

Heritability estimates for seed yield and its components in *Cynodon dactylon* var. *dactylon* (L.) Pers.

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Abstract

Bermudagrass [*Cynodon dactylon* var. *dactylon* (L.) Pers.] is a major warm-season turf and forage grass worldwide. Seed yield is an important trait targeted for improvement in bermudagrass breeding programs because of the increased interest in seed-propagated cultivars. Understanding the nature of genetic variation for seed yield and its components in bermudagrass would aid the development of seed-propagated cultivars. The objective of this study was to estimate the genetic variation and narrow-sense heritability for seed yield and its two major components, inflorescences prolificacy and seed set percentage in bermudagrass. Twenty-five half-sib families and their respective clonal parents were evaluated at two Oklahoma locations, Perkins and Stillwater (Oklahoma, USA), over two years. Half-sib families were different for seed yield, inflorescences prolificacy and seed set percentage, indicating the expression of additive genes in controlling these traits. Family × location effects were observed for seed set percentage and seed yield. All three traits showed family × year interaction effects. There was a significant family × location × year interaction in inflorescences prolificacy and seed set percentage. Narrow-sense heritability estimates for seed yield was 0.18 based on variance component analysis among half-sib families and ranged from 0.26 to 0.68 based on parent-offspring regressions, indicating genetic complexity of seed yield. Heritability estimates were moderate (0.30–0.55) for inflorescences prolificacy and moderate to relatively high (0.41–0.78) for seed set percentage. The results indicate that sufficient magnitudes of additive genetic variation for seed set percentage and inflorescence prolificacy permit positive response to selection and conventional progeny-based genotypic evaluation is necessary for seed yield improvement.

Citation: Tan C, Wu Y, Taliaferro CM, Bell GE, Martin DL, et al. 2022. Heritability estimates for seed yield and its components in *Cynodon dactylon* var. *dactylon* (L.) Pers.. *Grass Research* 2:7 <https://doi.org/10.48130/GR-2022-0007>

INTRODUCTION

Bermudagrass [*Cynodon dactylon* var. *dactylon* (L.) Pers.] is economically the most important and genetically most diverse species in the genus *Cynodon* Rich. It has been widely used for turf, forage, soil conservation and remediation of contaminated soil in southern United States, other temperate and tropical regions of the world^[1,2]. Bermudagrass has long been characterized as an outcrossing species^[3,4].

Sexual reproduction via cross-pollination and self-incompatibility is responsible for the immense genetic and phenotypic variability among bermudagrass^[3,5,6]. The broad genetic diversity within the species has been primarily derived from combinational functions of mutations, sexual reproduction, and natural selection during its dispersion and subsequent adaptation around the world. The sexual reproduction capability of individual bermudagrass plants varies from none to very high^[7]. In general, seed production of bermudagrass is low, but most plants have the ability to produce some seed that effects genetic recombination and segregation. According to Harlan & de Wet^[7], the variability within *C. dactylon* for many characteristics, including fertility, was enormous and generated by population fragmentation based on chromosomal changes such as translocations and deletions. As one of the most prominent causes of the variation in seed yield in bermudagrass, the

chromosomal irregularities are sufficient to cause high, but usually not complete sterility.

Extensive variability among selected genotypes of bermudagrass for components of seed yield has been documented^[3,8–11]. Burton^[3] studied variation in many characteristics of 147 bermudagrass polycross progenies, including seedhead abundance, seed set and seed yield. He concluded that a considerable amount of variation existed among polycross progenies for the three traits. Seed yield was correlated ($r = 0.59$) with seed set percentage. Ahring et al.^[8] collected data from seed yield and its components in bermudagrass using seven single-crosses with seven male clones and one cultivar as maternal parent. The components included number of racemes per head, number of florets per raceme, number of florets per head and number of florets containing a caryopsis per head (seed set percentage). Significant differences were found between progenies and parents for all components except florets per head. Paternal parentage could affect the seed set, because the differences in progenies were a result of different male clones. Seed yield of any offspring did not exceed that of the highest yielding parents.

Wu et al.^[11] reported an enormous amount of genetic variability and relationships for seed yield and its components existing in Chinese tetraploid *C. dactylon* accessions. Using path coefficient analyses, they concluded that inflorescence

prolificacy ($r = 0.51$) and seed set percentage ($r = 0.38$) were significantly positively correlated with seed yield and had the highest direct effects on seed yield. They indicated that selection for increased inflorescence prolificacy and seed set should be the best indirect method for the improvement of seed yield.

Since the 1980s, the number of seed-propagated turf bermudagrass cultivars released for commercial production has dramatically increased, especially in the breeding programs belonging to commercial companies in the US^[2]. According to Ahring et al.^[8], seed-propagated bermudagrass cultivars are needed because commercial planting equipment and establishment technology for vegetative propagation are not effective for confined areas, such as home lawns or on steep embankments such as dam faces or roadsides. In addition, vegetative propagation requires more time and physical labor than seeding. Establishment of bermudagrass turf is less expensive by seeding than by sodding^[12]. With the increased interest in breeding seed-propagated bermudagrass cultivars, seed yield has become a major trait targeted by bermudagrass breeding programs.

Heritability is a measure of the magnitude to which genetic factors contribute to the quantitative phenotypic variation in a population. In breeding programs, information regarding heritability is most useful as a measure of potential response to selection, i.e. predicted genetic gains per selection cycle. Broad sense heritability (H) measures the magnitude to which phenotypic variance (V_p) is determined by variation in genetic factors (V_g) of additive, dominant and interactive effects. Narrow sense heritability (h^2) only quantifies the proportion of phenotypic variation that is due to additive genetic effects. Robust information on narrow sense heritability estimates for seed yield and its components is warranted to increase the selection efficiency for such traits during the development of improved seed-propagated bermudagrass cultivars. Accordingly, the objectives of this study were: (i) to determine if significant genetic variability existed for seed yield and its related components among selected half-sib families of *C. dactylon* accessions, (ii) to calculate narrow-sense heritability estimates for seed yield and its two major components using

variance components analysis and parent-offspring regression, and (iii) to use this information to suggest appropriate breeding strategies for the development of seed-propagated bermudagrass cultivars.

RESULTS AND DISCUSSION

Weather conditions

Severe drought prevailed during the summer of 2012 while the 2013 summer received consistent rainfall during May, June and July. The monthly precipitation at the Stillwater site was 2.84, 5.49 and 0.18 cm in May, June and July of 2012 respectively, while 15.80, 10.03 and 14.15 cm rainfall occurred in the respective months of 2013. At the Perkins site the monthly rainfall was 2.84, 7.39 and 0.66 cm in May, June and July of 2012, compared to 17.81, 10.52 and 15.42 cm precipitation in the respective months of 2013. It has been documented that too much rainfall during these months can be detrimental to seed production^[13]. The average air temperatures during May (23.06, 23 °C), June (26.22, 26.22 °C) and July (30.83, 30.89 °C) 2012 at Perkins and Stillwater respectively were similar. In 2013, the average air temperatures during May (18.89, 19.06 °C), June (25.44, 25.56 °C) and July (26.28, 26.44 °C) at Perkins and Stillwater respectively were lower on average than those in 2012.

Phenotypic variation

Means, standard errors and ranges of seed yield and its components in parents and progeny half-sib families are given in Table 1. For inflorescence prolificacy rating, the ranges of offspring observations fell within the ranges of the parents from either single year or two year data combined. Considering seed set percentage, only the range of offspring at the Stillwater site in 2013 fell within the range of the parents. The ranges of offspring for seed yield fell within the ranges of the parents except the data at the Perkins site in 2013. The means of offspring for seed set percentage and seed yield were mostly greater than the means of parents at the same site in the same years. The ranges and means for these two variables indicate that transgressive segregation may exist in the offspring population.

Table 1. Means, standard errors and ranges of seed yield and its components in parents and progeny half-sib families.

Variables	Year	Site [‡]	Parent			Offspring		
			Mean	SE [§]	Range	Mean	SE	Range
Inflorescence prolificacy rating [†]	2012	Pks	6.31	0.24	1.00–9.00	5.17	0.14	2.00–8.00
		Stw	6.29	0.21	1.00–9.00	5.40	0.16	3.00–8.00
	2013	Pks	6.24	0.25	1.00–9.00	6.17	0.19	2.00–9.00
		Stw	6.08	0.24	1.00–9.00	5.59	0.18	2.00–8.00
	Combined		6.23	0.12	1.00–9.00	5.59	0.09	2.00–9.00
Seed set (%)	2012	Pks	21.58	1.91	0.73–63.69	37.66	2.23	1.83–86.29
		Stw	27.37	2.34	0.00–85.55	44.28	2.40	4.16–89.54
	2013	Pks	18.06	0.02	0.14–62.78	30.01	2.07	1.38–68.89
		Stw	29.41	2.34	0.20–82.14	24.63	2.00	0.10–73.29
	Combined		24.11	1.07	0.00–85.55	34.15	1.17	0.10–89.54
Seed yield (kg ha ⁻¹)	2012	Pks	152.23	16.29	1.26–742.44	198.26	9.50	31.75–373.86
		Stw	114.39	11.23	0–419.67	165.75	9.10	4.31–403.18
	2013	Pks	10.54	1.54	0–70.75	23.47	3.65	0–136.30
		Stw	8.05	0.95	0–39.37	7.80	0.84	0.33–33.61
	Combined		71.30	6.16	0–742.44	98.82	5.94	0–403.18

[†]Rating scale was 1–9, where 1 indicated the least inflorescences while 9 was the greatest inflorescence prolificacy.

[‡]Sites were Stw = Stillwater, Pks = Perkins.

[§]Standard error of the group mean.

Bermudagrass (*C. dactylon*) is a cross-pollinated species. Its seed yield largely depends on water conditions during pollination^[13]. Dry and wet cycles enhance seed set, seedhead prolificacy, and seed yield. In this experiment, the bermudagrass seed yields in 2012 in two locations were similar to that previously reported^[11]. However, seed yields in 2013 were very low due to abundant rainfall in the flowering season of bermudagrass from May to July. It is common to have low seed yields in bermudagrass if high soil moisture results in too much vegetative growth.

Estimated components of variation

Based on the data of offspring in 2012 (Table 2), half-sib families differed greatly in all the variables measured, indicating a significant role of additive genes in seed yield and its related components of bermudagrass. The fixed effect of location was only significant for seed yield. Seed set percentage showed a significant family \times location interaction. The effects of replication nested within location were observed for both seed set percentage and seed yield. In 2013, half-sib families were also different for all the variables measured (Table 2). The fixed location effects were shown for inflorescence prolificacy and seed yield. Seed set percentage and seed yield were also influenced by family \times location interaction. In both single-year analyses, a significant residual variance existed in all three variables, which may suggest that the phenotypic variation

Table 2. Tests of fixed effects due to location by year, location and year, and expected mean squares due to random effects of various sources for inflorescences prolificacy, seed set percentage and seed yield among half-sib families combined across locations (Stillwater and Perkins) or/and years (2012 and 2013).

Sources	Df	Inflorescence prolificacy [†]	Seed set (%)	Seed yield (kg ha ⁻¹)
2012 test of fixed effects (F values)				
Location (L)	1	1.53	3.73	10.16*
Expected mean squares				
Family (F)	24	4.16*	0.11*	23,960.13*
F \times L	24	1.26	0.04*	3,902.04
Rep/L	4	1.81	0.04	12,709.81*
F \times Rep/L	96	1.16*	0.02*	2,513.33*
2013 test of fixed effects (F values)				
Location (L)	1	4.59*	3.36	13.25*
Expected mean squares				
Family (F)	24	5.67*	0.09*	910.22*
F \times L	24	2.81	0.03*	694.42*
Rep/L	4	2.57	0.01	1,787.60*
F \times Rep/L	96	1.74*	0.02*	336.71*
Across 2-location and 2-year test of fixed effects (F values)				
Location (L)	1	0.81	0.06	7.99*
Year (Y)	1	9.20*	45.33*	199.86*
L \times Y	1	6.45*	9.55*	3.32
Expected mean squares				
Family (F)	24	6.97*	0.170*	14,483.50*
F \times L	24	2.15	0.048*	3,060.98*
Rep/L	4	2.33	0.007	3,986.73*
F \times Y	25	3.81*	0.085*	93,009.25*
F \times L \times Y	25	2.34*	0.038*	1,686.89
F \times Y \times Rep/L	196	1.46*	0.020*	1,610.44*

* Significant at the 0.05 probability level.

[†] Rating scale was 1–9, where 1 indicated the least inflorescences while 9 was the greatest inflorescence prolificacy.

involving some genetic variance associated with among individuals of the same half-sib families within plots. In order to exploit the within family genetic variance, individual data within a family is required, but were not collected in this experiment.

In the two-year combined analysis (Table 2), the year effect was of greater magnitude than the effects due to location or location \times year interaction for inflorescence prolificacy, seed set percentage and seed yield. The year effect was likely related to the uncommon rainfall that occurred in 2013. The results also demonstrated a significant amount of variation among half-sib families for inflorescence prolificacy and seed set percentage, suggesting a significant contribution of additive genes in these two components associated with the seed production. For seed yield, however, the expected means square due to half-sib families did not exceed the expected mean square due to family \times year interaction. This could indicate greater genotype \times environment interaction in controlling seed yield variation than its two components. The family \times year interaction effect was likely due to different responses of the families to the obvious climate difference between the two years. On average, the seed yield in 2013 was a 10th to 15th of the yield in 2012 (Table 1). This significant year effect is likely caused by the unusually high precipitation during the seed production season (May, June and July) in 2013 compared to 2012 with intermittent rainfall under drought conditions. Growth-stress cycles with alternate wet and dry conditions are needed to stimulate bermudagrass seed production and flowering during May, June and July, which afterwards could produce a good seed crop in August^[13]. In 2013, the weather provided consistent rather than intermittent precipitation during the seed production season.

The significant genetic variances in the half-sib families for inflorescences prolificacy and seed set percentage indicated that additive genetic components account for these two traits comparing with small interaction variances. Thus, breeding strategies commonly used for bermudagrass improvement, such as recurrent phenotypic selection, should be effective in improving these two seed yield related components.

Estimates of narrow sense heritability

From the single year data, narrow-sense heritability estimates based on half-sib families' variance components for inflorescence prolificacy, seed set percentage and seed yield in 2012 were 0.70, 0.61% and 0.84 kg ha⁻¹ respectively, while in 2013 were 0.50, 0.63% and 0.23 kg ha⁻¹ respectively (Table 3). A large decline occurred in the seed yield estimates between 2012 and 2013. In 2013, when unusually consistent precipitation was received and no growth-stress cycles occurred during the seed production season, the seed yields of families at two locations were significantly affected compared to the

Table 3. Narrow-sense heritability estimates for seed yield and its components in bermudagrass based on component of genetic variation among half-sib families.

Variables	2012 [†]	2013 [†]	Combined [‡]
Inflorescence prolificacy	0.70	0.50	0.55
Seed set (%)	0.61	0.63	0.78
Seed yield (kg ha ⁻¹)	0.84	0.23	0.18

[†] Estimates were based on the single year data across locations.

[‡] Estimates were based on the two-year data across locations.

relatively drought conditions in 2012. Greater family \times location effect was shown in both 2013 than 2012, which could be accounted for by differences in precipitation pattern. Some families at Perkins may have been influenced more severely than those at Stillwater due to the difference between soil types at the two locations. In the combined year analysis, the narrow-sense heritability estimates were 0.55, 0.78 and 0.18, respectively, for inflorescence prolificacy, seed set percentage and seed yield. Seed set percentage showed relatively high heritability estimates with single year and year combined analysis. Low narrow-sense heritability estimates for seed yield in this study were comparatively lower than the result ($h^2 = 0.42$) reported by Cluff & Baltensperger^[14]. This could be attributed to the large family \times year interaction and residuals associated with random effects from replications nested within location, including sampling error. Low heritability estimates may be the result of large phenotypic variability caused by differing microenvironments and are indicated by a large residual variance term.

The heritability estimates based on parent-offspring regression for all variables are given in Table 4. The regressions were only performed with half-sib families and parents from different locations in the same year to exclude the family \times location interaction effect and the significant amount of year effect in reverse year analysis. The heritability estimates were statistically different from zero ($p < 0.05$) for inflorescence prolificacy, seed set percentage and seed yield in 2012 when regressing half-sib families performance at one location on parents at another location, except the estimate for seed set percentage obtained by regression with half-sib families at the Perkins site. In 2013, only estimates for seed set percentage were statistically different from zero. The estimates based on parent-offspring regressions for inflorescence prolificacy ranged from 0.30–0.53, and the estimates for seed set percentage ranged from 0.41–0.76, which were fairly comparable with the estimates for both traits obtained from variation among half-sib families. This may suggest the low effect of non-additive gene actions in influencing inflorescence prolificacy and seed set. The heritability estimates for seed yield ranged from 0.26–0.68, which were only statistically significant in 2012. The heritability estimates for seed yield based on parent-progeny regressions in 2012 were from 0.26 to 0.68 while 2013 heritability values were not different from zero. The inconsistent heritability estimates for seed yield by years and in two methods indicate the genetic complexity of the trait.

Table 4. Narrow-sense heritability estimates and their standard errors (in parentheses) for inflorescences prolificacy, seed set percentage and seed yield in 2012 and 2013 based on parent-offspring regression.

Traits	Stillwater [†]	Perkins [‡]	Stillwater [†]	Perkins [‡]
	2012	2012	2013	2013
Inflorescence prolificacy	0.30*(0.15)	0.53*(0.14)	0.21(0.16)	0.33(0.18)
Seed set (%)	0.76*(0.28)	0.33(0.21)	0.66*(0.27)	0.41*(0.20)
Seed yield (kg ha ⁻¹)	0.26*(0.13)	0.68*(0.18)	-0.10(0.13)	1.38(0.88)

[†]Data for half-sib families were at the Stillwater site, and for parents at the Perkins site.

[‡]Data for half-sib families were at the Perkins site, and for parents at the Stillwater site.

* Significant at the 0.05 probability level.

Predicted genetic gain

Narrow-sense heritability estimates based on half-sib families' variance components were used to predict genetic gain for all the traits. Predicted genetic gains for inflorescence prolificacy were 0.86 and 0.72 for the years of 2012 and 2013, respectively. With two-year data combined, the predicted genetic gain was 0.62 for inflorescence prolificacy. For seed set percentage, predicted genetic gains were 11.14, 11.36 and 13.00% for 2012, 2013 and two-year combined data respectively. Predicted genetic gains for seed yield were 77.87, 4.30 and 9.29 kg/ha for 2012, 2013 and both year combined. The lowest predicted genetic gain for seed yield in 2013 was resulted from the much smaller phenotypic variance 151.70 than 3,993.36 for 2012 and 1,214.94 for 2012 and 2013 combined, respectively (data not presented). The consistent rainfall pattern in 2013 compared with the drought conditions in 2012 resulted in the obvious differences in predicted gains for seed yield obtained individual year separately and combined. The result indicated the risks of selecting for the improvement of seed yield that requires intermittent rainfall pattern to predict seed production using one year's data. Seed yield selection using this population in 2012 would have resulted in greater progress than the predicted gain of the trait in 2013. For accurate selection of seed yield that requires particular environment conditions, the use of multiple years of data would probably result in more reliable progress.

CONCLUSIONS

The population of 25 half-sib families used in the current study was derived from open pollination in a field planting in a randomized complete block design with three replications. The families were selected because of relatively high fertility, winter survivability and spring green-up of their maternal parents. Relatively high to moderate narrow-sense heritability estimates for inflorescence prolificacy and seed set percentage in this population indicated not only that a substantial genetic variation existed in the two traits, but also the variability was significantly controlled by additive gene action in nature and therefore of value to breeders. The results suggest that a significant improvement for seed yield could be possible when applying phenotypic selection to the two components. Low and unstable heritability estimates for seed yield indicated the sole phenotypic recurrent selection when obtaining seed yield directly may not be very effective to improve the trait in bermudagrass. Conventional genotypic selection procedures are necessary to achieve improvement for seed yield increase.

MATERIALS AND METHODS

Plant materials

Plant materials used in the study included 25 *C. dactylon* clonal accessions introduced from China and half-sib progeny from the accessions. The 25 clonal accessions were selected from a larger population of Chinese accessions based on their winter hardiness and relatively high fertility. Half-sib seed from the 25 respective clonal accessions was harvested from plots in a replicated nursery in 2002^[11].

About 0.1g (~2,000 seeds/g) seed of each half-sib family was planted in Metro Mix 250 growing medium (Sun Gro Horticulture, Bellevue, WA, USA) in labeled 12.4 cm \times 19.7 cm black

Bermudagrass seed yield traits heritability

pots placed inside a 26.7 cm × 53.3 cm white tray in a greenhouse at the Agronomy Research Station, Oklahoma State University (OSU, USA). Forty-eight progeny seedlings from each pot were transplanted to two 24-cell trays (26.7 cm × 53.3 cm) representing one half-sib family. After a 2–3 months growing period, 40 plants were randomly selected, and each of the selected plants was split into six sprigs (shoots with attached roots) to grow six identical plants, which were used in establishing experiments on the OSU Agronomy Research Station, Stillwater, OK, USA and the Cimarron Valley Research Station, Perkins, OK, USA. Propagating material for each of the 25 maternal parent plants was dug from the '2007 OSU turf bermudagrass germplasm nursery'. Six identical potted plants were vegetatively prepared for each of the 25 parents in a greenhouse at the OSU Agronomy Research Station, Stillwater (OK, USA).

Experimental design

The experimental design for the Stillwater and Perkins experiments was a randomized complete block with three replications. Within each replication block, a total of 50 entries (one plot for each entry), including 25 randomly selected half-sib families and their respective 25 maternal clones were randomly arranged and planted into each 1.52 m × 2.44 m (5 feet × 8 feet) plot with 1.52 m (5 feet) bare borders between neighboring plots. Each of 40 progeny plants per family was planted on 30.5 cm (one foot) centers in each progeny plot. Each potted maternal plant was cut into four equal plugs (shoots and attached roots and soil) in the field. The four plugs of each maternal parent were transplanted to its respective parent plot.

Management procedures

The soil type at the Stillwater research site is an Easpor loam while the soil type at the Cimarron Valley Research Station is a Teller fine sandy loam (Natural Resources Conservation Service at <http://websoilsurvey.nrcs.usda.gov>). Based on the soil test reports for the two locations, fertilizers [N-P(P₂O₅)-K(K₂O)] were applied at 56-112-112 kg ha⁻¹ respectively to both fields to achieve optimum rates for bermudagrass seed production before transplanting. The Stillwater and Perkins experiments were respectively established on July 7–8 and July 22, 2011. Dual® herbicide (metolchlor) was applied to both fields at 3.36 kg ha⁻¹ a.i. Weeds within the alleys were suppressed by applying 2.24 kg ha⁻¹ a.i. Roundup® (glyphosate, N-phosphonomethyl glycine) plus surfactant (0.5% v:v⁻¹) and 2.24 kg ha⁻¹ (NH₄)₂SO₄ herbicide in the middle of September.

In 2012 there was no mowing of plant residues before initiation of spring regrowth due to early spring green up following the establishment. In early March 2013, plant residues in the plots were mowed off at a 5.08 cm height. Before the initiation of bermudagrass spring green up, Roundup® (glyphosate, N-phosphonomethyl glycine) at 4.68 L a.i. ha⁻¹, 2,4-D [(2,4-dichlorophenoxy) acetic acid] at 1.17 L a.i. ha⁻¹ and Barricade® (prodiamine) at 2.58 kg a.i. ha⁻¹ with 1.17 L ha⁻¹ of surfactant were applied in early March according to the labels of each herbicide. In early May for both years of 2012 and 2013, nitrogen fertilizer was applied at a rate of 67 kg ha⁻¹ for both plots in Stillwater and Perkins. During the growing season, glyphosate tank mixed with a surfactant and ammonium sulfate was applied to control weeds in alleys if needed on a weekly basis.

Data collection

Data were collected in August and September in both 2012 and 2013. Measured and visually rated response variables were: (i) inflorescence prolificacy, (ii) seed set percentage [total seed number per inflorescence and collective raceme length (mm) per inflorescence], and (iii) seed yield (kg ha⁻¹).

Inflorescence prolificacy were visually assessed for each plot with a rating scale from 1 to 9, with 1 indicating no inflorescences and 9 the most abundant inflorescences. This variable was taken at the beginning of August 2012 and early September 2013 due to the difference at inflorescence maturity. To obtain seed set percentage on the plot mean basis, 80 inflorescences were randomly hand-picked from 40 30.5 cm (one foot) centers within the offspring plot using a 30.5 cm × 30.5 cm (one square foot) grid, where originally the 40 individual progeny were planted. For the parent plots, 20 individual inflorescences collected to obtain this variable. For achieving seed set for each plot, 10 inflorescences per replication of each entry were randomly chosen to determine seed number and raceme length (mm) per inflorescence, which were used to calculate seed set percentage. Seed set percentage was calculated as: (number of caryopses inflorescence⁻¹ / number of spikelets inflorescence⁻¹) * 100. The number of spikelets inflorescence⁻¹ was estimated with a linear formula: $Y = 8.4 + 0.79X$ ($r^2 = 0.68$, $p < 0.01$)^[11]. The number of caryopses inflorescence⁻¹ was counted by soaking the seedhead samples in a 20% (v/v) bleach solution then the seedhead was examined under a dissecting microscope at 10× magnification^[11]. For seed yield data collection in September 2012, the variable was estimated by harvesting all biomass of each progeny plot using a sickle-bar mower. All harvested biomass was bagged, dried thoroughly and then threshed by hammermilling at 800 rpm using a 0.371 cm round hole screen^[15]. Due to incomplete coverage for some parent plots in 2012, the biomass from 30.5 cm × 30.5 cm fully covered area was randomly selected and hand-clipped within each plot. The parent plot samples were threshed by rubbing in pans lined with ridged rubber matting. In 2013, all parent and progeny plots were harvested by a sickle-bar mower to obtain the seed yield for each plot. All bagged biomass samples were threshed following the same procedure as in 2012. All threshed samples from both parent and progeny plots were cleaned into pure seed with a Model B South Dakota seed blower using an air-valve setting of 15°^[15].

Statistical analyses

Data were analyzed using the MIXED procedure of SAS version 9.3^[16] to obtain estimates of variance components and GLM procedure to obtain mean squares and significance for each of various sources of variation. Estimates of narrow-sense heritability were computed for all three variables, inflorescence prolificacy, seed set percentage and seed yield. Narrow-sense heritability was estimated for the three variables based on the genetic components of variation among half-sib families. In this experiment, the genetic variance of half-sib families predominantly measured the additive genetic variation in the population. Estimates of narrow-sense heritability were obtained for two individual years 2012 and 2013 and for both years combined. For single year data analysis, the estimates of variance components of half-sib families were based on combined data at two locations. The half-sib families data were collected on the plot mean basis, the narrow-sense heritability on a phenotypic variance among half-sib family mean basis averaging over replications, years, and locations can be estimated as:

$$h_{PFM}^2 = \sigma_F^2 / (\sigma_F^2 + \sigma_{FL}^2/l + \sigma_{FY}^2/y + \sigma_{FLY}^2/ly + \sigma_r^2/rl + \sigma_e^2/ryl)^{[17]}$$

For single year analysis, the estimates of narrow-sense heritability on a phenotypic mean basis is

$$h_{PFM}^2 = \sigma_F^2 / (\sigma_F^2 + \sigma_{FL}^2/l + \sigma_r^2/rl)^{[17]}$$

Parent-offspring regression was the other method used for the estimates of narrow sense heritability. Regression of progeny means on parental means evaluated under different environments can remove the potential bias due to non-genetic covariance between parent and offspring. The estimate in this case would be free of genotype \times environmental interaction effect. In our study, the parent offspring regression was performed with parent and offspring data from different locations for the single year data to reduce upward bias caused by genotype \times environment interactions^[18]. The estimates of h_n^2 were calculated by the following formula: $h_n^2 = 2 \times \beta_1$, where β_1 = the slope of the parent offspring regression^[19].

Predicted genetic gain was calculated for seed yield and its two components using the formula: $\Delta G = ck h_{PFM}^2 \sigma_{PFM}$, where c represents parental control factor, k represents the standardized selection differential, h_{PFM}^2 and σ_{PFM} represent heritability and phenotypic standard deviations on a phenotypic mean basis^[17]. Parental control factor $c = 2$ in this experiment, because superior parents are selected based on the mean performance of their half-sib progenies and intermated in isolation to produce the improved population. For a selection intensity of 30%, $k = 0.736$ ^[19].

ACKNOWLEDGMENTS

The authors would like to acknowledge Mr. Gary Williams, Ms. Sharon Williams and lab colleagues for their help with the inflorescence sampling and biomass harvest. The work has been supported, in part, by the United State Department of Agriculture Specialty Crop Research Initiative award 2010-51181-21064, the Oklahoma Agricultural Experiment Station, and the United States Golf Association.

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

Received 1 August 2022; Accepted 26 October 2022; Published online 22 November 2022

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