameter estimates of the logistic function $Y = 1/[1 + \exp(\alpha - \beta^*x)]$, time to 50% maximum germination (α/β), and mean square error of the regression of cumulative germination over time for the three genotypes of *Sorghum bicolor* (SO = sorghum, SH = shattercane, and F_1 = the hybrid) as influenced by temperature treatment.

Temperature treatment (°C)	Genotype	Den df	α	β	α/β (*d*) [a]	MSE
20	SO	214	8.43	1.46	5.82*	0.017
	SH	429	8.89	1.29	6.97*	0.023
	F_1	214	7.23	0.94	7.80	0.020
	Average	861	7.24	1.06	6.89†	0.024
25	SO	214	12.64	3.16	4.00*	0.019
	SH	429	7.26	1.71	4.30	0.018
	F_1	214	6.26	1.40	4.50	0.018
	Average	862	6.87	1.64	4.27	0.019
30	SO	214	4.74	1.19	3.99	0.019
	SH	429	6.47	1.42	4.55	0.020
	F_1	214	5.96	1.39	4.34	0.019
	Average	862	5.74	1.32	4.36	0.020
35	SO	214	5.68	1.72	3.38*	0.019
	SH	429	6.24	1.68	3.80	0.019
	F_1	214	5.16	1.38	3.88	0.021
	Average	862	5.69	1.57	3.71†	0.020
(20–30)	SO	214	6.42	1.82	3.61*	0.019
	SH	429	6.20	1.28	4.81	0.021
	F_1	214	6.49	1.27	5.11	0.022
	Average	862	5.35	1.16	4.59	0.024
10 + (20–30)	SO	214	6.45	2.37	2.85*	0.019
	SH	429	7.98	2.12	3.88	0.020
	F_1	214	5.99	1.51	4.02	0.020
	Average	862	5.83	1.62	3.66†	0.022
43 + (20–30)	SO	214	5.67	2.69	2.36*	0.026
	SH	429	8.35	4.64	1.93	0.021
	F_1	214	9.19	5.17	1.92	0.022
	Average	862	6.85	3.73	2.03†	0.023

[a] The ratio of the α and β parameters estimated from the regression of cumulative germination on time (*d*) using $Y = 1/[1 + \exp(\alpha - \beta^*X)]$ represents the time to 50% maximum germination. An asterisk indicates that the time to 50% maximum germination of that parent differs (at $P < 0.05$ using orthogonal contrasts) from that of the F_1 hybrid within a temperature treatment. A dagger indicates that the average time to 50% maximum germination of all three genotypes differs (at $P < 0.05$) from that of the temperature-treatment control group (20–30°C).

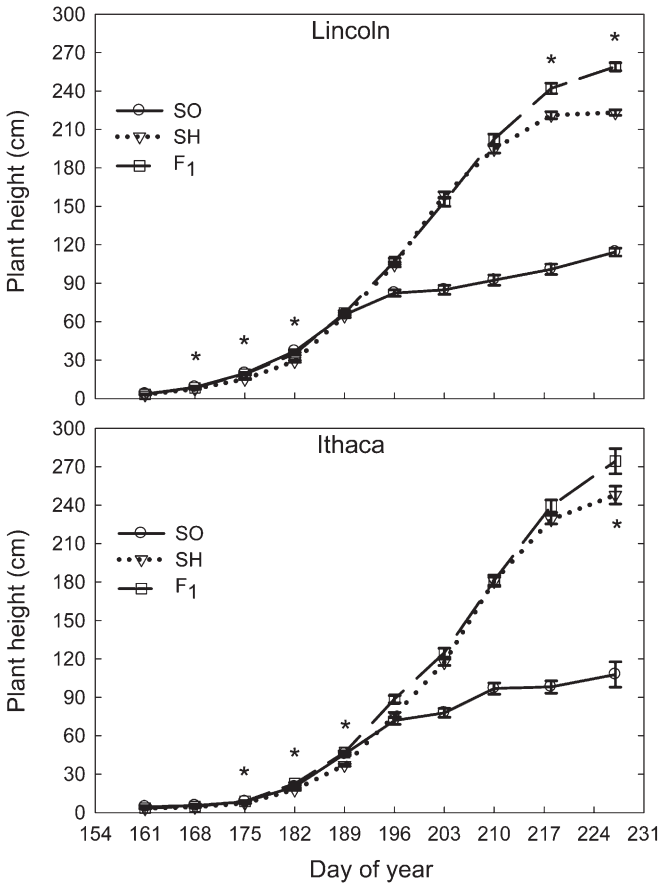

Fig. 2. Least-squares mean height (cm) of sorghum (SO, $n = 8$), shattercane (SH, $n = 16$), and their F_1 hybrid ($n = 8$) over time (day of year) at Lincoln and Ithaca, Nebraska. Bars represent the standard error of the mean. An asterisk at a specific date indicates that height differs between SH and F_1 at $P < 0.05$.

period. Therefore, the aim of the germination experiment was to determine whether the shattercane × sorghum F_1 hybrids displayed germination patterns more like their crop or wild-type parent.

We found that cooler temperatures (<25°C) result in lower total germination and a delay in germination of both parents and the hybrid, but the effect was greater for shattercane and the hybrid. Therefore, cool spring temperatures are likely to keep shattercane and the hybrid seeds in an enforced state of dormancy and extend their period of germination more than that of sorghum. We also found that total germination of sorghum was somewhat negatively affected by higher temperatures. High temperatures reduced total germination and delayed the time to 50% maximum germination in sorghum but resulted in more rapid germination in shattercane and the F_1 hybrid (Table 3). Together, these factors may contribute to the survival of both shattercane and the hybrid in a wide range of temperature environments. Total germination of both parents and the hybrid were reduced in the accelerated-aging treatment, though sorghum and the hybrid seeds were more severely affected by the heat treatment, as TZ tests showed that the nongerminated seeds were dead.

Overall, these results show that the shattercane × cultivated sorghum hybrid responds to low temperatures similarly to shattercane, but the hybrid responds to high temperatures similarly to sorghum. One reason for dormancy and seed protection in shattercane is the fact that the glumes of the spikelet completely encapsulate the seed, protecting it from damage and environmental extremes. Sorghum seeds are generally only subtended by their glumes, which exposes them to environmental extremes but makes them easier to harvest and mill. We observed that the glumes of the hybrid spikelet did not completely cover the seed. Therefore, it is possible that the hybrid seeds had physiological dormancy characteristics similar to those of shattercane (and hence the similar low-temperature response) but that the lack of protection from the glumes made them susceptible to the extreme conditions (heat and high humidity) of the accelerated-aging treatment, similar to the cultivated sorghum parent. Therefore, while the F_1 hybrid seed may display field germination patterns more like those of the weedy parent than those of the crop parent, it may also be more susceptible to mortality factors that would reduce its survival in the seedbank.

Many of the disturbed habitats where shattercane occurs are relatively rich in soil nutrients and water. Given adequate soil nutrients and water, competition for light is a primary determinant of plant fecundity (Wilson and Levin, 1986). Light absorption in mixed canopies is determined by the height of the plant as

TABLE 4. Least-squares mean (±SE) fitness characteristics of sorghum, shattercane, and their F_1 hybrids grown in the field at two locations in Nebraska using two seed treatments (D = dormant and ND = nondormant; within a location, $n = 32$ for grain sorghum and F_1, and $n = 64$ for shattercane). An asterisk indicates that the mean of that parent differs (at $P < 0.05$ using orthogonal contrasts) from the F_1 hybrid.

Trait	Location	Seed treatment [a]	Sorghum	Shattercane	F_1 hybrid
Leaf area index ($m^2 \cdot m^{-2}$)	Lincoln	D	6.2 ± 0.32	3.8 ± 0.22*	5.3 ± 0.32
		ND	6.8 ± 0.29*	3.6 ± 0.21*	5.1 ± 0.29
	Ithaca	D	7.1 ± 0.52*	3.8 ± 0.44*	5.4 ± 0.52
		ND	4.6 ± 0.54	3.6 ± 0.52*	5.3 ± 0.54
Biomass ($g \cdot plant^{-1}$)	Pooled	†	42.2 ± 2.43*	42.7 ± 1.72*	61.0 ± 2.43
Final plant height (cm)	Lincoln	†	114 ± 3.2*	223 ± 2.3*	259 ± 3.2
	Ithaca	†	108 ± 11.0*	245 ± 8.9	274 ± 11.0
Seed mass ($g \cdot 100\ seed^{-1}$)	Lincoln	†	3.45 ± 0.11*	1.30 ± 0.09*	2.16 ± 0.11
	Ithaca	†	3.11 ± 0.06*	1.37 ± 0.04*	2.45 ± 0.06
Spikelets $panicle^{-1}$	Lincoln	†	1079 ± 133.6*	2303 ± 107.5*	1815 ± 133.6
	Ithaca	†	838 ± 111.1*	2349 ± 78.6	2237 ± 111.1
Seeds $plant^{-1}$	Lincoln	†	1078 ± 141.1*	2321 ± 114.3*	1849 ± 141.1
	Ithaca	†	982 ± 152.9*	2408 ± 108.5	2549 ± 152.9

[a] Dagger indicates that seed treatments were pooled for this analysis.

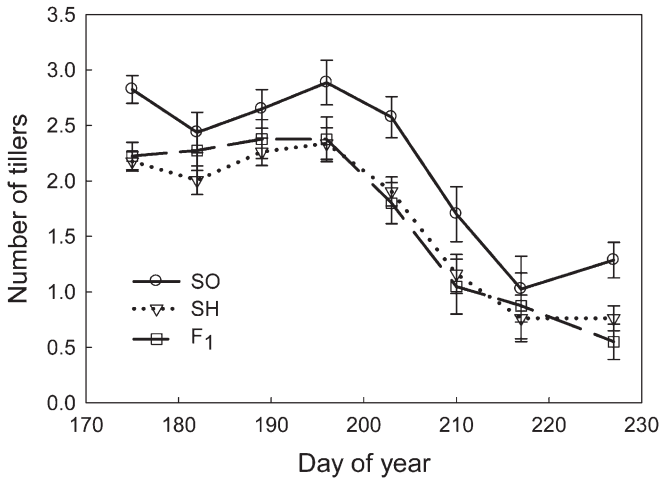

Fig. 3. Least-squares mean number of tillers of sorghum (SO, $n = 16$), shattercane (SH, $n = 32$), and their F_1 hybrid ($n = 16$) over time (day of year) at Lincoln and Ithaca, Nebraska. Bars represent the standard error of the mean.

well as by the LAI and where the leaves are displayed in the canopy (Traore et al., 2002). Our results indicate that both shattercane and F_1 hybrids are taller than cultivated sorghum throughout the reproductive period of growth and that the hybrid expressed heterosis and was even taller than shattercane toward the end of seed fill. While cultivated sorghum had the greatest and shattercane the smallest LAI, the F_1 hybrid expressed an intermediate LAI that was closer to that of sorghum. Moreover, leaf emergence in both the hybrid and cultivated sorghum was more rapid than that in shattercane, which may contribute to more rapid canopy closure. Combining the larger LAI in relation to shattercane, the earlier leaf emergence, and the substantially greater height compared with cultivated sorghum, the hybrid is likely to capture more light and be more competitive than its parents when grown in mixture in the field. However, factors such as herbivory, disease, and local weather conditions could alter these interactions.

Tillering characteristics are important for plant fecundity because the number and size of tillers will affect the number of panicles per square meter and the number of spikelets per panicle. On the other hand, profuse tillering is considered disadvantageous for seed production because it increases leaf area, self-shading, number of ineffective tillers, discontinuous ripening, and blanking (Jennings et al., 1979). We found that both parents and the hybrid produced relatively few tillers and were surprised that cultivated sorghum produced a greater number of tillers than shattercane or the hybrid, but this may be due to the relatively high planting density used in this experiment and the fact that sorghum mortality was greater than shattercane or the F_1. Under high-density conditions, the weedy characteristic is to partition most new growth into stems to produce a taller plant that exceeds the height of its neighbors and provides a better opportunity to produce a greater number of seeds.

The F_1 hybrid produced the greatest aboveground biomass, followed by shattercane and cultivated sorghum. While this appears to be inconsistent with our LAI results, it is consistent with the height data. Structural stem tissue is considerably denser than leaf tissue, so taller plants are likely to be more massive than shorter plants with greater leaf area. Plant fecundity is generally linearly related to total biomass within a species (Aarssen and Taylor, 1992), so these results imply that the F_1 hybrid will produce more seed than either parent. Despite having significantly greater biomass and height, hybrids produced about 20% fewer seeds than wild shattercane at Lincoln and had fecundity similar to that of wild plants at Ithaca.

Seed size has an important effect on establishment success, seedling growth rate, and fecundity of the resulting plants (Rees et al., 2001). Smaller-seeded species tend to be less successful at emerging from deeper in soil and surviving environmental constraints (Leishman et al., 2000) but tend to have greater relative growth rate of seedlings (Maranon and Grubb, 1993). Therefore, smaller-seeded species that survive to become established seedlings may have greater early-season success than larger-seeded species in early-successional environments. Given that the seeds of the F_1 hybrid were intermediate in size compared with those of its parents, it might be hypothesized that early-season success would be intermediate between the two parents. This was not the case; seedling survival and early height growth did not differ among parents and the hybrid. However, smaller seed size allows the production of greater numbers of seed for the same energy expenditure, which may explain the similarity in fecundity of the F_1 and its wild parent.

In closing, it is important to recognize that the heterosis observed in hybrids based on a single inbred shattercane line may not be typical of all potential shattercane hybrids. However, our results indicate that the relative fitness of shattercane × cultivated sorghum F_1 hybrids may be equivalent to that of the wild shattercane parent. Therefore, genes that flow from cultivated sorghum to F_1 shattercane hybrids will likely be in a plant that is competitive and likely to pass those genes on to the successive generation unless those genes have a specific deleterious effect on the fitness of the shattercane plant.

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