Rev. Brasil. Genet. 18, 2, 249-257 (1995)
(Brazil. J. Genetics)

Genetic mapping of quantitative trait loci for panicle characteristics and seed weight in sorghum*

M.G. Pereira[1], *D. Ahnert*[2], *M. Lee*[2] *and K. Klier*[3]

ABSTRACT

The objective of the sudy was to use restriction fragment length polymorphisms (RFLPs) to determine the genetic location and the inheritance of quantitative trait loci (QTL) controlling some morphological characteristics of the sorghum panicle, including panicle length, seed-branch length, sterile portion of the seed-branch, peduncle diameter, number of seed-branches per panicle, and 100-seed weight. F_2 plants (152) from the cross CK60 (*Sorghum bicolor* spp. *bicolor*) X PI229828 (*S. bicolor* spp. *drummondii*) were used. An RFLP map (111 loci distributed among 10 linkage groups with an average of 12.9 cM between adjacent loci) was employed. Interval mapping identified a total of 25 QTL: six for panicle length, five for seed-branch length, two for length of sterile portion of the seed-branch, six for peduncle diameter, three for number of seed-branches per panicle, and three for 100-seed weight. The "high" parent (with higher phenotypic mean) contributed to 64% of the alleles that increased the trait mean. QTL were unlinked, with no evidence for epistasis. Phenotypic variation for each QTL ranged from 8% to 37%. Multiple models accounted for from 28% (100-seed weight) to 69% (panicle length) of the phenotypic variation. Pleiotropy or linked QTL was evident for panicle morphology traits. Positive significant correlation coefficients corresponded to pleiotropic or closely linked QTL with the same direction of additive effects.

INTRODUCTION

Sorghum (tribe Andropogoneae; group Sorghastrae; and genus Sorghum; Doggett, 1988) has been classified according to several schemes. The most extensive classification (Snowden, 1936) defined 31 species, but, because of the complexity of the scheme, more simplified versions have been proposed (Harlan and De Wet, 1971, 1972; De Wet, 1978). De Wet (1978) established that the genus sorghum has three species: (1) *Sorghum halepense*, a perennial tetraploid; (2) *Sorgum propinquum*, a perennial diploid; and (3) *Sorgum bicolor*, an annual diploid (n=10). *Sorghum bicolor* includes three subspecies: *bicolor* (domesticated grain sorghums); *arundinaceum* (wild progenitors of grain sorghums); and *drummondii* (stabilized derivatives of hybridization between grain sorghum and its closest wild relatives. The subspecies *bicolor* includes five basic races (bicolor, guinea, caudatum, kafir, and durra) and 10 intermediate races, which are composed of all combinations of basic races. Traditionally, sorghum classification is based on spikelet charac-

---

* Journal Paper No. J-15729 of the Iowa Agric. and Home Econ. Exp. Stn., Ames; Project No. 3134.

[1] Universidade Estadual do Norte Fluminense, CCTA-LMGV, 28015-620 Campos, RJ, Brasil. Send correspondence to M.G.P.

[2] Department of Agronomy, Iowa State University, Ames, IA 50011, USA.

[3] Department of Biology, University of Northern Iowa, Cedar Falls, IA, USA.

teristics (seed size, seed shape, glume size, glume shape, glume covering, etc.), panicle characteristics (panicle length, panicle width, number of seed-branches per panicle, etc.), and plant characteristics (height, tillering, daylength response, etc.). However, panicle and spikelet characteristics have been deemed the most useful (more stable and least influenced by the environment) for assigning sorghum species into subspecies and races (Harlan and De Wet, 1972).

Precise genetic information about panicle and spikelet characteristics, not only are the basis for sorghum classification, but also are related (components) to grain yield - the major agronomic trait. Thus, these characteristics are helpful for both breeding and botanical purposes. A possible approach to generate such information is to use molecular markers to investigate the inheritance of these key traits. Such an approach has been successfully utilized to locate genetic factors that determine morphological differences between maize and teosinte (Doebley and Stec, 1993).

Genetic information about panicle and spikelet characteristics of the sorghum plant is limited. Panicle density (loose/compact panicle) and basal sterility are controlled by single genes (Ayyangar and Ayyar, 1938; Ghawchawe *et al.*, 1966). Panicle length and seed-branch length have generally been described as being highly heritable (Fanous *et al.*, 1971; Patel *et al.*, 1983; Kukadia *et al.*, 1983; Kumar and Singhania *et al.*, 1984; Wenzel, 1990). The number of seed-branches per panicle and 100-seed weight are also highly heritable, but generally not as highly as panicle dimensions (Fanous *et al.*, 1971; Wenzel, 1990). On the basis of estimates of combining ability, a major portion of the genetic variation for some panicle characteristics is due to the additive genetic effects (Kirby and Atkins, 1968).

Recent advances in sorghum genetics have been accomplished by using molecular markers. Restriction fragment length polymorphism (RFLP) mapping studies (Hulbert *et al.*, 1990; Binelli *et al.*, 1992; Whitkus *et al.*, 1992; Berhan *et al.*, 1993; Pereira *et al.*, 1994) have provided the means for more detailed characterization of the inheritance of important characteristics in sorghum. Pereira *et al.* (1994) identified 10 linkage groups, most likely corresponding to the haploid chromosome number of sorghum. Based on their map, 18 quantitative trait loci (QTL), related to plant height, tillering, leaf length, leaf width, stalk circumference, and anthesis (maturity) were found (Pereira and Lee, in press; Pereira *et al.*, in press). QTL for plant height and anthesis may correspond to previously identified genetic loci (*Dw*; Quinby and Karper, 1954 and *Ma*; Quinby, 1967). Genetic loci in sorghum for the other morphological traits have not been identified.

MATERIAL AND METHODS

Genetic material and phenotypic data collection

One hundred and fifty-two F_2 individuals from the cross CK60 X PI229828 were used (Pereira *et al.*, 1994). For the traits studied, genotypic information is unavailable for either parent. The phenotypes of the two parents, however, are quite distinct (Table I). CK60 has compact panicles and large seeds. PI229828 has a large, open panicle.

Table I - Summary of trait means and distribution of parents and progenies.

Traits	CK60	PI229828	F_1	F_2	F_2 range	W[g]
PAL[a]	246 ± 2	412 ± 67	320	320 ± 59	203-480	0.95
SBL[b]	97 ± 18	193 ± 41	180	168 ± 42	98-282	0.95
SLSB[c]	30 ± 24	49 ± 21	50	48 ± 21	12-125	0.92
PDI[d]	8.5 ± 0.7	9.2 ± 1.2	10.0	9.8 ± 1.3	6-13	0.94
NSB[e]	39 ± 24	69 ± 7	62	57 ± 11	33-88	0.98
SWT[f]	1.8 ± 0.3	1.1 ± 0.2	1.9	1.6 ± 0.4	0.7-2.6	0.98

[a] Panicle length (cm).
[b] Seed-branch length (cm).
[c] Sterile length of seed-branch (cm).
[d] Peduncle diameter (mm).
[e] Seed-branches/panicle (number).
[f] Seed weight.
[g] Shapiro and Wilk test of normality.

The seed was hand-planted at the Agronomy and Agriculture Engineering Research Center near Ames, IA, on 27 May, 1992. Parents, F_1 and F_2 seeds were planted in a rectangular uniform region in the field, with 91 cm between rows, and were thinned to 45 cm between plants within rows.

The main panicle of each plant was harvested, air-dried at ambient temperature for three days and kept at room temperature for approximately five weeks. The measurements were recorded for the main panicle of each plant:

- Panicle length (PAL): Measured from the basal node to the tip of the panicle to nearest 0.1 cm.

- Seed-branch length (SBL): The average (cm) of the two longest primary branches containing seeds.

- Sterile portion of the seed-branch (SLSB): The average (cm) length of the sterile portion (no florets) on same seed-branches used for the total length.

- Peduncle diameter (PDI): Measured (mm) directly below the basal node of the panicle.

- Number of seed-branches per panicle (NSB): Number of seed-bearing primary branches per panicle.

- Seed weight (SWT): Weight (g) of 100 seeds (glumes removed).

RFLP assays, and linkage map

Leaf samples were harvested from each plant about two weeks before flowering, freeze-dried, ground, and stored in a -20°C freezer. DNA isolated from this tissue was used for RFLP characterization and linkage map construction, as previously described (Pereira *et al.*, 1994). Genomic DNA isolation, digestion, Southern transfer, clone labeling, and filter hybridization were conducted as described (Veldboom *et al.*, 1994). Separate digests were performed by using restriction enzymes *Eco*RI and *Hin*dIII. Clones identifying polymorphism between parents were hybridized against filters containing DNA from the segregating population digested with the appropriate enzyme. Autoradiograms were scored twice, independently. Filters contained DNA from CK60 (score A), PI229828 (score B), F_1 (score H), and F_2 plants.

Probe selection, detection of RFLP loci, and map construction were previously described (Pereira *et al.*, 1994). Goodness of fit to a 1:2:1 ratio for loci with codominant alleles and to a 3:1 ratio for loci with dominant alleles was determined by means of Chi-square analysis performed by a program written with PC-SAS (Lamkey, K., personal communication). Linkage analysis was accomplished by means of the computer software program MAPMAKER/EXP version 3.0 (Lander *et al.*, 1987) as previously described (Pereira *et al.*, 1994). Linkage groups were declared with a minimum LOD score of 3.0 and maximum distance of 30% recombination. The Haldane function was used to determine the genetic distance between adjacent RFLP loci. The map (Pereira and Lee, in press; Figure 1) consisted of 111 RFLP loci covering 1299 cM, with an average interval length of 12.9 cM.

Data analysis

(a) Phenotypic data

The trait means of the F_2 population, parents, and F_1 (Table I) indicated substantial differences between the parents for most traits. The panicle of PI229828 was nearly twofold greater in terms of length (PAL), width (SBL), and number of seed-branches (NSB) in comparison with CK60. CK60 had higher seed weight (SWT).

The W statistic was used to test trait values of the F_2 plants for their fit to the normal distribution (Shapiro and Wilk, 1965; Table I). The data fit a normal distribution for NSB and SWT (W = 0.98). For PAL, SBL, SLSB, and PDI the data deviated slightly from the normal distribution, (W = 0.95, 0.95, 0.92, and 0.94, respectively). The panicle characteristics (PAL, SBL, and SLSB) were skewed toward high values, in agreement that loose panicle is dominant over compact panicle (Ghawchawe *et al.*, 1966). Despite the deviation, the original data were considered for QTL identification. Simple-Pearson correlations were calculated among traits (Table II).

Table II - Correlation coefficients among traits.

Traits	PAL[a]	SBL[b]	SLSB[c]	PDI[d]	NSB[e]	SWT[f]
PH[g]	0.09	-0.06	-0.03	0.05	0.22**	-0.20*
PAL		0.85***	0.48***	0.61***	0.17*	-0.18*
SBL			0.71***	0.61***	-0.13	-0.20*
SLSB				0.32***	-0.18*	-0.20*
PDI					0.23**	-0.02
NSB						-0.01

*, **, *** Significant at 0.05, 0.01, and 0.001 of probability level, respectively.

[a] Panicle length.

[b] Seed-branch length.

[c] Sterile length of seed-branch.

[d] Peduncle diameter.

[e] Seed-branches/panicle.

[f] Seed weight.

[g] Plant height.

(b) QTL identification

Interval mapping (Lander and Botstein, 1989) and single-factor analysis of variance (SFAOV; Edwards *et al.*, 1987) were used. Interval mapping was conducted with MAPMAKER/QTL 1.1 (Paterson *et al.*, 1988) as previously described (Pereira and Lee, in press). The unconstrained model (Lincoln and Lander, 1990) was used with a LOD threshold of 2.4 to declare the presence of a putative QTL in a given genomic region. This threshold level corresponds to a test at the 0.05 level of significance, according to the Lander and Botstein (1989) "sparse-map" case.

Log-likelihood plots were constructed for the entire length of linkage groups where interval mapping and SFAOV placed the QTL. LOD scores at 2.0 cM intervals were calculated and plotted against map distance for each linkage group. For each QTL,

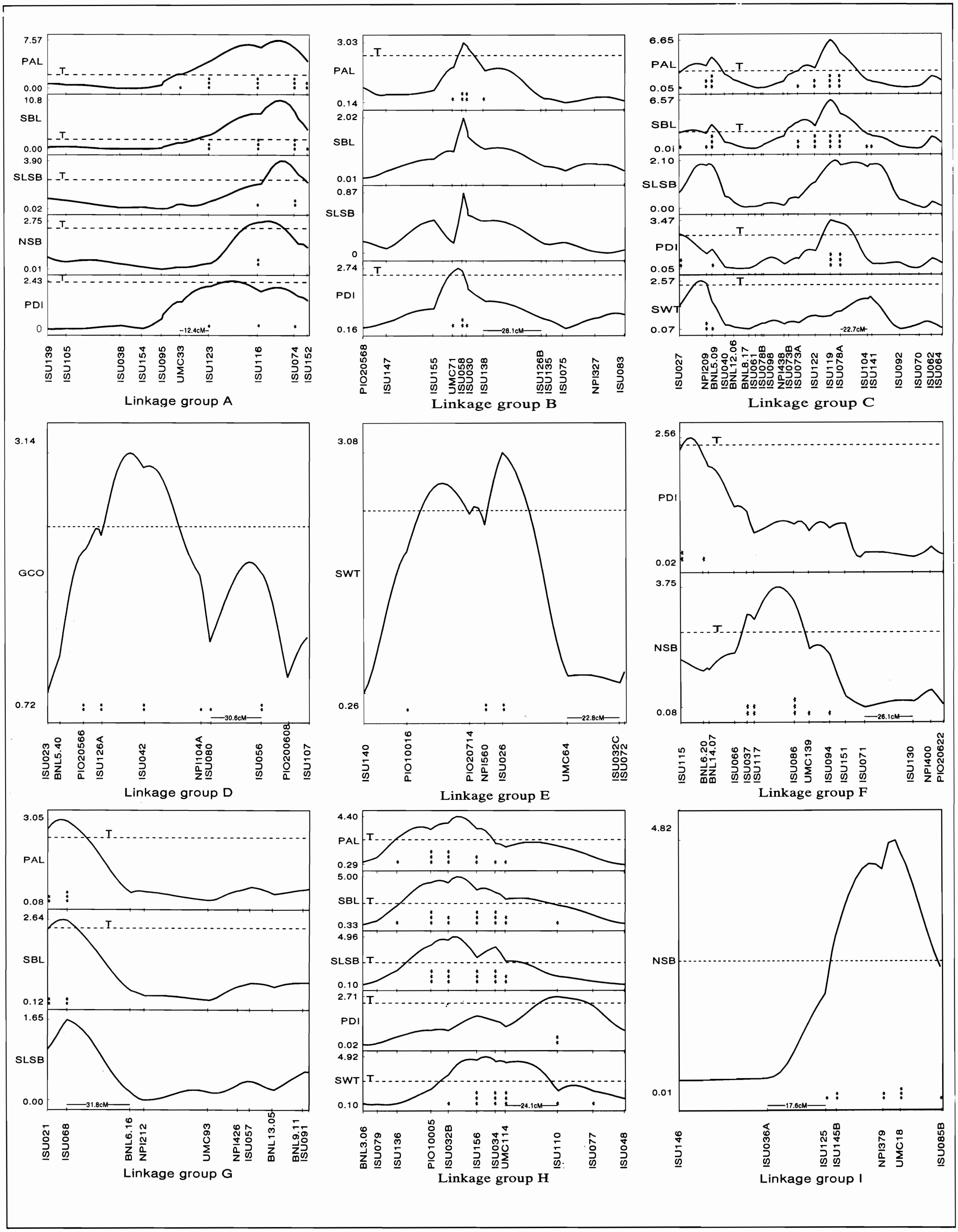

Figure 1 - Log-likelihood plots of linkage groups A, B, C, E, H, and I for panicle length (PAL) in cm, for seed-branch length (SBL) in cm, for sterile length of the seed branch (SLSB) in cm, for peduncle diameter (PDI) in mm, for number of seed-branches per panicle (NSB), and for 100-seed weight (SWT) in g. Vertical lines represent LOD score. (LOD of 2.40 used as threshold (T) for declaration of a QTL. *, **, *** indicate significance at 0.05, 0.01, and 0.001 levels, respectively for SFAOV.

MAPMAKER/QTL determined the map positions of the boundaries of the 10:1 "confidence interval" surrounding the peak. These confidence intervals indicate the region in which the model's probability of giving rise to the data is, at most, 10-fold less than at the most likely position (Paterson *et al.*, 1991).

Gene effects (a = additive effect; d = dominance effect) and percent of phenotypic variation attributable to individual putative QTL were estimated at the peaks (maximum likelihood QTL position). Average level of dominance for QTL was calculated as the ratio d/a. Gene action was determined according to guidelines presented by Stuber *et al.* (1987): additive gene action (A) = 0 to 0.20; partial dominance (PD) = 0.21 to 0.80; dominance (D) = 0.81 to 1.20; and overdominance (OD) = > 1.20. The sign of the additive component of the effect of the B allele (from PI229828) defined the contributing parent for each QTL: if positive, the allele for increased trait mean came from PI229828; if negative, the allele came from CK60.

SFAOV was used for each pair-wise combination of quantitative trait and RFLP locus (Edwards *et al.*, 1987). F-tests at 0.001, 0.01, or 0.05 level of significance determined if significant variation in the trait value was associated with differences among the three marker genotypes AA, AB, and BB for each locus. The reduction of type 1 error (false positives) increases the probability of type 2 errors (rejecting true association between a marker and a QTL). Thus, 0.05 of probability level has been used (Dudley, 1993).

RESULTS AND DISCUSSION

QTL mapping

A total of 25 QTL associated with panicle morphology and seed weight was identified: six, five, two, six, three, and three controlled PAL, SBL, SLSB, PDI, NSB, and SWT, respectively (Table III; Figure 1). Overall, QTL were placed to eight linkage groups (A, B, C, E, F, G, H, and I), but most of the QTL (17 of 25) were located to three linkage groups (A, C, and H). These linkage groups and two others (B and D) were also the predominant regions for QTL related to vegetative plant morphology: all (14) QTL were placed to five linkage groups (A, B, C, D, and H); 71% (10) at three linkage groups (A, C, and H) (Pereira *et al.*, in press). The results suggest that the sorghum linkage groups A, C, and H are heavily populated with loci responsible for the inheritance of vegetative and reproductive morphological traits in this population. Similar results have been reported in maize (Edwards *et al.*, 1992), maize and teosinte (Doebley and Stec, 1993), and tomato (Paterson *et al.*, 1991): QTL affecting different traits were located near one another more frequently than would be expected by chance.

The multiple QTL model explained a significant portion of the phenotypic variation, 69% in PAL, 69% in SBL, 34% in SLSB, 43% in PDI, 30% in NSB, and 28% in SWT. In general, the higher the heritability of a trait, the more variation was explained by the multiple model. All traits investigated herein are generally highly heritable.

The multiple QTL LOD scores for each of the traits closely corresponded to the arithmetic summation of the individual QTL LOD scores, which suggests cumulative effects of loci (possibly no epistasis; Lincoln and Lander, 1990).

SFAOV results (Figure 1) agree closely with those obtained by interval mapping. For each QTL recognized by interval mapping, the peak (most likely QTL position) was flanked by markers that exhibited significant association with the respective trait.

QTL gene action

Estimated gene action was, primarily, additive and with partial dominance. Among 25 QTL, 18 revealed additive to partial dominance gene action. Gene action was not the same for different QTL controlling a determined trait. Such specificity of gene action for each QTL instead of at the level of the whole genome explains the importance of genetic background to define gene action of a trait. As discussed in a previous report (Pereira *et al.*, in press), the gene action of a trait depends on which QTL are polymorphic in the population. Liang and Walter (1968) reported dominance effects as an important component of the genotypic variance for most traits in sorghum; however, in other studies (Beil and Atkins, 1967; Kirby and Atkins, 1968; Laosuwan and Atkins, 1977; Ibrahim *et al.*, 1985), the general combining ability (additive component) accounted for the main portion of the genotypic variance for most of the traits.

Gene action for QTL controlling PAL, SBL, and SLSB was typically additive to partially dominant. The current results agree with a previous study that reported an average degree of dominance of 0.08 for PAL (Wenzel, 1990). Gene action for QTL controlling 100-seed weight was primarily dominant, which agrees with a previous investigation that reported 0.78 for the

Table III - Location and effects of QTL affecting some panicle characteristics in F_2 plants of a CK60 X PI229828 sorghum population.

Linkage group	Interval[a]	R^2	LOD[b]	Gene effects[c]		d/a	Gene action	Dir[d]
				a	d			
Panicle length (cm)								
A	ISU116-ISU074	25%	7.6	-47.5	-9.9	0.21	PD	CK
B	ISU058-ISU030	9%	3.0	22.4	22.6	0.99	D	PI
C	BNL5.09-ISU040	12%	4.3	-29.8	-9.2	0.31	PD	CK
C	ISU119-ISU078A	19%	6.6	38.9	3.4	0.09	A	PI
G	ISU021-ISU068	9%	3.0	25.6	3.6	0.14	A	PI
H	ISU032B-ISU156	15%	4.4	34.3	4.7	0.14	A	PI
Multiple QTL model		70%	34.7					
Seed-branch length (cm)								
A	ISU116-ISU074	37%	10.8	-40.9	-25.0	0.61	PD	CK
C	BNL5.09-ISU040	9%	3.2	-18.8	-9.8	0.52	PD	CK
C	ISU119-ISU078A	19%	6.6	28.3	-0.6	-0.02	A	PI
G	ISU021-ISU068	8%	2.6	16.2	10.4	0.64	PD	PI
H	ISU032B-ISU156	17%	5.0	26.5	2.3	0.09	A	PI
Multiple QTL model		69%	33.5					
Length of the sterile portion of seed-branch (cm)								
A	ISU116-ISU074	17%	3.9	-13.9	-8.6	0.62	PD	CK
H	ISU032B-ISU156	17%	5.0	13.0	-2.2	-0.17	A	PI
Multiple QTL model		34%	9.8					
Peduncle diameter (mm)								
A	ISU123-ISU116	9%	2.4	-0.56	0.13	-0.23	PD	CK
B	UMC71-ISU058	9%	2.7	0.57	0.44	0.77	D	PI
C	ISU027-NPI209	7%	2.5	-0.54	0.10	0.18	A	CK
C	ISU119-ISU078A	10%	3.5	0.64	0.20	0.31	PD	PI
F	ISU115-BNL6.20	9%	2.6	0.53	-0.33	-0.62	PD	PI
H	UMC114-ISU110	8%	2.7	0.42	0.44	1.05	D	PI
Multiple QTL model		43%	17.0					
Seed-branches/panicle (number)								
A	ISU116-ISU074	9%	2.8	2.8	6.4	2.28	OD	PI
F	ISU117-ISU086	14%	3.8	5.7	-0.6	-0.10	A	PI
I	NPI379-UMC118	14%	4.8	2.90	7.2	2.48	OD	PI
Multiple QTL model		30%	10.0					
100-seed weight (g)								
C	ISU027-NPI209	11%	2.6	0.05	0.25	5.00	PD	PI
E	ISU026-UMC64	9%	3.1	0.13	0.13	1.00	D	PI
H	ISU156-ISU034	16%	4.9	-0.19	0.17	-0.89	D	CK
Multiple QTL model		28%	9.4					

[a] Flanking markers of the most likely QTL position.

[b] LOD threshold = 2.4.

[c] Additive effects are associated with the allele from PI229828. Thus, a negative value means that the PI229828 allele decreases the value of the trait.

[d] Direction of response is the parent whose additive value of a marker allele increased the value of the trait. (PI = PI229828; CK = CK60).

average degree of dominance for this trait (Wenzel, 1990). For the other traits gene action was variable, from additive to overdominance.

Most of the time, the donor parent for alleles that increased the trait mean ("high" alleles) was the "high" parent (with the higher trait value). The "high" parent contributed with 64% of the "high" alleles, and the "low" parent (with lower trait value) contributed 36%. In a study of transgressive segregation in an interspecific cross of tomato (De Vicent and Tanksley, 1993), the same proportion was reported; 36% of the QTL had alleles with effects opposite to those predicted by the parental phenotypes. The authors concluded that such a phenomenon, "high" alleles coming from both "high" and "low" parents for the same trait, could be directly responsible for the occurrence of transgressive phenotypes in the F_2 population. In an investigation of morphological differences between maize and teosinte (Doebley and Stec, 1993), "high" alleles at six (of 50) QTL came from the "low" parent, but most of the exceptions included QTL with small effects. In the present study, "high" alleles from the "low" parent had effects of similar magnitude in comparison with those from the "high" parent.

Linkage and pleiotropy

High coefficients of genotypic correlation between traits related to panicle measurements (PAL and SBL) have been reported (Fanous *et al*., 1971). Our results suggest that the high correlation coefficient involving these traits (Table II) is due to the same set of QTL with pleiotropic or linked effects for both traits. QTL for these two panicle traits were located in the same position (linkage groups A, B, C, G, and H; Figure 1). Also, for both traits, these QTL share the same donor parent for "high" alleles and very similar gene effects (Table III). SLSB is a component or SBL and, as expected displayed similar QTL likelihood plots in relation to the other two traits. These three traits (PAL, SBL, and SLSB) may be controlled by the same set of genes or the same cluster (closely linked) of genes.

Linkage or pleiotropic effects have been reported in other investigations. In maize, some flowering traits are controlled by the same QTL (Veldboom *et al*., 1994). In maize and teosinte populations (Doebley and Stec, 1993) the concentration of effects in five regions of the genome was attributed to be most likely due to a mixture of (i) QTL with pleiotropic effects on several traits and (ii) multiple linked QTL affecting the individual traits.

Correlation among traits

Correlation coefficients (Table II) were highly significant, especially for traits related to panicle dimensions (PAL, SBL, SLSB, and PDI). Because these traits are related to the size of the panicle (length, width, and diameter of the peduncle), these high correlation coefficients were expected. Paterson *et al*. (1991), and Veldboom *et al*. (in press) reported that correlated traits often have some of the same markers significantly associated with each trait. These four traits share common or closely linked QTL. PAL, SBL, and SLSB are controlled by a common set or closely linked QTL, and, for PDI, among six QTL, five are located at the same (or close) position of QTL for the other panicle dimension characteristics (linkage groups A, B, C, and H).

Common or closely linked QTL also occur for most of the other correlated traits in this population. Most often, a positive significant correlation coefficient corresponds to traits that have QTL closely linked, with the same direction of effects ("high" alleles having the same donor parent). Additionally, a negative significant correlation coefficient corresponds to QTL having an opposite direction of effects ("high" alleles having different donor parents). PAL and SWT were significantly correlated (Table II), but the respective linked QTL (linkage groups C and H) had an opposite direction of effect: alleles that increased the trait mean in linkage groups C and H came from CK60 and PI229828, and from PI229828 and CK60 for PAL and SWT, respectively. Fanous *et al*. (1971) also reported significant genetic correlation involving panicle length and seed weight. These results (previous and here reported) suggest that a fraction of the genes controlling SWT may be linked to genes controlling panicle dimensions.

Our results support the importance of panicle characteristics for sorghum taxonomy. The high proportion of the variation explained by the multiple QTL model indicated that the environment has a small effect on the expression of these traits. Therefore, these traits may be used with confidence, even in adverse conditions. Also, the possible pleiotropy or close linkage involving QTL controlling panicle dimension characteristics may simplify the procedures of evaluations for selection and classification purposes.

ACKNOWLEDGMENTS

This research was supported by Pioneer Hi-Bred International, the Iowa Agriculture and Home Economics Experiment Station (Project 3134), and CEPLAC-CNPq.

RESUMO

O objetivo deste estudo foi usar "restriction fragment length polymorphisms" (RFLPs) para determinar a localização genômica e a herança de loci de caracteres quantitativos (QTL) controlando alguns caracteres morfológicos da panícula de sorgo. Plantas F_2 (152) do cruzamento CK60 (*Sorghum bicolor* spp. *bicolor*) X PI229828 (*S. bicolor* spp. *drummondii*) foram usadas. Um mapa genético baseado em RFLPs (111 loci distribuídos em 10 grupos de ligação com uma média de 12,9 cM entre loci adjacentes) foi usado. O procedimento "interval mapping" identificou um total de 25 QTL: seis para comprimento de panículas, cinco para comprimento de ramos com sementes, dois para comprimento da porção esteril dos ramos com sementes, seis para diâmetro do pedúnculo, três para número de ramos por panícula e três para o peso de 100 sementes. O progenitor de maior média fenotípica contribuiu com 64% dos alelos que aumentaram a média do carater na progênie. Não foi detectado ligação gênica entre QTL, também não houve evidência de ocorrência de epistasia. Variância fenotípica explicada por cada QTL variou de 8 a 37%. Modelos múltiplos explicaram de 28% a 69% da variância fenotípica. Pleiotropismo ou ligação gênica foi evidente para caracteres relacionados com a morfologia da panícula. Significantes coeficientes de correlação positivos corresponderam com pleiotropismo ou íntima ligação gênica entre QTL dos correspondentes caracteres, tendo a mesma direação do efeito aditivo.

REFERENCES

Ayyangar, G.N.R. and **Ayyar, M.A.S.** (1938). Linkage between a panicle factor and the pearly chalky mesocarp factor *Zz* in sorghum. *Proc. Indian Acad. Sci. 8*: 100-107.

Beil, G.M. and **Atkins, R.E.** (1967). Estimates of general and specific combining ability in F_1 hybrids for grain yield and its components in grain sorghum, *Sorghum vulgare* Pers. *Crop. Sci. 7*: 225-228.

Berhan, A.M., Hulbert, S.H., Butter, L.G. and **Bennetzen, J.L.** (1993). Structure and evolution of the genomes of *Sorghum bicolor* and *Zea mays. Theor. Appl. Genet. 86*: 598-604.

Binelli, G.L.P.E., Gianfranceschi, M.E., Taramino, G., Busso, C., Stenhouse, J. and **Ottaviano, E.** (1992). Similarity of maize and sorghum genomes as revealed by maize RFLP probes. *Theor. Appl. Genet. 84*: 10-16.

De Vicent, M.C. and **Tanksley, S.D.** (1993). QTL analysis of transgressive segregation in an interspecific tomato cross. *Genetics 134*: 585-596.

De Wet, J.M.C. (1978). Systematics and evolution of sorghum sect. sorghum (gramineae). *Amer. J. Bot. 65*: 477-484.

Doebley, J. and **Stec, A.** (1993). Inheritance of the morphological differences between maize and teosinte: Comparison of results for two F_2 populations. *Genetics 134*: 559-570.

Doggett, H. (1988). *Sorghum.* Longman Group UK Ltd., Essex, England.

Dudley, J.M. (1993). Molecular markers in plant improvement: manipulation of genes affecting quantitative traits. *Crop Sci. 33*: 660-668.

Edwards, M.D., Stuber, C.W. and **Wendel, J.F.** (1987). Molecular-marker-facilitated investigations of quantitative-trait loci in maize. I. Numbers, genomic distribution and types of gene action. *Genetics 116*: 113-125.

Edwards, M.D., Helentjaris, T., Wright, S. and **Stuber, C.W.** (1992). Molecular-marker-facilitated investigations of quantitative trait loci in maize. *Theor. Appl. Genet. 83*: 765-774.

Fanous, M.A., Weibel, D.E. and **Morrison, R.D.** (1971). Quantitative inheritance of some head and seed characteristics in sorghum (*Sorghum bicolor* (L.) Moench). *Crop Sci. 11*: 787-789.

Ghawchawe, B.G., Bhale, N.L. and **Shekar, V.P.** (1966). Linkage groups in sorghum. *Indian J. Genet. 26*: 317-326.

Harlan, J.R. and **De Wet, J.M.J.** (1971). Toward a rational classification of cultivated plants. *Taxon. 20*: 509-517.

Harlan, J.R. and **De Wet, J.M.J.** (1972). A simplified classification of cultivated sorghum. *Crop Sci. 12*: 172-176.

Hulbert, S.H., Richter, T.E., Axtell, J.D. and **Bennetzen, J.L.** (1990). Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. *Proc. Natl. Acad. Sci. USA 87*: 4251-4255.

Ibrahim, O.E., Nyquist, W.E. and **Axtell, J.D.** (1985). Quantitative inheritance and correlations of agronomic and grain quality traits of sorghum. *Crop Sci. 25*: 649-654.

Kirby, J.S. and **Atkins, R.E.** (1968). Heterotic response for vegetative and mature plant characters in grain sorghum, *Sorghum bicolor* (L.) Moench. *Crop Sci. 8*: 335-339.

Kukadia, M.U., Desai, K.B., Desai, M.S., Patel, R.H. and **Rajak, R.V.** (1983). Estimates of heritability and other related genetic parameters in sorghum. *Sorghum Newsletter 26*: 31-32.

Kumar, S. and **Singhania, D.L.** (1984). Genetic advance and heritability estimates for grain yield and its components. *Sorghum Newsletter 27*: 15-16.

Lander, E.S. and **Botstein, D.** (1989). Mapping mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics 121*: 185-199.

Lander, E.S., Green, P., Abrahamson, J., Barlow, A., Daly, M.J., Lincoln, S.E. and **Newburg, L.** (1987). MAPMAKER: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics 1*: 174-181.

Laosuwan, P. and **Atkins, R.E.** (1977). Estimates of combining ability and heterosis in converted exotic sorghums. *Crop Sci. 17*: 47-50.

Liang, G.H. and **Walter, T.L.** (1968). Heritability estimates and gene effects for agromic traits in grain sorghum, *Sorghum vulgare* Pers. *Crop Sci. 8*: 77-81.

Lincoln, S.E. and **Lander, E.S.** (1990). Mapping Genes Controlling Quantitative Traits Using MAPMAKER/QTL. Whitehead Institute for Biomedical Research, Cambridge, MA.

Patel, R.H., Desai, K.B. and **Desai, S.P.** (1983). Heritability estimates in grain sorghum. *Sorghum Newsletter 26*: 89-90.

Paterson, A.H., Lander, E.S., Hewitt, J.D., Peterson, S., Lincoln, S.E. and **Tanksley, S.D.** (1988). Resolution of quantitative traits into mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature 335*: 721-726.

Paterson, A.H., Damon, S., Hewitt, J.D., Zamir, D., Rabinowitch, H.D., Lincoln, S.E., Lander, E.S. and **Tanksley, S.D.** (1991). Mendelian factors underlying quantitative traits in tomato: Comparison across species, generatisons, and environments. *Genetics 127*: 181-197.

Pereira, M.G. and **Lee, M.** Identification of genomic regions affecting plant height in sorghum and maize. *Theor. Appl. Genet.* (in press).

Pereira, M.G., Lee, M., Bramel-Cox, P., Woodman, W., Doebley, J. and **Whitkus, R.** (1994). Construction of an RFLP map in sorghum and comparative mapping in maize. *Genome 37*: 236-243.

Pereira, M.G., Lee, M. and **Ahnert, D.** Genetic mapping of quantitative trait loci for morphological and physiological traits in sorghum. *Theor. Appl. Genet.* (in press).

Quinby, J.R. (1967). The maturity genes of sorghum. *Advanc. Agron. 19*: 267-305.

Quinby, J.R. and **Karper, R.E.** (1954). Inheritance of height in sorghum. *Agron. J. 46*: 211-216.

Shapiro, S.S. and **Wilk, M.B.** (1965). An analysis of variance for normality (complete samples). *Biometrika 52*: 591-611.

Snowden, J.D. (1936). *The Cultivated Races of Sorghum.* Allard and Son, London.

Stuber, C.W., Edwards, M.D. and **Wendel, J.F.** (1987). Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. *Crop Sci. 27*: 639-648.

Veldboom, L.R., Lee, M. and **Woodman, W.L.** (1994). Molecular marker-facilitated studies in an elite maize population. I. Linkage analysis and determination of QTL for morphological traits. *Theor. Appl. Genet. 88*: 7-16.

Wenzel, W.G. (1990). Inheritance and interrelationships of quantitative traits in sorghum. *Sorghum Newsletter 31*: 1-3.

Whitkus, R., Doebley, J. and **Lee, M.** (1992). Comparative genome mapping of sorghum and maize. *Genetics 132*: 1119-1130.

(Received September 2, 1994)