Theor Appl Genet (1995) 90:380–388

M. G. Pereira · M. Lee

Identification of genomic regions affecting plant height in sorghum and maize

Received: 4 November 1993 / Accepted: 17 May 1994

Abstract The objective of this study was to use restriction fragment length polymorphisms (RFLPs) to determine the genetic location and effects of genomic regions controlling plant height in sorghum. F_2 plants (152) from the cross CK60 × PI229828 were used. Genomic and cDNA clones (106) identified 111 loci distributed among ten linkage groups covering 1299 cM. Interval mapping identified four regions, each in a separate linkage group. These regions may correspond to loci (*dw*) previously identified by alleles with qualitative effects. Also, these regions identified in sorghum may be orthologous to those previously reported for plant height in maize. Gene effects and gene action varied among genomic regions. In each region, PI229828 alleles resulted in increased plant height. Each region accounted for 9.2–28.7% of the phenotypic variation. Positive, additive effects ranged from 15 to 32 cm. Tallness was dominant or overdominant and conferred by alleles from PI229828 for three quantitative trait loci (QTL). At the fourth QTL, PI229828 contributed to increased plant height, but short stature was partially dominant. One digenic interaction was significant. The presence of a PI229828 allele at one region diminished the effects of the other region. A multiple model indicated that these four regions collectively accounted for 63.4% of the total phenotypic variation. The utility of this information for germplasm conversion through backcross breeding is discussed.

Key words Genetics · Breeding · *Sorghum bicolor* *Zea mays*

Journal Paper No. J. 15649 of the Iowa Agriculture and Home Economic Experiment Station, Ames, Iowa. Project No. 3134

Communicated by F. Salamini

M. G. Pereira · M. Lee ✉
Department of Agronomy, Iowa State University, Ames, IA 50011, USA

Introduction

Restriction fragment length polymorphisms (RFLPs) have been successfully employed to construct linkage maps and to locate genes with qualitative and quantitative effects. The usefulness of the maps for basic and applied aspects of plant genetics has been summarized (Paterson et al. 1991a). In sorghum [*Sorghum bicolor* (L.) Moench], RFLPs have been used for linkage map construction and comparative analysis of genome structure with maize (Hulbert et al. 1990; Binelli et al. 1992; Whitkus et al. 1992; Berhan et al. 1993; Pereira et al. 1994). In the investigation presented here, we report the detection of genomic regions with major effects on plant height in sorghum and compare them to regions with similar effects in maize.

Genetic control of plant height in sorghum has been characterized in terms of factors with qualitative (Karper 1932; Quinby and Karper 1954) and quantitative (Hadley 1957) effects. Tallness is partially dominant to shortness (Hadley 1957). Four independent loci, *Dw1*, *Dw2*, *Dw3*, and *Dw4*, have been defined by alleles with qualitative effects (Quinby and Karper 1954). At each locus, the tall phenotype is completely dominant. The effects of the loci are cumulative (Quinby and Karper 1954) but unequal (Hadley 1957). Genetic factors at other loci may also influence plant height: varieties genetically identical at the four *Dw* loci may differ greatly in height. Quinby and Karper (1954) attributed this difference to modifier loci.

Alleles at *Dw* loci primarily influence plant height by affecting internode length. Also, through the use of isogenic lines, pleiotropic effects have been attributed to the *Dw* loci. Alleles at *Dw3* have pleiotropic effects on yield components (number of seeds per panicle and seed weight), tiller number, and panicle size (Casady 1965). The *Dw2* locus may have pleiotropic effects on panicle length, main head yield, seed weight, and leaf area (Graham and Lessman 1966). Studies of pleiotropic effects for the other 2 loci (*Dw1* and *Dw4*) were not

identified. However, in an investigation comparing tall revertants with nonrevertants at the *Dw4* locus (Quinby and Karper 1954), pleiotropic effects were not observed (Karper 1932).

Comparisons of sorghum and maize genomes have revealed a high degree of homology and synteny (Hulbert et al. 1990; Whitkus et al. 1992; Berhan et al. 1993; Pereira et al. 1994). The conserved molecular and genetic composition suggests that such regions could code for similar functions. For example, Fatokun et al. (1992) located major quantitative loci for seed weight in cowpea and mung bean. In both species, the respective map positions with greatest effect on seed weight were identified by the same RFLP probes, suggesting that the structure and function of the regions have been conserved. In maize, loci defined by alleles with qualitative effects on plant height have been mapped and related to quantitative trait loci (QTL) (Beavis et al. 1991; Edwards et al. 1992; Veldboom et al. 1994). Integration of maize genetic maps based on DNA markers, mutant phenotypes, quantitative trait loci, and comparative mapping with other monocotyledons should elucidate many examples of conserved gene order and function (Ahn and Tanksley 1993). In this study we present evidence of orthologous regions controlling plant height in maize and sorghum.

Materials and methods

Genetic material and phenotypic data collection

F_2 plants (152) from the cross CK60 × PI229828 were used. This population has been described previously (Pereira et al. 1994). CK60 is an inbred line from the species *Sorghum bicolor* spp. *bicolor* with the genotype *dw1 Dw2 dw3 dw4* (Quinby and Karper 1954). PI229828 is representative of *Sorghum bicolor* spp. *drummondii* (Duncan et al. 1991; de Wet 1978). The genotype of PI229828 has not been determined, but the phenotype suggests that it is homozygous at each of the 4 *Dw* loci for alleles conferring increased plant height. The plant height for CK60 and PI229828 is about 109 and 262 cm, respectively (Table 2).

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

Plant height was recorded at anthesis. Height of the main stem was measured in centimeters to the nearest 1 cm from the soil level to the tip of the panicle. Also, at anthesis we recorded the number of tillers per plant, leaf length and width, stalk circumference, and anthesis. After harvesting, we recorded panicle length and width, number of primary branches per panicle, peduncle diameter, and seed weight. Traits other than plant height will be presented in a related manuscript.

RFLP assays and linkage map

Leaf samples were harvested from each plant about 2 weeks before flowering, freeze-dried, ground, and stored at −20 °C in a freezer. 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 hybridizations were conducted as described in Veldboom et al. (1994). Separate digests were performed using restriction enzymes *Eco*RI and *Hin*dIII. Clones identifying polymorphism between parents were hybridized against filters containing DNA from the segregating sorghum population digested with the appropriate enzyme. Autoradiograms were scored independently twice. Filters contained DNA from CK60 (score A), PI229828 (score B), F_1 (score H), and F_2 plants.

Six sorghum genomic probes, 34 maize genomic probes, and 66 maize cDNA probes were used to detect 111 RFLP loci (Pereira et al. 1994). Goodness-of-fit to a 1:2:1 ratio of genotypic classes 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 (K. Lamkey, personal communication). Linkage analysis was accomplished with 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 estimate the genetic distance in centiMorgans (cM) between adjacent RFLP loci.

Data analysis

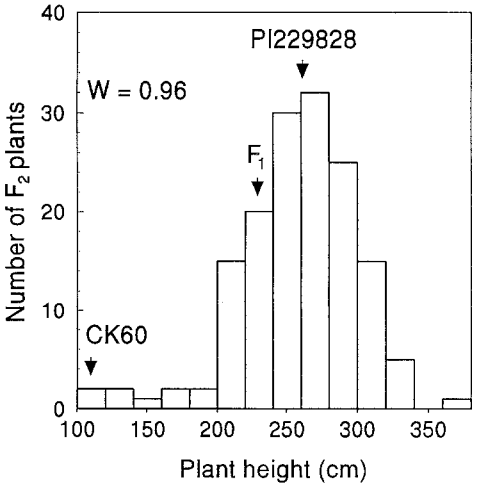
Phenotypic data

Plant height values approximated a normal distribution ($W = 0.96$; Shapiro and Wilk 1965) but were skewed slightly toward tall plants (Fig. 1). The skewness is expected because tall genotypes are partially or completely dominant in sorghum (Quinby and Karper 1954; Hadley 1957). Because data transformations, i.e., arc sin and $\log_{10}$, failed to completely normalize the distribution and may be inapplicable to this situation, untransformed data were used in the analysis. The slight deviation from normality should not cause significant bias in QTL identification (Knott and Haley 1992).

QTL identification

Interval mapping (Lander and Botstein 1989) and single factor analysis of variance (SFAOV; Edwards et al. 1987) were used in the present investigation. SFAOV was performed using SAS (SAS 1988). Interval mapping was conducted with MAPMAKER/QTL 1.1 (Paterson et al. 1988). The unconstrained model (Lincoln and Lander 1990) was used. The "sequence" and "scan" commands were used to scan the genome to detect individual QTL. The "sequence" and "map" commands were used to determine the total phenotypic variation of plant height accounted for by a multiple QTL model that included all significant QTL.

Fig. 1. Histogram of plant height (PH) for 152 F_2 plants of a CK60 × PI229828 population. W *is* the Shapiro-Wilk test of normality. The *arrows* indicate the phenotypic means



When more than one peak occurred within a linkage group, the presence of additional (linked) QTL was assessed. The peak with the largest LOD was "fixed" (Lander and Botstein 1989), and the genome was rescanned to compute the QTL likelihood plot showing the LOD score for a two-QTL model. If the LOD for the combined model was significantly higher (according to the significance threshold) than for one QTL, the presence of two QTL is likely (Paterson et al. 1991a).

There were 101 intervals in this study. An LOD threshold of 2.4 was used to declare the presence of a putative QTL in a given genomic region. This threshold level corresponds to a test of the presence of a QTL at the 0.05 level of significance according to the "sparse-map" case (Lander and Botstein 1989).

Log-likelihood plots were constructed for the entire length of linkage groups A, B, E, and H [where interval mapping and single factor analysis of variance (SFAOV) placed QTL for plant height]. LOD scores at 2.0-cM intervals were calculated and plotted against map distance for each linkage group. For each QTL, MAPMAKER/QTL determined the map positions of the boundaries of the 10:1 "confidence interval" surrounding the peak (Paterson et al. 1991).

Gene effects (a = additive effect; d = dominance effect) and percent of phenotypic variation attributable to individual 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) = 0–0.20; partial dominance (PD) = 0.21–0.80; dominance (D) = 0.81–1.20; 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 plant height came from PI229828; if negative, the allele came from CK60.

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

Two-factor analysis of variance (Edwards et al. 1987) was used to test for possible digenic epistasis among the four putative QTL (in linkage groups A, B, E, and H) identified by interval mapping. The analysis was performed by using SAS's GLM procedure, considering a factorial arrangement of the four QTL and the three marker genotypes (Fatokun et al. 1992).

Results

Allele segregation and linkage map

Linkage groups, locus order, and relative genetic distance were congruent with a previous report (Pereira et al. 1994). Ten linkage groups were identified by 111 loci, covering a total of 1299 cM, with an average interval of 12.9 cM between adjacent loci (Fig. 2). Ratios of genotypic classes at 16 loci deviated from expectations, indicating deficiency of the homozygous CK60 class. Of the loci with deviant ratios, 10 were placed consecutively in linkage groups A (6 loci) and B (4 loci). At all 10 loci, a greater frequency of PI229828 alleles was observed. The average allelic ratio (CK60:PI229828) was 0.43:0.53 and 0.37:0.63 in linkage groups A and B, respectively.

QTL identification

Interval mapping and single-factor analysis of variance identified four unlinked genomic regions in linkage groups A, B, E, and H with significant effects on plant height (Table 1; Fig. 3). Each of these regions accounted for 9.2–28.7% of the total phenotypic variation. The multiple QTL model indicated that these QTL, collectively, accounted for 63.4% of the total variation for plant height. When the genome was rescanned, additional significant genomic regions were not identified. This suggests that the two small peaks in linkage group A (Fig. 3) are associated with the main peak instead of representing additional QTL.

The QTL displayed unequal gene effects. Additive effects ranged from 15 (linkage groups B) to 32 cm (linkage group A). Genotypic class averages (Table 2) illustrates the magnitude and effects of the four QTL. Differences among homozygous genotypes (CK60/

Table 1 Location and effects of QTL affecting plant height

Linkage group	Interval[a]	R^2	LOD[b]	Gene effects[c]		d/a	Gene action	Dir[d]
				Additive	Dominance			
				cm				
A	*ISU123* *ISU116*	29%	8.4	32.5	33.1	1.02	D	PI
B	*ISU155* *UMC71*	9%	2.7	15.0	23.7	1.57	OD	PI
E	*ISU140* *PIO100016*	20%	5.6	20.1	25.2	1.25	OD	PI
H	*ISU032B* *ISU156*	12%	3.8	21.3	−10.9	−0.51	PD	PI
Multiple QTL model		63%	25.6					

[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

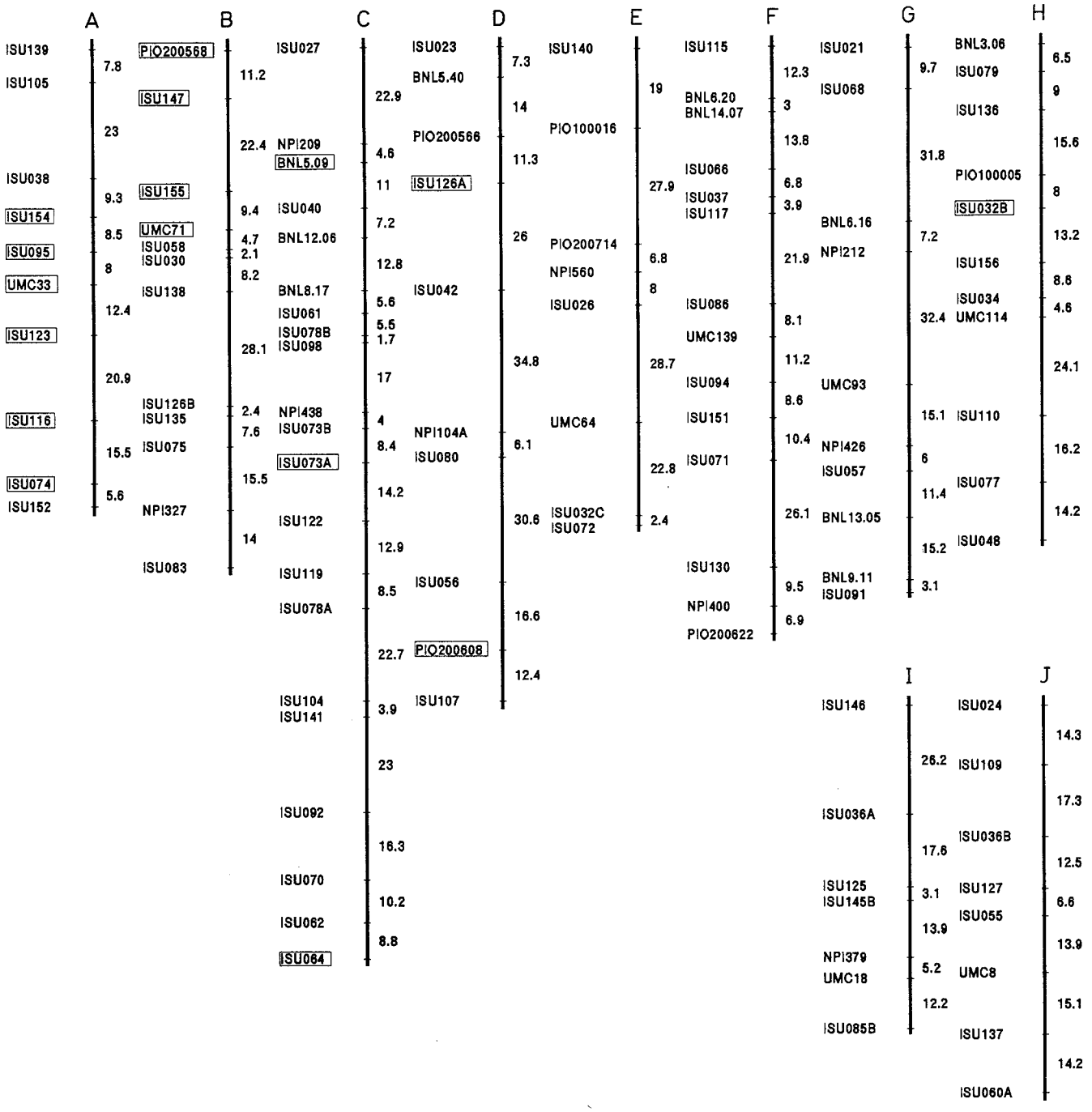


Fig. 2 RFLP linkage map of *Sorghum bicolor* L. Moench population CK 60 × PI229828. Loci (111) were distributed to ten linkage groups (*A* – *J*). The *numbers* to the *right* of each linkage group represent the map distance in cM (Haldane). Loci identified by *open boxes* displayed distorted ratios

CK60 versus PI229828/PI229828) ranged from 30 cm for QTL in linkage group B to 65 cm for QTL in linkage group A. The dominant effects ranged from 11 cm for QTL in linkage group H to 33 cm for QTL in linkage group A.

Each QTL exhibited specific gene action. In each region, PI229828 alleles resulted in increased plant height. Alleles from PI229828 were dominant or overdominant, except in linkage group H where the CK60 allele was partially dominant. At that region, heterozygotes had an average plant height closer to that of homozygous CK60 genotypes than homozygous PI229828 genotypes. Gene action indicated by the multiple QTL model was partially dominant ($d/a = 0.66$) toward increased plant height.

In agreement with interval mapping, SFAOV identified the same four unlinked genomic regions in linkage groups A, B, E, and H with significant effects on plant height (Fig. 3). Three genomic regions (linkage groups A, E, and H) were significant at the 0.001 probability level, and one (linkage group B) was significant at the

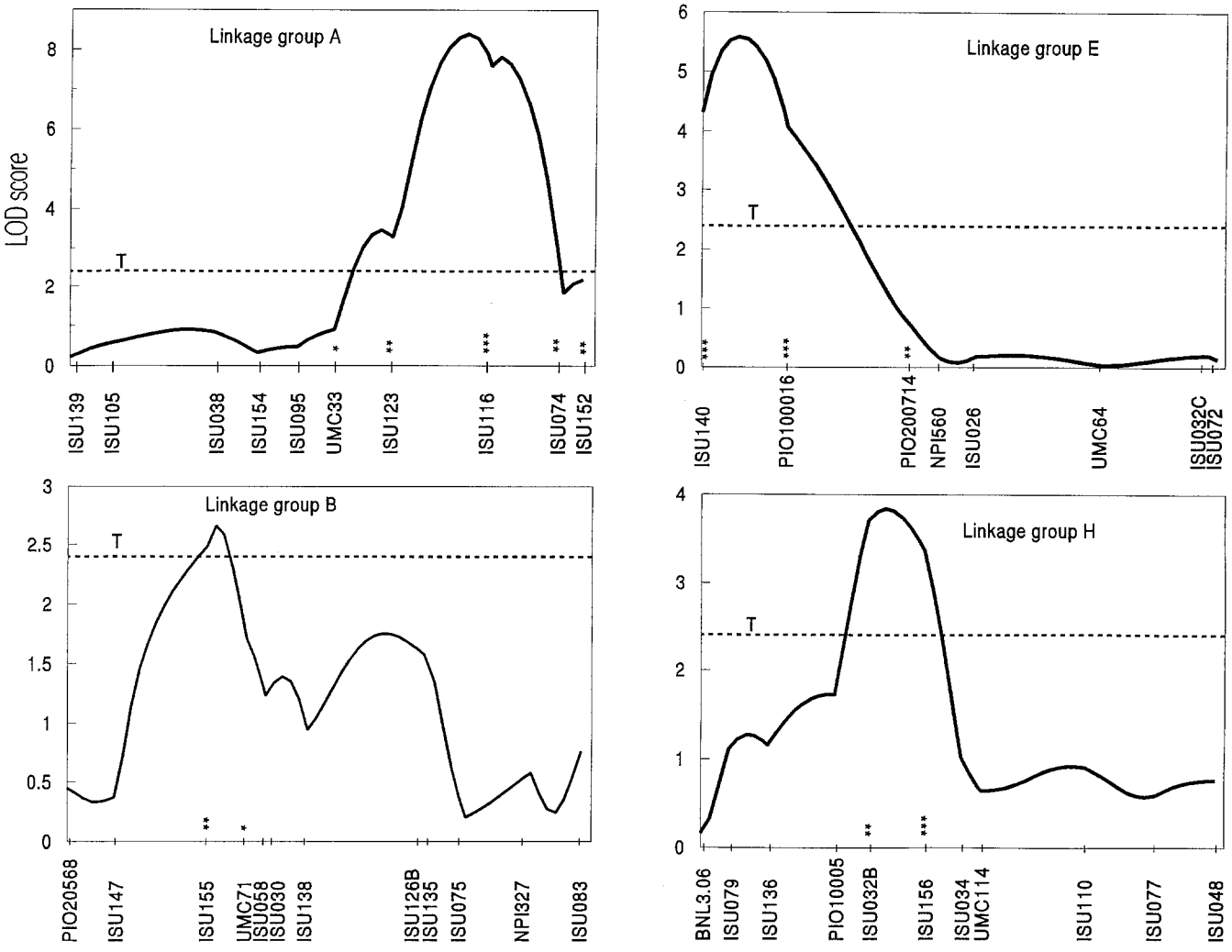


Fig. 3 Log-likelihood plots of linkage groups A, B, E, and H for plant height. *Vertical axes* represent LOD score. *, **, *** indicate significance at 0.05, 0.01, and 0.001 levels respectively, for SFAOV

Table 2 Class averages of QTL affecting plant height

Linkage group	Interval[a]	CK/CK (*u*AA)[b]	CK/PI (*u*AB)[c]	PI/PI (*u*BB)[d]
		cm		
A	*ISU123 – ISU116*	201 ± 35[e]	266	266
B	*ISU155 – UMC71*	226 ± 39	265	256
E	*ISU140 – PIO100016*	224 ± 37	299	264
H	*ISU032B – ISU156*	244 ± 39	254	286

CK60 = 109 cm PI229828 = 262 cm F_1 = 232 cm

[a] Flanking markers of the most likely QTL position
[b] Trait mean for a homozygous CK60 with no effect of that QTL
[c] Trait mean for a heterozygous genotype (CK60/PI229828). Calculated as *u*AA + *a* (additive effect) + *d* (dominance effect)
[d] Trait mean for a homozygous PI229828. Calculated as *u*AA + 2*a*
[e] Standard deviation associated with the estimated mean of that interval

0.01 probability level. In linkage group A, interval mapping placed the most likely QTL position (likelihood peak) closer to *ISU116*. In concordance, SFAOV indicated *ISU116* had the strongest association ($P < 0.001$) with plant height in that linkage group. Similar relationships can be observed for the other three linkage groups containing plant height QTL: SFAOV indicated that flanking markers for each most likely QTL position identified by interval mapping are significantly associated with variation in plant height.

Digenic epistasis was identified between regions in linkage groups A and E, represented by loci *ISU116* and *ISU140*, respectively (Table 3). As illustrated in Table 3, the gene effects of one QTL are dependent on the allelic constitution at the other locus. The presence of a PI229828 allele at QTL of linkage group E is associated with a reduction in the gene effects of the QTL of linkage group A (from 54 to 7 cm of additive effect). Also, the presence of the PI229828 allele at QTL of linkage group A reduces the estimated gene effects of the QTL of linkage group E (from 60 to 13 cm of additive effect). The other five possible digenic interactions involving QTL for plant height were not significant.

Table 3 Digenic interaction between QTL from linkage groups A (*ISU116*) and E (*ISU140*)

Genotype at *ISU140*	Genetic effects *ISU116*		Genotype at *ISU116*	Genetic effects *ISU140*	
	a[a]	d[b]		a[a]	d[b]
CK60/CK60	54	66	CK60/CK60	60	10
CK60/PI[c]	40	28	CK60/PI	16	3
PI/PI	7	25	PI/PI	13	29

[a] Additive effect in centimeters
[b] Dominance effect in centimeters
[c] PI229828

Discussion

Linkage mapping

Linkage groups, locus order, and relative genetic distance were in good agreement with those presented in a previous report (Pereira et al. 1994). However, ratios of genotypic classes at a higher proportion of loci (5% versus 16%) deviated from expectations. Previously, loci with deviant ratios were predominantly at one region of linkage group B. In the present investigation, the loci with deviant ratios were placed not only at that region, but also at another region in linkage group A. The same population was used in both studies, but F_2 plants were grown in different environments (greenhouse versus field). Also, seed of the F_2 generation was produced in different environments (field in Manhattan, Kansas, 1990 for the previous study and in the greenhouse, Ames, Iowa, 1991 for this study). Perhaps biotic or abiotic stress encountered in the field environment affected germination of the homozygous CK60 genotypes and caused deviant ratios at loci in linkage group A. At all loci with deviant ratios in linkage group A, alleles contributed by PI229828 were recovered at a greater frequency than expected. Segregation distortion of this magnitude or greater has been observed in other studies involving interspecific crosses of tomato (Paterson et al. 1991b; de Vicente and Tanksley 1993), and maize (Doebley and Stec 1993), and intraspecific crosses of maize (Edwards et al. 1987). Loci with deviant ratios should not affect QTL identification, but would have a minor effect on estimates of the variance due to additive and dominance effects (Edwards et al. 1987).

Genetic effects

The genomic regions controlling plant height were associated with relatively large effects: one QTL (linkage group A) accounted for almost 29% of the phenotypic variation, while the smallest amount of variation accounted for by a single QTL was 9.2%. The magnitude of effects differed among QTL. These results agree with those in a previous report of unequal effects for plant height genes in sorghum (Hadley 1957). The high proportion of variation accounted by the multiple model (63.4%) agrees with previous heritability estimates (progeny mean basis) of plant height in sorghum (Vasudeva-Rao and Goud 1977; Kukadia et al. 1983; Patel et al. 1983; Kumar and Singhania 1984; Knapp et al. 1987; Wenzel 1990).

Interval mapping and SFAOV methods were congruent in the identification of genomic regions controlling plant height (Fig. 3). For each QTL identified by interval mapping, SFAOV indicated that the flanking markers of the most likely QTL position were significantly associated with plant height. Such correspondence between the two methods concurs with simulation studies (Darvasi et al. 1993) and empirical observations (Stuber et al. 1992).

Gene action

PI229828 contributed alleles that increased main effects for plant height at all QTL. The multiple model exhibited partial dominance, which is in agreement with results from previous studies (Quinby and Karper 1954; Hadley 1957; Vasudeva-Rao and Goud 1977). Gene action varied among individual QTL. In linkage group H, the allele with dominant effects was derived from CK60, and it reduced plant height. For the other QTL, tallness was dominant or overdominant and conferred by alleles from PI229828. Quinby and Karper (1954) found partial dominance for plant height. However, some variation in the degree of dominance was attributed to modifiers specific to the genetic background of the population.

The multiple QTL model indicated a lack of interaction among QTL. The LOD score (25.55) and the total phenotypic variation (63.4%) were equivalent to the summation of these parameters from individual QTL. The lack of interaction was also reported by Hadley (1957), who suggested that nonallelic interactions, if present, were either balanced or too small to be detected. In another investigation (Quinby and Karper 1954), epistasis was not directly identified, but in strains of very short stature the effect of a dwarfing allele ranged from 10 to 100 cm. The identification of interaction between QTL in linkage groups A and E by the analysis of variance in the present study is in agreement with such variation of effects of the dwarfing alleles previously reported (Quinby and Karper 1954). The additive effect of the PI229828 allele ranged from 7 to 54 cm and from 13 to 60 cm in QTL linkage groups A and E, respectively.

Relating quantitative and qualitative inheritance

The four QTL detected in the current investigation may correspond to loci identified by alleles with qualitative

effects (*Dw1*, *Dw2*, *Dw3*, and *Dw4*). The genotype for PI229828 is unknown, although the phenotype suggests that it does not contain dwarfing alleles at the known *Dw* loci. Also, the locations of the *Dw* loci in the sorghum genome are not established. As a result, direct comparisons between QTL and *Dw* loci (loci with major effects on plant height), as in maize (Beavis et al. 1991), are limited. However, putative pleiotropic effects of the *Dw* loci (Karper 1932; Quinby and Karper 1954; Casady 1965; Graham and Lessman 1966; Shertz 1973), and linkages involving QTL for plant height and other morphological traits (Pereira et al., in prep.) provide some basis for relating the plant height QTL reported herein and the *Dw* loci.

In the present study, the plant height QTL are usually associated with QTL for other morphological traits. Briefly, in linkage group A, there are QTL for tiller number, stem diameter, panicle dimensions, and number of seed-branches closely linked to or at the plant height QTL. In linkage group E, the plant height QTL is not linked to any other QTL. In linkage group H, QTL for maturity (anthesis), leaf length and width, and panicle dimensions have been placed at the same region as the QTL for plant height.

Pleiotropic effects of the *Dw* loci have been reported. The *Dw3* locus has pleiotropic effects on yield components (number of seeds per panicle and seed weight), tiller number, and panicle length (Casady 1965; Schertz 1973). Thus, *Dw3* may correspond to the QTL in linkage group A. The *Dw2* locus has pleiotropic effects on leaf area, panicle length, and seed weight, but not on tiller number (Graham and Lessman 1966). Therefore, *Dw2* may correspond to the plant height QTL of linkage group H. Pleiotropic effects (Karper 1932; Quinby and Karper 1954) at *Dw4* have not been reported. Thus, *Dw4* may correspond to the QTL in linkage group E.

According to the reported (CK60) and assumed (PI229828) parental genotypes, 3 *Dw* loci (*Dw1*, *Dw3*, and *Dw4*) are possibly segregating in the present population; however, four QTL were identified. One explanation would be that the *Dw2* locus is also segregating; and, as alleles from PI229828 increased the main effect, the PI229828 allele should be different from *Dw2* (of CK60; Quinby and Karper 1954) and from *dw2* (conferring a dwarf recessive phenotype). An allelic series at the 4 height loci may well exist (Quinby 1975). Another possible explanation should be the presence of another locus controlling plant height in the current population, but not yet reported in sorghum.

QTL in sorghum and maize

Maize and sorghum share a high level of homology and synteny. Thus, regions of the sorghum genome associated with plant height may be directly compared with regions of the maize genome also related to this trait (Fig. 4).

RFLP loci of linkage group A associated with plant height exhibit collinearity to a genomic region of the long arm of the maize chromosome 1. QTL for plant height in maize have been reported in the same region of the long arm of the chromosome 1 (Beavis et al. 1991; Edwards et al. 1992; Veldboom et al. 1994). The genomic region identified by Beavis et al. (1991) and Veldboom et al. (1994) includes some of loci that define the region in sorghum (Fig. 4). For example, locus *ISU116* is included by the QTL confidence interval in both instances. Two genetic loci defined by alleles with highly qualitative effects (*br1* and *an1*) are located within the same region in the maize genome (Beavis et al. 1991). The mutant phenotype of *an1* is an andromoneocius, gibberellin-responsive dwarf with short, broad leaves and few tassel branches (Neuffer et al. 1968; Emerson and Emerson 1922). Sorghum QTL in that region (linkage group A) have significant effects on the number of primary branches per panicle in the sorghum plant. The region of sorghum linkage group H controlling plant height may correspond to a region of the short arm of maize chromosome 9. The corresponding regions share 6 RFLP loci, 3 in conserved and 3 in inverted order. This sorghum QTL may be related to a maize QTL reported by Beavis et al. (1991). The *d3* locus is located in the same region in the maize genome (Beavis et al. 1991). The *d3* mutant is also characterized by thick, broad leaves and a compact tassel (Neuffer et al. 1968; Demerec 1926). The sorghum QTL in that region (linkage group H) affects leaf and panicle dimensions in sorghum. For the QTL identified in sorghum linkage group E, 1 of the loci flanking the most likely QTL position is *PIO100016*. That probe also detects a locus mapped to the long arm of maize chromosome 6. Edwards et al. (1992) and Veldboom et al. (1994) identified QTL affecting plant height in that region. The confidence interval of the region reported by Veldboom et al. (1994) includes locus *PIO100016*. Maize locus *py1* is placed to the same region in the maize genome (Veldboom et al. 1994). The *py1* mutant has a pleiotropic effect on the length of the maize leaves (Neuffer et al. 1968; Suttle 1924; cited by Maize New 1993). However, the sorghum QTL in that region (linkage group E) does not affect any trait besides plant height in this population.

Marker-assisted selection and introgression of exotic germ plasm

The current investigation identified genomic regions that individually and cumulatively accounted for significant portions of the toal phenotypic variation for plant height in sorghum. The utility of RFLP maps for a plant breeding program depends, in part, on the identification of RFLP markers that are closely linked to desirable genes. For each QTL reported here, there is an RFLP marker, within approximately 10 cM of desirable genes. Sorghum is originally a tropical species and unadapted to machine harvesting for grain. To grow this crop for

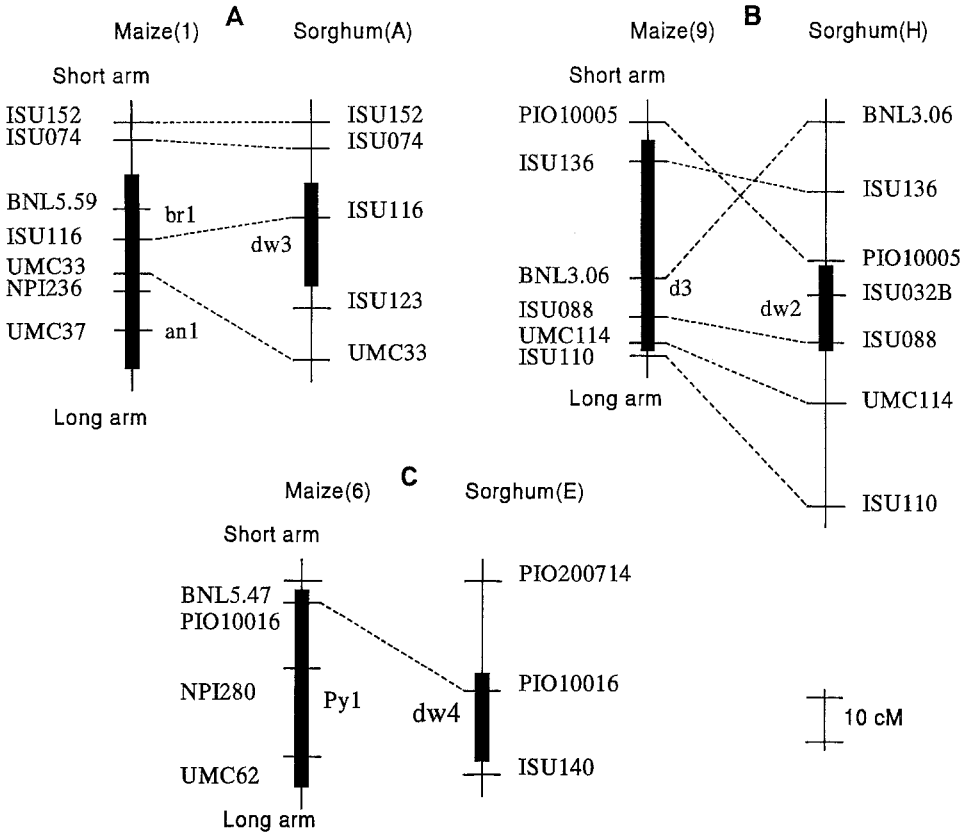


Fig. 4A–C Conserved regions of maize and sorghum genome having the same RFLP markers (joined by *broken lines*). *Numbers* and *letters* in parentheses indicate maize chromosome numbers and sorghum linkage groups, respectively. The *shaded areas* are the confidence intervals (1.0 log unit as indicated by Mapmaker-QTL program) for plant height QTL. In **A** and **B**, the maize QTL were identified by Beavis et al. (1991), and in **C**, the maize QTL was identified by Veldboom et al. (1994). *br1*, *an1*, *d3*, and *py1* are maize plant height genes with qualitative alleles approximately located in that position of the maize genome (Maize Newsl 1992). *dw2*, *dw3*, and *dw4* are sorghum plant height loci with qualitative alleles possibly corresponding to sorghum plant height QTL. Positions of the *dw* loci are hypothetical

grain in latitudes of temperate regions, some adaptation is necessary. Important traits for adaptation are photoperiod sensitivity (maturity genes) and machine harvestability (plant height genes). The U.S. Sorghum Conversion Program (Miller 1982; Duncan et al. 1991) utilizes a backcrossing scheme in which genes at up to 8 loci (4 for plant height and 4 for maturity) are introgressed from the temperate, domestic parent to the exotic, recurrent parent. Identification of four QTL for plant height, possibly corresponding to the 4 *Dw* loci, may be very useful in accelerating the process of germ plasm introgression via a marker-assisted backcross scheme. For example, in the present study 1 F_2 plant has a phenotype closely resembling CK60 for plant height (127 cm) but contains a high proportion of the PI229828 genotype. The ratio CK60/PI229828, in terms of percentage of homozygous loci, is 0.5 for genomic regions unlinked to the four plant height QTL (twice as many homozygous PI229828 loci as homozygous CK60 loci) and 1.1 for the total genome. In another F_2 plant with a phenotype closely resembling that of CK60 for plant height (110 cm), the ratios were 1.6 and 2.8 for the unlinked and the total genome, respectively. As the objective of the Sorghum Conversion Program is to introgress as many genes as possible from the exotic, unadapted parent while maintaining the desired plant stature and maturity, knowledge of the genotype (RFLP loci) of the segregating progeny could facilitate the selection of appropriate individuals to be backcrossed.

Acknowledgements This research was supported by Pioneer Hi-Bred Int., Iowa Agricultural and Home Economics Experiment Station Project 3134, and CEPLAC-CNPq. The authors thank Paula Bramel-Cox for providing F_1 seed, and Keith Schertz, John Axtell, and Gary Hart for helpful comments.

References

Ahn S, Tanksley SD (1993) Comparative linkage maps of the rice and maize genomes. Proc Natl Acad Sci USA 90:7980–7984

Beavis WD, Grant D, Albertsen M, Fincher R (1991) Quantitative trait loci for plant height in four maize populations and their associations with qualitative genetic loci. Theor Appl Genet 83:141–145

Berhan AM, Hulbert SH, Butter LG, Bennetzen JL (1993) Structure and evolution of the genomes of *Sorghum bicolor* and *Zea mays*. Theor Appl Genet 86:598–604

Binelli GL PE, Gianfranceschi ME, Taramino G, Busso C, Stenhouse J, Ottaviano E (1992) Similarity of maize and sorghum genomes as revealed by maize RFLP probes. Theor Appl Genet 84:10–16

Casady AJ (1965) Effect of a single height (*Dw*) gene of sorghum on grain yield, grain yield components, and test weight. Crop Sci 5:385–389

Darvasi A, Weinreb A, Minke V, Weller JI, Soller M (1993) Detecting marker-QTL linkage and estimating QTL gene effect and map location using a saturated genetic map. Genetics 134:943–951

De Vicente MC, Tanksley SD (1993) QTL analysis of transgressive segregation in an interspecific tomato cross. Genetics 134: 585–596

De Wet JMC (1978) Systematics and evolution of sorghum sect. sorghum (gramineae). Am J Bot 65:477–484

Demerec M (1926) Notes on linkages in maize. Am Nat 60:172–176

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

Dudley JW (1993) Molecular markers in plant improvement: manipulation of genes affecting quantitative traits. Crop Sci 33: 660–668

Duncan R, Bramel-Cox PJ, Miller FR (1991) Contributions of introduced sorghum germplasm to hybrid development in the USA. (CSSA special publ no. 17:69–101)

Edwards MD, Stuber CW, Wendel JF (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 MD, Helentjaris T, Wright S, Stuber CW (1992) Molecular-marker-facilitated investigations of quantitative trait loci in maize. Theor Appl Genet 83:765–774

Emerson RA, Emerson SH (1992) Interactions of two andromonoecious types of maize, dwarf and anther ear. Genetics 7:203–236

Fatokun CA, Menancio-Hautea DI, Danesh D, Young ND (1992) Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. Genetics 132:841–846

Graham D, Lessman KJ (1966) Effect of height on yield and yield components of two isogenic lines of *Sorghum vulgare* Pers. Crop Sci 6:372–374

Hadley HH (1957) An analysis of variation in height in sorghum. Agron J 49:144–147

Hulbert SH, Richter TE, Axtell JD, Bennetzen JL (1990) Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. Proc Natl Acad Sci USA 87:4251–4255

Karper RE (1932) A dominant mutation of frequent recurrence in sorghum. Am Nat 66:511–529

Knapp SJ, Ross WM, Stroup WW (1987) Precision of genetic variance and heritability estimtes from sorghum populations. Crop Sci 27:265–268

Knott SA, Haley CS (1992) Aspects of maximum likelihood methods for mapping of quantitative trait loci in line crosses. Genet Res 60:139–151

Kukadia MU, Desai KB, Desai MS, Patel RH, Raja KRV (1983) Estimates of heritability and other related genetic parameters in sorghum. Sorghum Newsl 26:31–32

Kumar S, Singhania DL (1984) Genetic advance and heritability estimates for grain yield and its components. Sorghum Newsl 27:15–16

Lander ES, Botstein D (1989) Mapping mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121: 185–199

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lincoln SE, Lander ES (1990) Mapping genes controlling quantitative traits using MAPMAKER/QTL. Whitehead Institute for Biomedical Research, Cambridge, Mass.

Miller FR (1982) Genetic and environmental response characteristics of sorghum. In: House LR, Munghogho LK, Peacock JM (eds) Sorghum in the eighties. ICRISAT, Patancheru, India, pp 393–402

Neuffer MG, Jones L, Zuber MS (1968) The mutants of maize. Crop Sci Soc Madison, Wis.

Patel RH, Desai KB, Desai SP (1983) Heritability estimates in grain sorghum. Sorghum Newsl 26:89–90

Paterson AH, Lander ES, Had JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726

Paterson AH, Tanksley SD, Sorrells ME (1991a) DNA markers in plant improvement. Adv Agron 46:39–90

Paterson AH, Damon S, Hewitt JD, Zamir D, Rabinowitch HD, Lincoln SE, Lander E, Tanksley SD (1991b) Mendelian factors underlying quantitative traits in tomato: comparison across species, generations, and environments. Genetics 127:181–197

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

Quinby JR (1975) The genetics of sorghum improvement. J Hered 66:56–62

Quinby JR, Karper RE (1954) Inheritance of height in sorghum. Agron J 46:211–216

SAS Institute Inc (1988) SAS/STAT users' guide, 6.03 edn. SAS Institute Inc, Cary, N.C.

Shapiro SS, Wilk MB (1965) An analysis of variance for normality (complete samples). Biometrika 52:591–611

Shertz KF (1973) Single height-gene effects in hybrids of double haploid *Sorghum bicolor* (L.) Moench. Crop Sci 13:421–423

Stuber CW, Edwards MD, Wendel JF (1987) Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. Crop Sci 27:639–648

Stuber CW, Lincoln SE, Wolf DW, Helentjaris T, Lander ES (1992) Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 132:823–839

Suttle AD (1924) Genetic interrelations of different types of dwarf corn. PhD thesis Cornell University, USA

Tanksley SD, Bernatzsky DR, Lapitan NL, Prince JP (1988) Conservation of gene repertoire but not gene order in pepper and tomato. Proc Natl Acad Sci USA 85:6419–6423

Vasudeva-Rao MJ, Goud JV (1977) Inheritance of plant height and maturity in sorghum. I. Influence of height, maturity and their components. Mysore J Agric Sci 11:269–275

Veldboom LR, Lee M, Woodman WL (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 WG (1990) Inheritance and interrelationships of quantitative traits in sorghum. Sorghum Newsl 31:1–3

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