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ABSTRACT

Pearl millet, *Pennisetum americanum* (L.) Leeke, is often established under stressful environmental conditions. Thus, establishment capability is crucial to success of the crop. Objectives of this study were (i) to verify previous results associating establishment of the crop with density and size of seed, and (ii) to identify other seed and seedling traits of pearl millet that are related to seed density and size. Seed of four populations was divided by gravity table into three density fractions, each of which was then separated, by dockage sieves, into three size fractions. Seed representing each population-density-size fraction was evaluated in a field study at Manhattan, KS in 1981 and in the laboratory. Seedling emergence increased from 40% with small, low-density seed, to 62% with large, high-density seed. Days from seeding to anthesis decreased from 70 with small, low-density seed, to 62 with large, high-density seed. In both cases, density and size interacted in such a manner that each factor had most effect at low levels of the other. Seed weight, a germination index that emphasized speed of germination, and seed diameter were positively affected by both seed density and size. In addition, germination, seedling height 24 days after seeding, and proportion of vitreous starch in seed endosperm were positively related to seed density. Seedling respiration rate, on a per-seed basis, was associated positively with seed density and size. With a fixed weight of seed, however, there was little effect. Results indicated that seed density and seed size were effective criteria of field establishment and of seed quality as determined by a number of laboratory tests. In some cases, however, the nature of the density × size interaction implied that the major effects of both factors were effectively integrated in seed weight.

Additional index words: Germination, Grain yield, Seed diameter, Seedling respiration, Seed protein content, Seed weight, *Pennisetum americanum* (L.) Leeke.

PEARL MILLET, *Pennisetum americanum* (L.) Leeke, is an important food crop in semiarid parts of Africa and Asia (Rachie and Majmudar, 1980). Usually, the crop must be established under conditions of uncertain rainfall and without benefits of advanced tillage and seeding technology. Superior seed quality and seedling vigor are, therefore, requisites to consistent establishment of satisfactory stands. Study of those traits should be a part of any comprehensive effort to improve pearl millet.

In many crops, seed germination, seedling vigor, and other traits considered important in establishment capability have been found to be associated positively with size, density, and/or weight of seeds (Abdullahi and Vanderlip, 1972; Kauffmann and Guitard, 1967; Kneebone and Cremer, 1955; Ries and Everson, 1973; Sung and Delouche, 1962). Gardner (1980) found that seed germination, seedling emergence, and eventual grain yield were related positively to seed size and seed density in pearl millet. Superior seedling vigor of heavy seeds of barley, *Hordeum vulgare* L., has been attributed to an increased quantity of mitochondrial protein and higher respiratory activity of mitochondria (McDaniel, 1969). Bartee and Kreig (1974) reported that in upland cotton, *Gossypium hirsutum* L., quantities of organic and inorganic materials available to germinating seedlings were greater in seeds of high density than in those of low density. A positive relationship between seedling vigor and seed protein content has been noted in wheat, *Triticum aestivum* L., (Lowe et al., 1972; Ries and Everson, 1973).

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Objectives of this study were (i) to verify findings of Gardner (1980) relative to effects of seed density and seed size on seed germination, field emergence, and final grain yield; and (ii) to identify other seed and seedling traits related to seed density and seed size.

MATERIALS AND METHODS

Seed Lots

Seed sources (populations) were: RMP 1 (RMP), HMP 550 (HMP), Serere 3A (SER), and Senegal Bulk (SEN). Seed of each population was separated into fractions of high, medium, and low density by gravity table. Subsequently, each density fraction was separated into three size fractions by means of dockage sieves. Size fractions were large (retained on 2.8-mm round-hole sieve), medium (passed 2.8-mm round-hole sieve but retained on 2.4-mm round-hole sieve), and small (passed 2.4-mm round-hole sieve).

Field Study

A field study was planted at the Kansas Agricultural Experiment Station Agronomy Farm, Manhattan on 5 June 1980. Soil at the site was an Ivan silty clay loam (fine-silty, mixed, mesic Cumulic Hapludoll). The experimental area received 84 kg N and 34 kg P ha^{-1} on 30 Apr. 1980. Mean monthly temperatures during the growing season were 25.8, 31.0, 28.8, and 22.5 °C for June, July, August, and September, respectively. Mean monthly precipitation for the four months was 66.8, 29.7, 68.3, and 42.9 mm, respectively. That was < 50% of normal for the period and was especially deficient in July, but drought stress was not apparent.

Experimental design was a split plot in which the main-plot arrangement was a randomized complete block. Populations were main-plot treatments and the nine possible density-size combinations were subplot treatments. There were three replications. Each plot consisted of two rows 6.1 m long. Row spacing within and between plots was 0.76 m. Seeding was by means of a two-row vacuum planter and 110 seeds were placed in each row of each plot.

Field emergence was expressed as a percentage of the number of seeds planted with seedlings counted on 24 or 25 June, when most were in the three- to five-leaf stage. Seedling height was measured from the ground to the highest point of the extended foliage 24 days after seeding on three random plants from each row of each plot. Measurements for the six plants in each plot were averaged to give a mean height. Days to anthesis was the number of days from seeding until at least 50% of the plants produced heads and 50% of emerged heads were in full anthesis. Heads were hand harvested from each plot and threshed. Grain yield was adjusted to a moisture content of 125 g H_2O kg^{-1} of total weight and expressed as kg ha^{-1}.

Laboratory Determinations

Lots of 50 seeds were placed on moist filter paper in petri dishes and maintained at 27 °C in a germinator for 7 days. Germination counts were made daily beginning with the second day. A seed was considered germinated when it had produced a plumule and a radicle. Germination index, designed to emphasize speed of germination as well as total germination, was calculated from daily germination counts according to a formula described by Maguire (1962), with the exception that counts were based on 50 rather than 100 seeds. Seed weight was determined on 50 seeds dried to constant weight at 65 °C. An independent measure of seed size (diameter) was obtained by sizing 50 seeds with a series of five dodder sieves with hole diameters of 3.51, 2.62, 2.01, 1.65, and 1.45 mm. All seeds passed the coarsest (top) sieve while none passed the finest (bottom). Seeds retained on each sieve were counted and average seed diameter calculated by assuming seeds to be of the same diameter as the holes of the retaining sieves. Lots of 50 seeds were classified visually according to shape as (1) elongate, (2) medium-elongate, (3) medium-spheroid, and (4) spheroid. Individual seeds, in samples of 10, were sectioned longitudinally through the germ face. Halved seeds were examined under a 10x stereomicroscope, and the apparent proportion of chalky to vitreous starch in the endosperm was rated as 0(0 to 20% chalky), 1(21 to 40% chalky), 2(41 to 60% chalky), 3(61 to 80% chalky), and 4(81 to 100% chalky). Observations for the 10 seeds of each sample were averaged.

Seedling respiration was determined on samples of 50 seeds placed in serum bottles with 5000 mm^3 of vermiculite and 5 mL of water. Samples of 0.5 mL of gas were withdrawn for determination of CO_2 content at intervals of 48, 72, 96, and 120 h following introduction of the seed. Carbon dioxide content of the extracted gas was determined by means of a modified Carle 8501 thermal conductivity gas chromatograph[3], with a 1.83 m column of Porapak S at 30 °C, and a N carrier gas at a flow rate of 720 mL h^{-1}. Respiration rate was computed by means of the following formula:

$$\text{Rate} = \frac{\text{Peak height of observation for } CO_2}{f(\text{stoppered time in hours})}$$

where f is a standardization factor including corrections for the aliquot taken and the peak size per μmole of CO_2 injected into the machine. Rates were expressed in two ways: (i) as μmoles of CO_2 produced per hour by 50 seeds, and (ii) as μmoles of CO_2 produced per hour by 1 g of seed. Total N was determined spectrophotometrically (Technicon Industrial Systems, 1977), and multiplied by 6.25 to obtain seed protein content.

Data on seedling respiration were analyzed in two ways: (i) with CO_2 production averaged across times of extraction, and (ii) with times of extraction treated as a factor in the model. In the second analysis, the model was a three-replicate split plot, with populations as main-plot treatments and the nine possible combinations of seed density and seed size as subplot treatments. In the latter case, data from each population were analyzed separately as a three-replicate split plot, with combinations of seed density and seed size as main-plot treatments and times of CO_2 extraction as subplot treatments. Design for the study of relative embryo size was a three-replicate, randomized complete block with treatments consisting of all available combinations of populations, seed density, and seed size. Only populations of HMP, SEN, and SER were available for this study. In all other laboratory determinations, design was a three-replicate split plot in which main-plot treatments were the four populations and subplot treatments were combinations of seed density and seed size. Deficiency of seed in some of the population-density-size fractions resulted in missing cells in several of the laboratory analyses and necessitated pooling of certain nonerror interactions. Pooled interactions are indicated in the analysis of variance tables. Data on seed shape were clearly nonparametric and were not subjected to variance analysis.

RESULTS

Field Study

Field Emergence. Number of seedlings emerged in the field was affected by population, seed density, and the density × size interaction (Table 1). Percent emergence for RMP, HMP, SER, and SEN was 36, 57, 66, and 53, respectively [LSD(0.05) = 5%]. Generally,

[3] Mention of a trade mark or proprietary product does not imply approval by the Kansas Agric. Exp. Stn. to the exclusion of other products that also may be suitable.

Table 1. Analysis of variance summaries for field variables and seed starch appearance.

Source of variation	df	Mean square: Field emergence	Seedling height	Days to anthesis	Grain yield	Seed starch appearance
		%	mm		kg ha⁻¹	
Replication	2	186.4	202	91.34**	118 433	0.256
Population (*P*)	3	2 042.6**	15 235*	415.52**	407 226	3.524**
Error a	6	45.1	1 743	3.70	104 118	0.063
Seed density (*D*)	2	1 319.9**	14 586**	131.13**	702 881**	5.188**
Seed size (*S*)	2	98.2	742	36.13*	130 780	0.338*
DS	4	225.7**	257	33.87*	123 792	0.086
PD	6	78.2	463	6.46	41 716	0.327**
PS	6	17.5	1 847	16.36	36 353	0.364**
PDS	10	55.7	466	18.38	127 301**	0.142
Error b	59	47.6	855	9.90	76 625	0.083
CV (error a)		12.6	17.6	3.2	57	10.2
CV (error b)		12.9	12.3	5.2	49	11.8

*,** Significant at the $P < 0.05$ and $P < 0.01$ levels, respectively.

emergence was associated positively with both seed density and seed size, but the density × size interaction was such that each factor had most effect at low levels of the other. Thus, emergence from high-density seeds was unaffected by seed size, and emergence from large seeds was unaffected by seed density (Table 2).

Seedling Height. Average seedling height 24 days after seeding was affected by population and seed density (Table 1). Average height for RMP, HMP, SER, and SEN was 193, 248, 251, and 214 mm, respectively [LSD(0.05) = 29 mm]. Average height of seedlings from seed of low, medium, and high density was 205, 235, and 247 mm, respectively [LSD(0.05) = 14 mm].

Days to Anthesis. Number of days from seeding to anthesis was affected by population, seed density, seed size, and the density × size interaction (Table 1). Means for RMP, HMP, SER, and SEN were 66, 67, 58, and 65 days, respectively [LSD(0.05) = 2 days]. Generally, time required to reach anthesis was associated negatively with both seed density and seed size, but, as with field emergence, the effect of each factor was significant only at low levels of the other (Table 2).

Grain Yield. Mean yields for stands from seed of low, medium, and high density were 410, 636, and 714 kg ha⁻¹, respectively [LSD(0.05) = 135 kg ha⁻¹], but applicability of density mean differences was complicated by significance of the population × density × size interaction. Other real effects in the grain-yield data may have been obscured by the high CV (Table 1).

Laboratory Determinations

Germination. Total germination after 7 days was affected by population and seed density (Table 3). Germination tended to increase with seed density, but the effect was significant only with HMP, creating a significant population × density interaction (Tables 3 and 4).

Germination Index. In all populations, the index was higher with seed of medium and high density than with seed of low density. That relationship, however, was more pronounced with HMP than with the other populations, contributing to a significant population × density interaction (Tables 3 and 4). The significant

Table 2. Effects of seed density and seed size on field emergence and days to anthesis.†

Seed density	Field emergence (%): Small	Medium	Large	Days to anthesis: Small	Medium	Large
Low	40	43	59	70	66	63
Medium	57	57	58	63	63	63
High	59	57	62	63	63	62

† LSD (0.05) for comparing interaction means: field emergence = 6%, days to anthesis = 3.

Table 3. Analysis of variance summaries for five laboratory variables.

Source of variation	df	Mean square: Germination	Germination index	Seed weight	Seed diameter	Seed protein
		%		g	mm	g kg⁻¹
Replication	2	79.5	1 591	0.0086	0.0066*	1.9
Population (*P*)	3	1 197.4**	18 901**	0.1740**	0.1515**	8 971.2**
Error a	6	21.6	500	0.0014	0.0009	11.8
Seed density (*D*)	2	583.2**	9 915**	0.0535**	0.0187**	20.5
Seed size (*S*)	2	32.6	1 234*	0.2532**	1.3127**	155.3**
DS	4	55.4	708*	0.0011	0.0242**	115.9**
PD	6	125.2**	1 176**	0.0115**	0.0248**	74.1**
PS + *PDS*	13	28.5	263	0.0060*	0.0168**	184.0**
Error b	54	36.2	257	0.0026	0.0024	11.4
CV (error a)		5.3	9.2	9.3	2.1	6.2
CV (error b)		6.8	6.6	12.8	3.4	6.1

*,** Significant at the $P < 0.05$ and $P < 0.01$ levels, respectively.

density × size interaction (Table 3) reflected a complex relationship, which could not be generalized.

Seed Weight. Weight of 50 seeds was affected by population, seed density, and seed size (Table 3). Seed weight generally increased with density, but the effect was more pronounced with some populations than with others, resulting in a significant population × density interaction (Tables 3 and 4). Seed weights for small, medium, and large seed were 0.34, 0.45, and 0.58 g, respectively [LSD(0.05) = 0.03 g]. Although the estimate for the pooled population × size and population × density × size interactions was significant (Table 3), examination of the second-order-interaction means showed no gross departures from the foregoing observations.

Seed Diameter. Average seed diameter varied with population, seed density, seed size, and all interactions among those factors (Table 3). Seed diameter increased rather regularly with seed size. Examination of second-order-interaction means showed that significant interactions involving size reflected relatively minor deviations from that relationship. The relationship between seed diameter and seed density could not be generalized, showing pronounced inconsistency across populations (Table 4) as well as size classes.

Seed Shape. Average ratings for RMP, HMP, SER, and SEN were 4.0, 2.6, 2.9, and 3.8, respectively (nonparametric data). Density and size effects, though apparent in HMP, SER, and SEN were inconsistent.

Seed Starch Appearance. Apparent proportion of chalky to vitreous starch varied with population, seed density, seed size, and the population × density and population × size interactions (Table 1). Proportion of chalky starch generally was higher in seeds of low density than in those of high density. Seed size affected starch appearance only in RMP, where small- and me-

Table 4. Effects of population and seed density on germination, germination index, seed weight, and seed diameter.†‡

	Density			Density			Density			Density		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
Population	Germination (%)			Germination index			Seed weight (g)			Seed diameter (mm)		
RMP	70	78	74	179	207	199	0.26	0.29	0.34	1.94	1.94	1.97
HMP	74	92	94	205	270	279	0.46	0.47	0.46	2.08	2.10	2.06
SER	88	94	96	244	269	279	0.53	0.54	0.60	2.28	2.22	2.24
SEN	84	90	82	221	254	234	0.34	0.38	0.52	2.03	2.08	2.20

† LSD (0.05) for comparing density means in the same population: germination = 10%, germination index = 26, seed weight = 0.08 g, seed diam = 0.08 mm.
‡ LSD (0.05) for comparing population means at the same or different seed density: germination = 10%, germination index = 36, seed weight = 0.08 g, seed diam = 0.08 mm.

Table 5. Effects of population, seed density, and seed size on seed starch appearance.†‡

	Seed density			Seed size		
Population	Low	Medium	High	Small	Medium	Large
RMP	3.3	2.3	1.9	2.5	2.7	1.9
HMP	3.0	2.6	2.4	2.7	2.7	2.6
SER	3.2	2.9	2.8	3.1	3.0	2.8
SEN	2.6	2.1	1.7	2.0	2.1	2.3

† Scale = 0 (0 to 20% chalky) to 4 (81 to 100% chalky).
‡ LSD (0.05) for comparing population × density or population × size interaction means = 0.5.

Table 6. Analysis of variance summaries for seedling respiration averaged across times of CO_2 extraction.

Source of variation	df	Mean square for μmol CO_2 h^{-1} 50 seeds	1 g seed
Replication	2	40.86	114.56
Population (*P*)	3	48.52	76.16
Error a	6	16.22	56.26
Seed density (*D*)	2	96.05**	61.58
Seed size (*S*)	2	23.66*	46.06
DS	4	11.23	53.79
PS	6	33.70**	102.46**
PD + *PDS*	9	6.59	22.74
Error b	42	5.03	22.56
CV (error a)		32.0	30.8
CV (error b)		17.8	19.5

*,** Significant at the $P < 0.05$ and $P < 0.01$ levels, respectively.

dium-sized seed were higher than large seed in proportion of chalky starch (Table 5).

Seedling Respiration. Variance analysis results for individual populations, with times of extraction treated as subplots, showed that rate of CO_2 evolution varied significantly with time of extraction, being low at 48 h and reaching a maximum at 96 to 120 h. In no case, however, did time of extraction interact significantly with either seed density or seed size. Analysis of variance results for seedling respiration averaged across times of CO_2 extraction are shown in Table 6. Amount of CO_2 produced per hour by 50 seeds was affected by seed density, seed size, and the population × size interaction. Seedlings from seed of low, medium, and high density produced CO_2 at rates of 11.21, 12.92, and 13.72 μmol h^{-1}, respectively [LSD(0.05) = 1.25 μmol h^{-1}]. Respiration rate generally increased with seed size, but the relationship was not consistent across populations. When CO_2 production was placed on a fixed-weight-of-seed basis, most significant effects disappeared with only the population × size interaction remaining significant at the 0.05 level.

Seed Protein. Protein content of seeds was affected by population, seed size, and all interactions among those factors and seed density (Table 3). Mean contents for RMP, HMP, SER, and SEN were 106, 113, 82, and 129 g kg^{-1}, respectively [LSD(0.05) = 3 g kg^{-1}].

DISCUSSION

Limitations of methods for separating density and size classes of seed should be considered in interpretation of results. Gravity-table separation divided seed lots into density classes, but provided no measure of the actual density of those classes. Size separation through use of sieves probably was affected by differences in seed shape. Shape differences probably also affected gravity table separation of seed density classes. Effects of seed density and seed size on seed weight and seed diameter indicate that density and size separations were effective and meaningful. The significant effect of seed density on seed diameter, as measured by dodder sieves, indicates that density classes differed in seed size or shape as well as in seed density, and persistence of that effect after seed sizing by dockage sieves reflects limitations of sieving.

Field results are in general agreement with those of Gardner (1980), who found field emergence of pearl millet to be associated positively with both seed density and seed size. Grain yield also was affected by both density and size in that study. In this experiment, effects of size on grain yield were not significant. Gardner (1980) found that, while superior emergence and grain yield usually were obtained with seeds from the upper half of the size range, exceptionally large seeds frequently gave poor results. That effect was not observed in this study.

The nature of the density × size interaction implies a compensatory relationship between those factors in seedling emergence. Low-density seeds gave satisfactory emergence provided they were sufficiently large; small seeds performed satisfactorily, provided they were high in density. There also appeared to be a compensatory relationship between density and size in days to anthesis. Such a relationship suggests that seed density and seed size are important, primarily as components of seed mass and that there is a threshold level above which mass is unimportant. The tendency for density and size effects to lose significance when weight of seed is held constant, as occurred in seedling respiration, implies that the major effects of seed density and size are effectively integrated in those of seed weight.

No compensatory relationship was apparent, however, in seed germination, seedling height, or grain yield, where neither size effects nor the density × size

interaction was significant; nor in germination index, where a density × size interaction with noncompensatory features occurred.

Results indicate a strong positive association of seed density and proportion of vitreous starch in the endosperm of pearl millet. That is in general agreement with observations on wheat, where vitreous endosperm long has been asociated with high test weight (Shollenberger and Coleman, 1926). According to Yamazaki and Briggle (1969), differences in kernel density of wheat are due, at least in part, to variation in the amount of air space within the kernel. Those authors noted that in low-protein wheat there may be insufficient protein to fill the intergranular spaces in the endosperm, resulting in low kernel density. They pointed out that most soft (chalky) wheats are lower in both protein and test weight than hard (vitreous) wheats. De Francisco et al. (1982), however, found no relationship in pearl millet starch between vitreousness and physical hardness as determined by particle-size distribution after grinding.

This study indicated no well-defined relationship between seed density and seed protein content of pearl millet. The possibility of complications resulting from seed shrivelling warrants consideration. Since shrivelled seeds probably would be low in density and high in protein, due to incomplete filling of the protein matrix with starch, their presence would tend to mask any positive association of density and protein content that might exist among normal seeds. Shrivelled seeds would tend to accumulate in low-density, small-size fractions where their relative abundance would vary with the seed-density and seed-size characteristics of individual populations. The likelihood of statistically significant interactions under such circumstances is obvious. Gardner (1980) observed a negative correlation between field emergence and protein content of pearl millet seed.

Results indicate that seed density and size are effective criteria of field establishment capability and that density and size measurements generally agree with results of other tests of seed quality. Since, in seedling emergence, density and size were important primarily as components of seed mass or weight, choice of seed weight vs. density and size as a criterion of establishment capability appears to be largely a matter of convenience. Precise measurement of density and size is technically difficult, and, for that reason, plant breeders and other workers evaluating large numbers of small seed lots may find seed weight a more practical criterion. On the other hand, primitive as well as advanced methods of processing seed for planting usually involve procedures that separate seeds on the basis of density (fanning, winnowing) and size (screening). It is important to understand the mechanical as well as genetic effects that such practices may have on seed quality.

Design of this study permitted analysis of only intrapopulation effects of seed density and seed size. It has not been established that intra- and interpopulation effects of those traits are the same. Therefore, population differences in seed density and size should be interpreted with caution when those traits are used as criteria of establishment capability.

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