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Inheritance of height and maturity in crosses between pearl millet landraces and inbred Tift 85DB

J. P. Wilson, G. W. Burton and K. Bondari

USDA-ARS and University of Georgia, Coastal Plain Experiment Station, Tifton, GA 31793, USA

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Summary. Over 300 landraces of pearl millet were collected in Burkina Faso and grown at the Coastal Plain Experiment Station in Tifton/GA. At Tifton, these landraces are predominantly tall and late-maturing. The photoperiod requirements of these landraces hinder evaluation of their performance in the field and their use in breeding programs. A conversion program has been initiated to transfer genes for dwarf stature and early flowering into the tall, late-maturing landraces. The inbred Tift 85DB is being used as a donor of genes for the dwarf and early characteristics, and was crossed to nine randomly selected landraces from Burkina Faso. The parents, F_1, F_2, and backcrosses to each parent were grown in the field and evaluated for plant height at anthesis and time in days from planting to anthesis. In general, plant height of F_1s was taller than the tallest parent, and in all crosses the maturity of F_1s was intermediate between the parents. Numbers of loci conferring height varied among crosses, ranging from 0 to 9.6, and averaged 1.6. Estimated numbers of loci conferring maturity ranged from 0 to 12.8 and averaged 3.4. Broad-sense heritability estimates for height and maturity averaged 60.2 and 65.7%, respectively. Corresponding narrow-sense estimates averaged 23.8 and 48.2%. Joint scaling tests revealed that additive-genetic effects were highly significant for both traits, but dominance and epistatic-genetic effects contributed to the inheritance of each trait in some crosses. The low gene numbers, high heritability estimates, and preponderance of additive-genetic effects suggest that selection for these traits should be effective.

Key words: *Pennisetum glaucum* – Plant height – Plant maturity – Gene number – Gene action

Introduction

Exotic germ plasm can be a source of useful genes for crop improvement, but the preponderance of undesirable traits can impose constraints on effective evaluation. Seed of more than 300 landraces of pearl millet [*Pennisetum glaucum* (L.) R. Br.] collected in Burkina Faso were received by the USDA-ARS Forage and Turf Research Unit at Tifton/GA, for evaluation and preservation. Evaluation of these landraces in field plantings at Tifton is difficult because under these environmental conditions the plants are almost exclusively tall and late maturing. Most of the landraces will flower when grown in south Georgia, but will not mature seed before frost. Because seed does not mature on many of these lines, and the time of flowering differs greatly from that of improved inbreds, the chance of obtaining successful crosses in the field is small.

The expression of photoperiodism in these landraces is similar to sorghum [*Sorghum bicolor* (L.) Moench] from subtropical environments. The conversion of sorghum germ plasm in Texas (Stephens et al. 1967) has allowed exotic sorghums to be more easily evaluated by and accessible to plant breeders. The value of the pearl millet collection from Burkina Faso would be more apparent if the accessions were of dwarf stature and photoperiod insensitive. A conversion program has been initiated at the Coastal Plain Experiment Station to transfer genes for dwarfness and photoperiod insensitivity from south Georgia-adapted inbreds into the landraces from Burkina Faso (Burton et al. 1989).

One source of genes for dwarfness and photoperiod insensitivity being used in the program is the inbred Tift $85D_2B_1$ (Tift 85DB) (Hanna et al. 1987). In the conversion program, landrace plants are crossed in the greenhouse to Tift 85DB. F_1 progeny are grown in the green-

house, and F_2 populations are grown in the field where short, early-flowering plants are selfed. Seed from selfed plants are screened in the greenhouse for resistance to rust caused by *Puccinia substriata* Ell. & Barth. var. *indica* Ramachar & Cumm., and Pyricularia leaf spot, caused by *Pyricularia grisea* (Cke.) Sacc. Resistant plants are crossed with pollen collected from landrace plants. Backcross F_1 plants are screened for resistance to both pathogens, and selfed in the greenhouse to produce backcross F_2 populations.

The ability to successfully select for plant height and maturity in segregating populations is the major determinant for the success of this program. The inheritance of these traits in this collection of pearl millets has not been examined. Because of the specific goals of our program, it would be desirable to determine the genetic basis of plant height and maturity in landrace plants crossed to Tift 85DB, so that we can better estimate population sizes required to obtain dwarf, early plants. Small population sizes will reduce the probability that the desired genotypes will occur, and large populations will not allow efficient use of our field space and other resources. The objectives of this experiment were: (1) to determine the inheritance of height and maturity in crosses between tall, late-maturing pearl millets from Burkina Faso and Tift 85DB, and (2) to estimate the effectiveness of our conversion program aimed at genetic improvement of the African pearl millet germ plasm.

Materials and methods

At least three S_0 plants of nine pearl millet accessions from north Burkina Faso (BF nos. 17, 20, 26, 35, 36, 48, 52, 57, and 78) were crossed to inbred Tift 85DB. Selfed seed of the parents and a portion of F_1 seed were stored at 5 °C. F_1 plants were grown in the field in 1987 and selfed, and pollen was collected, frozen, and stored as described by Hanna et al. (1983). F_2 seed was stored at 5 °C, and stored F_1 pollen was used to pollinate plants of the landraces and of Tift 85DB growing in the greenhouse in the fall of 1987. Although seed was produced during different seasons, our experience indicates that seed vigor would be relatively unchanged after controlled storage.

On June 29, 1988, the parents, F_1, F_2, and backcrosses of the F_1 to both parents (BC_1F_1) of each of the nine crosses were planted in the field in a randomized, complete block design with six replications. Randomized within each block for each cross were one plot of each of the parents and F_1, six plots of F_2, and three plots of each backcross population. Plots were 3-m long single rows, with row spacing alternating between 0.6 and 1.2 m. Plants were thinned to a spacing of approximately 30 cm 18 days after emergence. The date at which individual plants reached anthesis, as a measure of maturity, and the height of the plant (dm) at anthesis were recorded.

Least-squares means and variances of plant height and maturity of the generations of each cross were computed by the general linear model (GLM) and variance components (VARCOMP) procedures of SAS (SAS 1985). The statistical model included effects due to replication ($df=5$), cross ($df=8$), and replication × cross. Standard errors of least-squares means were similar for each generation among crosses, but varied slightly due to differing numbers of observations between crosses. Means of standard errors were calculated for presentation in Table 1. Least-squares means and variance components were used to calculate degrees of dominance and broad-sense heritabilities (Falconer 1981). Standard errors of the heritability estimates were calculated by the equation of McNew, as given by Van Ginkel and Scharen (1987). Variance components of the F_2 and backcross populations were used to estimate narrow-sense heritabilities (Warner 1952).

Genetic theory and assumptions

Number of loci. Minimum numbers of loci involved in genetic control of height and maturity were calculated by six different methods using least-squares means and variances. The first method (Burton 1951) assumes no linkage between relevant loci, each parent contributes only "+" or "−" alleles, effects of all loci are equal, the degree of dominance is the same for all loci, and no epistatic interactions exist between loci. With these assumptions, minimum number of loci (n_1) was estimated by

$$n_1 = [0.25(0.75-h+h^2)\,D^2]/\sigma^2_{F_2}-\sigma^2_{F_1} \quad (1)$$

where $h=(F_1-P_1)/(P_2-P_1)$ and $D=P_2-P_1$.

Method 2 (Wright 1968) assumes no linkage between pertinent loci, each parent contributes only "+" or "−" alleles, each allele at all loci has an equal, additive effect, and all loci have an equal effect on the phenotype. Number of loci (n_2) based upon these assumptions was estimated by:

$$n_2 = (P_2-P_1)^2/[8(\sigma^2_{F_2}-\sigma^2_E)] \quad (2)$$

where $\sigma^2_E=(\sigma^2_{P_1}+\sigma^2_{P_2}+\sigma^2_{F_1})/3$.

The assumptions for method 3 (Wright 1968) differ from those of the second by assuming a constant degree of dominance, h, rather than equal and additive effects of alleles at each locus. Number of loci (n_3) based on these assumptions was estimated by:

$$n_3 = [1.5-2h(1-h)]\,n_2 \quad (3)$$

where n_2 is the number of loci estimated by Eq. (2).

The assumptions for method 4 (Wright 1968) differ from those of the second in that the effects of the loci are assumed to be unequal and fall off in arithmetic progression, rather than being equal. For these assumptions, minimum number of loci (n_4) is estimated by:

$$n_4 = [4n_2-3+\sqrt{(16n_2^2+9)}]/6 \quad (4)$$

where n_2 is the number of loci estimated by Eq. 2.

Methods 5 and 6 use backcross variances. Method 5 (Wright 1968) assumes no interaction or linkage between loci, and the degree of dominance is not assumed to be uniform. With these assumptions, minimum number of loci (n_5) is estimated by:

$$n_5 = (P_1-P_2)^2/\{8[2\sigma^2_{F_2}-(\sigma^2_{B_1}+\sigma^2_{B_2})]\} \quad (5)$$

Variances of the backcrosses may be used without $\sigma^2_{F_2}$ to estimate the number of loci by which the F_1 differs from either parent (Wright 1968). In method 6, S_1 and S_2 estimate the number of loci by which F_1 differs from P_1 and P_2, respectively, assuming that all "+" alleles are of equal effect, irrespective of their distribution among the parents. These values are calculated by:

$$S_1 = (F_1-P_1)^2/[4(\sigma^2_{BC_1}-\sigma^2_E)$$

$$S_2 = (F_1-P_2)^2/[4(\sigma^2_{BC_2}-\sigma^2_E)$$

where σ^2_E is defined as in Eq. 2. If complete dominance at all loci is assumed, the total number of loci involved should equal

S_1+S_2. If there is semidominance at all loci, S_1 and S_2 should be equal. Because height and maturity of the parents and F_1s suggested that these traits were expressed as dominant and partially dominant traits, respectively, numbers of loci (n_6) for height and maturity were estimated by sums and averages of S_1 and S_2, respectively.

In all the methods used, the relative potence of the parental gene sets was assumed to be the best estimate of the degree of dominance.

Table 1. Least-squares means of height (dm) and maturity (days after planting) of parental, F_1, F_2, and backcross generations in crosses of inbred Tift 85DB with nine pearl millet landraces

Cross (♀)×(♂)	Generation					
	P_1	P_2	F_1	F_2	$P_1\times F_1$	$P_2\times F_1$
	Plant height					
BF17×85DB	19.5	7.3	28.1	20.1	24.5	16.2
BF20×85DB	21.8	6.2	22.0	17.4	19.6	13.6
BF26×85DB	15.5	6.1	23.5	17.2	21.5	15.4
BF35×85DB	20.0	8.3	18.9	16.7	23.1	15.4
BF36×85DB	19.6	7.9	27.6	19.3	20.6	15.0
BF48×85DB	15.6	6.5	25.5	18.3	17.6	14.9
BF52×85DB	15.9	5.9	22.0	16.9	23.2	14.2
BF57×85DB	20.4	6.1	25.6	19.0	25.8	14.9
BF78×85DB	26.3	8.6	25.1	17.4	20.9	14.5
SE	1.1	0.9	1.5	0.5	1.1	0.6
	Plant maturity					
BF17×85DB	133.7	79.2	93.6	101.3	111.5	87.9
BF20×85DB	124.1	79.1	99.5	97.1	112.6	89.9
BF26×85DB	113.0	80.9	85.0	91.9	94.0	84.9
BF35×85DB	125.8	80.6	84.9	100.7	111.6	87.0
BF36×85DB	130.6	79.5	94.1	100.7	118.1	89.1
BF48×85DB	129.2	82.6	105.7	105.8	121.4	92.9
BF52×85DB	140.7	86.1	100.2	104.6	118.6	88.6
BF57×85DB	137.2	78.3	102.3	110.0	120.0	91.1
BF78×85DB	129.2	79.1	102.7	106.3	114.2	91.4
SE	2.6	2.7	2.0	1.5	2.3	1.3

Gene action. Parental, F_1, F_2, and backcross means and variances of each cross were used to determine additive, dominance, and epistatic gene effects with joint-scaling tests (Mather and Jinks 1982). Gene effects were defined in Gamble's notation (Gamble 1962). Thus, the m, $[d]$, $[h]$, $[i]$, $[j]$, and $[l]$ effects of Mather and Jinks (1982) are referred to as m=mean value, $[d]=a$=additive gene effects, $[h]=d$=dominance gene effects, $[i]=a\,a$=additive × additive-epistatic gene effects, $[j]=a\,d$=additive × dominance-epistatic gene effects, and $[l]=d\,d$=dominance × dominance-epistatic gene effects. The genetic components calculated were an estimate of the net effect of all the loci at which the parents differ for the measured characteristic. The data were used to test the additive-dominance genetic models. The simplest model ($m\,a\,d$) estimated m, the additive-genetic component (a), and the dominance-genetic component (d), while assuming that epistatic effects were not significant. All seven extensions of the basic model, involving one or more of the epistatic effects, $a\,a$, $a\,d$, and $d\,d$, were subsequently evaluated by weighted least-squares analysis (Rowe and Alexander 1980). A Chi-square test ($df=6-$no. parameters in the model) was used to determine the goodness of fit of each genetic model. For some crosses, all simplified models resulted in significant Chi-square values. For these crosses, perfect-fit solutions (Mather and Jinks 1982) were used to estimate the genetic parameters and their standard errors. The simplest model that fit the data was accepted based on a Chi-square test with $P>0.05$, even though a more complex model may have had a lower Chi-square value and a higher probability. Genetic parameters of appropriate models were tested for significance within the limits of their standard errors by the t-test. Only those parameters determined to be different from zero ($P<0.05$) were considered to contribute significantly to the model.

Results

Plant height

In general, the net effect of genes controlling plant height was expressed as overdominance. All F_1s were taller than the midparental values, with six of the F_1s being taller the landrace parent (Tables 1 and 2). Gene segregation in the

Table 2. Degrees of dominance and heritabilities (%) of height and maturity in crosses of inbred Tift 85DB with nine pearl millet landraces

Cross (♀)×(♂)	Height			Maturity		
	Degree of dominance	Heritability[a]		Degree of dominance	Heritability	
		Broad	Narrow		Broad	Narrow
BF17×85DB	1.10	53± 6	49.7	−0.12	68± 4	93.5
BF20×85DB	0.57	62± 4	48.8	−0.02	68± 4	26.5
BF26×85DB	1.18	66± 4	−16.5[b]	−0.12	62± 4	−38.1
BF35×85DB	0.34	42±11	31.5	−0.18	24±15	35.3
BF36×85DB	1.01	54± 5	−25.1	−0.10	51± 5	6.3
BF48×85DB	1.31	76± 3	4.6	0.00	87± 1	35.6
BF52×85DB	1.02	65± 5	27.3	−0.17	79± 3	95.2
BF57×85DB	0.93	69± 4	42.7	−0.05	76± 4	42.6
BF78×85DB	0.44	55± 6	10.0	−0.01	76± 3	98.6

[a] Broad-sense heritability ± standard error and narrow-sense heritability
[b] Negative values for heritability are assumed to be 0

F_2 and $P_2 \times F_1$ generations reduced plant height significantly (Table 1). Estimates of broad-sense heritability for height ranged from 42 to 76%, with a mean value of 60.2% (Table 2). Narrow-sense heritabilities (Table 2) ranged from 0 to 49.7%, with a mean value of 23.8%. Negative estimates were assumed to be 0.

Estimates of the number of loci controlling plant height varied among and within crosses, depending upon which method was used (Table 3). Estimates obtained from Eq. 1 ranged from 1.9 to 4.7 loci except in cross BF35 × 85DB, where an extreme value of 84.3 loci was computed. Equations 2, 3, and 4 were more consistent, yielding estimates ranging from 0.3 to 1.9 loci. Although there was little similarity between estimates for specific crosses, ranges for loci numbers over all crosses computed from Eq. 5 were similar to those of Eq. 6. Estimates for Eq. 5 ranged from 0 (negative values considered to be 0) to 9.6, and estimates for method 6 ranged from 0 to 6.8. Disregarding the extreme value of 84.3 and considering the negative estimates from Eq. 5 to be 0, the mean number of loci controlling height was estimated to be 1.6.

Additive-genetic effects for height were significant in all crosses (Table 4). Dominance effects were significant in crosses to BFs 17, 36, and 78. Epistatic effects were significant in crosses to BFs 17, 36, 48, and 78. Perfect-fit solutions ($P = 1.00$) were used to estimate the genetic

Table 3. Number of loci conferring height and maturity in crosses of inbred Tift 85DB and pearl millet landraces from Burkina Faso

Cross (♀) × (♂)	Number of loci estimated by equation					
	1	2	3	4	5	6
	Plant height					
BF17 × 85DB	1.9	0.7	1.3	0.7	0.8	6.8
BF20 × 85DB	2.3	1.1	1.1	1.2	1.5	0.0
BF26 × 85DB	3.7	0.6	1.2	0.6	–[a]	1.6
BF35 × 85DB	84.3	1.3	1.4	1.4	1.8	0.1
BF36 × 85DB	4.1	0.8	1.2	0.7	–	1.3
BF48 × 85DB	2.3	0.3	0.7	0.3	5.4	1.6
BF52 × 85DB	4.7	0.5	0.8	0.4	1.2	1.0
BF57 × 85DB	2.3	0.9	1.2	0.9	1.5	0.7
BF78 × 85DB	3.7	1.7	1.7	1.9	9.6	0.0
Range	2–5	1–2	1–2	1–2	1–10	1–7
	Plant maturity					
BF17 × 85DB	2.4	3.0	5.3	3.5	2.2	11.2
BF20 × 85DB	2.2	1.9	3.0	2.2	5.0	2.2
BF26 × 85DB	2.9	2.7	4.8	3.2	–	3.9
BF35 × 85DB	–	6.7	12.8	8.4	4.5	–
BF36 × 85DB	5.3	3.6	6.3	4.4	–	65.6
BF48 × 85DB	1.9	1.9	2.8	2.1	4.5	1.3
BF52 × 85DB	2.6	2.0	3.6	2.3	1.7	7.4
BF57 × 85DB	2.5	2.9	4.6	3.4	5.3	2.9
BF78 × 85DB	1.4	1.7	2.6	1.9	1.3	2.9
Range	2–6	2–7	3–13	2–9	2–6	2–12

[a] Negative estimates

Table 4. Estimates ± standard errors and significance of gene effects[a] for height in pearl millet, determined from the joint-scaling test

Cross	m	a	d	aa	ad	dd	χ^2	P
BF17 × 85DB	11.8 ± 1.03**	7.7 ± 0.66**	16.1 ± 1.39**	3.1 ± 1.34**	...	...	5.909	$0.05 < P < 0.10$
BF20 × 85DB	14.0 ± 0.54**	7.8 ± 0.53**	3.7 ± 2.42	...	−3.4 ± 2.32	4.3 ± 2.63	3.585	$0.05 < P < 0.10$
BF26 × 85DB	5.8 ± 26.00	4.7 ± 1.91*	27.9 ± 62.59	5.0 ± 25.93	2.8 ± 15.84	−10.2 ± 38.08	...	...
BF35 × 85DB	4.0 ± 26.42	5.9 ± 2.38*	36.1 ± 62.27	10.2 ± 26.31	3.7 ± 15.10	−21.1 ± 38.10	...	...
BF36 × 85DB	19.5 ± 0.53**	5.8 ± 0.12**	−9.0 ± 1.36**	−5.9 ± 0.53**	...	17.1 ± 0.90**	0.135	$0.50 < P < 0.75$
BF48 × 85DB	16.1 ± 2.32**	4.4 ± 0.46**	−0.5 ± 6.05	5.1 ± 2.41*	...	10.0 ± 3.92*	1.902	$0.10 < P < 0.25$
BF52 × 85DB	3.7 ± 29.63	5.0 ± 1.69**	34.5 ± 69.81	7.2 ± 29.58	8.0 ± 16.59	−16.2 ± 42.35	...	...
BF57 × 85DB	7.9 ± 30.43	7.2 ± 2.49**	26.9 ± 71.05	5.4 ± 30.33	7.5 ± 16.87	−9.1 ± 42.18	...	...
BF78 × 85DB	17.5 ± 0.35**	8.9 ± 0.35**	−7.1 ± 1.28**	...	−5.1 ± 1.02**	14.8 ± 1.24**	0.390	$0.50 < P < 0.75$

[a] m, a, and d represent mean, additive, and dominance genetics components, respectively
*, ** indicate significance at $P = 0.05$ and 0.01, respectively

Table 5. Estimates ± standard errors and significance of gene effects[a] for maturity in pearl millet, determined from the joint-scaling test

Cross	m	a	d	aa	ad	dd	χ^2	P
BF17 × 85DB	108.8 ± 1.30**	24.0 ± 0.87**	−15.2 ± 1.51**	−5.5 ± 1.76**	...	...	3.445	$0.10 < P < 0.25$
BF20 × 85DB	85.9 ± 0.55**	22.5 ± 0.08**	33.9 ± 1.39**	16.6 ± 0.55**	...	−19.4 ± 0.89**	0.023	$0.75 < P < 0.90$
BF26 × 85DB	106.8 ± 44.42*	16.1 ± 4.06**	−37.7 ± 107.92	−9.8 ± 44.24	−13.9 ± 28.21	15.9 ± 65.54	...	...
BF35 × 85DB	113.5 ± 3.64**	23.2 ± 0.91**	−25.0 ± 6.01**	−9.7 ± 3.79*	...	...	5.011	$0.05 < P < 0.10$
BF36 × 85DB	93.5 ± 65.64	25.6 ± 6.14**	28.4 ± 157.48	11.6 ± 65.36	6.9 ± 40.1	−27.7 ± 96.01	...	...
BF48 × 85DB	106.1 ± 0.79**	23.6 ± 0.80**	−0.6 ± 1.10	...	...	...	7.200	$0.05 < P < 0.10$
BF52 × 85DB	114.4 ± 1.29**	28.6 ± 1.07**	−27.7 ± 4.97**	...	...	13.5 ± 4.80*	4.091	$0.10 < P < 0.25$
BF57 × 85DB	125.3 ± 1.35**	29.3 ± 0.26**	−38.1 ± 3.38**	−17.7 ± 1.34**	...	15.2 ± 2.10**	0.191	$0.50 < P < 0.75$
BF78 × 85DB	117.9 ± 7.36**	24.2 ± 1.08**	−31.2 ± 17.07	−13.0 ± 7.17	...	16.0 ± 10.13	2.930	$0.05 < P < 0.10$

[a] m, a, and d represent mean, additive, and dominance genetics components, respectively
*, ** indicate significance at $P = 0.05$ and 0.01, respectively

parameters for crosses to BFs 26, 35, 52, and 57. Although additive-genetic effects were significant for these crosses, all other effects were associated with large standard errors and could not be estimated with adequate precision.

Maturity

The net effects of genes for maturity resulted in early maturity being partially dominant to lateness. Mean F_1 values for maturity were either equal to or earlier than midparental values (Tables 1 and 2). Broad-sense heritability estimates ranged from 24 to 87%, with a mean of 65.7% (Table 2). Estimates of narrow-sense heritability ranged from 0 to 98.6%, with a mean value of 48.2%. Some estimates of narrow-sense heritability were greater than the corresponding broad-sense estimates. This is probably an artifact of the methods used to calculate these values, and not possible in reality by definition of the heritabilities. Heritability estimates of 0 were negative values, but 0 was assumed to best estimate the ratio of additive to total genetic variance.

Estimates of number of loci controlling plant maturity were relatively consistent among the six methods used (Table 3). If negative estimates are regarded as 0, all methods estimated locus number between 0 and 12.8, with the exception of an extreme value of 65.6 estimated by method 6. When the extreme value of 65.6 was disregarded and negative values were assumed to be 0, the mean number of loci involved in the genetic control of plant maturity was estimated to be 3.4.

Results of the scaling tests indicated that additive-genetic effects were significant in all crosses. Dominance and epistatic genetic effects were significant in crosses to BFs 17, 20, 35, 52, and 57. Perfect-fit solutions were used to estimate genetic parameters for crosses to BFs 26 and 36. In these crosses, additive-genetic effects were significant, but all other parameters were associated with large standard errors and could not be estimated with adequate precision.

Discussion

Inbred Tift 85DB is a BC_5 backcross derivative of Tift 23DB, into which genes for resistance to rust and *Pyricularia* leaf spot resistances have been transferred (Hanna et al. 1987). Tift 23DB is homozygous for the recessive d_2 allele, which confers the dwarf character (Burton 1969). Because Tift 85DB is near-isogenic to Tift 23DB, Tift 85DB should be homozygous for the d_2 allele as well. The mean value for loci numbers computed from Eqs. 2, 3, and 4 ($\bar{x} = 1.0$) confirms that a single major gene conferring height was segregating in the F_2 of Tift 85DB × the Burkina Faso landraces. The other equations indicated

that some other loci may be involved which may not affect height per se, but their pleiotropic effects can be correlated with height. For example, the experimental plots were grown on a sandy soil and were not irrigated. In addition, high populations of chinch bug [*Blissus leucopterus* (Say)] were observed on some plants. Genes conferring drought tolerance, tolerance to chinch bug, or nonpreference by chinch bug might have all influenced the final plant height. Under the growing conditions of this experiment, the number of loci controlling plant height was determined to be between one and two.

The inheritance of plant height in other pearl millets was examined previously. When the short inbred 18 was crossed to tall inbreds 710, 717, and 782, numbers of loci conferring plant height were estimated to be 4.8, 25.8, and 3.5, respectively (Burton 1951). It is difficult to compare the results of these two studies because of genetic differences among cultivars and also differences in environmental conditions. The cultivars in the present study were approximately half the height of the cultivars in Burton's 1951 study, which might be due in part to genetics as well as differences in soil fertility and water availability. In general, estimates of locus numbers conferring plant height in the present study using the first method are similar to the 1951 study, however, this method may not be the most applicable. One of the assumptions of the method is that no epistasis exists, but the joint-scaling tests indicated that epistatic effects were significant in many of the crosses.

In the present study, the expression of height in the F_1 was overdominant, which is consistent with a previously published study concerning crosses between dwarf and tall inbreds (Burton and Fortson 1966). In that study, however, height of F_1s between inbreds near-isogenic for the recessive d_2 dwarfing allele was not reported. The F_2 data suggested that the dwarfing gene is recessive, but F_1 and parental data are necessary to determine if simple dominance or intra-locus epistasis is occurring at the D_2 locus. Dominance and epistatic genetic effects for height could frequently be detected in these populations.

Maturity in crosses between early- and late-maturing millets was previously reported to be conferred by 2.2–7.6 loci, with an average of 4.1 (Burton 1951). As was found in the present study, earliness in the F_1 was partially dominant to late maturity. In comparing the present results to the earlier study, it is interesting that we did not find greater differences in numbers of loci. The average flowering date of the late-maturing cultivars in the 1951 experiment was approximately mid-September, but the average flowering dates of the Burkina Faso landraces ranged from mid-October to mid-November. In the present study, it is likely that we have examined the inheritance of photoperiod insensitivity of Tift 85DB. A single gene that confers early maturity to pearl millet has been identified (Burton 1981), however, this gene is not present in Tift 85DB. Maturity, as defined by the flowering date at Tifton/GA was determined to be controlled by three to four loci. This differs from results indicating that photoperiod insensitivity is conferred by a single locus in some millets (Bilquez 1963), but is similar to conclusions regarding the inheritance of photoperiod insensitivity of Tift 23A (Burton 1966).

Assuming two and four loci control differences in plant height and maturity, respectively, between the landraces and Tift 85DB, then theoretically one out of 4,096 F_2 progeny would be homozygous for the alleles found in Tift 85DB at those six loci. To recover the homozygote in a segregating population ($P=0.05$), 12,269 F_2 progeny are required (Hanson 1959). Populations of this size may be the upper limits required for the conversion program, since some heterozygosity may be acceptable when selecting S_1 and backcross S_1 progeny. Field-grown plants are selfed and S_2 progeny are grown in the greenhouse, where backcrosses are made to the earliest dwarf progeny of selected plants. The cycle of selfing between selection and backcrossing increases the probability that plants used in crosses are homozygous at the desired loci.

The magnitude of heritability is one determinant in predicting the effectiveness of selection. Our estimates of broad-sense heritability are rather high and should be considered the upper limits for narrow-sense heritability. If nearly all of the genetic variance was additive, then both estimates would have been identical. Although maturity was conferred by a greater number of loci than was height, the mean narrow-sense heritability was greater for maturity (48.2%) than for height (23.8%). However, estimates of heritability in most cases were moderately high in magnitude, and additive genetic effects were highly significant in all crosses, indicating that both plant height and maturity should respond to mass selection.

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