

Genetics of Tassel Branch Number in Maize and its Implications for a Selection Program for Small Tassel Size*

S.H. Schuetz and J.J. Mock

Agronomy Department, Iowa State University, Ames, Iowa (USA)

Summary. Tassel branch numbers of six crosses of maize (*Zea mays* L.) were analyzed to determine inheritance of this trait. Generation mean analyses were used to estimate genetic effects, and additive and nonadditive components of variance were calculated and evaluated for bias due to linkage. Both narrow-sense and broad-sense heritabilities were estimated. Additive genetic variance estimates were significant in five of the six crosses, whereas estimates of variance due to nonadditive components were significant in only three crosses. Additionally, estimates of additive variance components usually were larger than corresponding nonadditive components. There was no evidence for linkage bias in these estimates. Estimates of additive genetic effects were significant in four of six crosses, but significant dominance, additive \times additive and additive \times dominance effects also were detected. Additive, dominance, and epistatic gene action, therefore, all influenced the inheritance of tassel branch number, but additive gene action was most important. Both narrow-sense and broad-sense heritability estimates were larger than those reported for other physiological traits of maize and corroborated conclusions concerning the importance of additive gene action inferred from analyses of genetic effects and variances. We concluded that selection for small-tasseled inbreds could be accomplished most easily through a mass-selection and/or pedigree-selection system. Production of a small-tasseled hybrid would require crossing of two small-tasseled inbreds. We proposed two genetic models to explain unexpected results obtained for two crosses. One model involved five interacting loci and the other employed two loci displaying only additive and additive \times additive gene action.

Key words: *Zea mays* L. – Tassel branch number – Selection program

Introduction

One solution to the problem of increasing the efficiency with which maize converts solar energy into grain is to increase solar-energy interception by the maize canopy. Most contemporary maize genotypes are barren when grown at high plant densities that maximize solar-energy interception; therefore, barrenness must be overcome to maximize grain yield.

Small tassels often are associated with density tolerance (decreased barrenness at high densities) in maize. For example, Buren et al. (1974) found correlations between dry weight of the tassel at pollen shed and grain yield ranging from -0.41 to -0.81 for three sets of maize hybrids grown at a plant density of 98,800 plants/ha. A correlation of -0.82 between mean tassel branch number of pairs of inbred parents and grain yield of their respective F_1 hybrids was reported by Sharma and Dhawan (1968). Evaluation of correlated responses to recurrent selection for grain yield in three Iowa maize breeding populations showed that six to seven cycles of selection had increased grain yield and decreased both tassel branch number and tassel dry weight significantly (Fakorede and Mock 1978).

The relationship between tassels and grain yield in maize was first detected in comparisons of grain yields of detasseled plants with yields of their nondetasseled counterparts. Watson (1892) observed a grain-yield increase of 50.6% associated with detasseling. In a more recent paper, Hactrjan (1965) reported that detasseling resulted in grain-yield increases ranging from 11 to 20%. According to Grogan (1956) and Hunter et al. (1969), yield advantages of detasseled plants were greater at high than at low

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plants densities. Eliminating pollen production of the tassel through male sterility has a similar effect on yield. Duvick (1958) found that, compared with male-fertile plants, male-sterile plants displayed yield advantages that were more pronounced at high than at low plant densities. Similarly, grain-yield increases of 17 and 41% were reported by Chinwuba et al. (1961) for male-sterile relative to male-fertile genotypes grown at 33,000 and 68,000 plants/ha, respectively. Meyer (1970) found that, at 44,000 plants/ha, there were no grain-yield differences among male-fertile and male-sterile genotypes, but at 89,000 plants/ha, male-sterile genotypes averaged 7% more grain than their male-fertile counterparts.

The tassel may also intercept light. Duncan et al. (1967) found that, at 27,000 plants/ha, maize tassels intercepted 4.2% of incident sunlight, but at 60,500 plants/ha, they intercepted 7.5%. Furthermore, a computer-simulation experiment (Duncan et al. 1967) showed that shading of upper leaves by the tassel reduced photosynthesis by 4% at 17,000 plants/ha and by 19% at 99,000 plants/ha.

Several studies have demonstrated that decreasing tassel size, rather than completely eliminating the tassel or pollen production, may have a positive effect on yield. Shekhawat et al. (1964) reported that partial detasseling (removal of tassel branches) gave an increase in yield of grain. Similarly, Hunter et al. (1969) obtained a significant increase in grain yield (0.4 tons/ha) at a density of 72,000 plants/ha by removing tassel side branches. Johnson and Lambert (1975) genetically reduced the number of tassel branches by 96% and estimated this procedure increased the potential yield of the maize crop by 5.9 quintals/ha. Clearly, breeding programs designed to reduce barrenness in maize grown at high plant densities should consider reduction of tassel size as a primary criterion for selection. Maize breeders, however, must know which types of gene action control tassel size before initiating a small-tassel selection program.

Materials and Methods

A previous study (Mock and Schuetz 1974) indicated that: 1) tassel branch number of F_1 hybrids relative to midparent values probably was genotype-dependent and 2) genotype \times environment interaction was relatively unimportant in determining tassel branch number. We decided, therefore, that the best allocation of resources for our present study would involve evaluating several crosses in single-environment experiments. Also, on the basis of data from our earlier study (Mock and Schuetz 1974), we selected four crosses for detailed study because they exhibited a variety of F_1 responses relative to their midparent values. A257 \times B75 displayed a lack of dominance, BSSS-101 \times B75 showed complete dominance of the large-tasseled parent, and mean values for both B75 \times H19 and (M14 \times C103) - 1505 \times B75 were larger than either parent (Table 1). Furthermore, preliminary observations

and data suggested that a reciprocal effect on tassel branch number might exist for crosses involving BSSS-36 and BSSS-78 (Table 2); therefore, these crosses were included in the study reported herein.

We grew nine generations for each of the six crosses evaluated. These generations included the parents (arbitrarily designated P_1 and P_2), the F_1 's and F_2 's, backcrosses to P_1 and P_2 (designated B_1 and B_2 , respectively), plus varying numbers of F_3 , B_1 S and B_2 S families produced by selfing random plants of the F_2 , B_1 and B_2 generations, respectively. All six experiments (one experiment per cross) were grown in randomized complete blocks with two replications. Plots for parental inbreds, the F_1 's and each F_3 , B_1 S and B_2 S family contained two 17-plant rows (34 plants with perfect stands). Plots for B_1 and B_2 contained four 17-plant rows (contained 68 plants), and F_2 generations were grown in eight-row plots (136 total plants). All plots were hand-planted and contained one plant per hill. Missing hills occurred in some plots, but perusal of the data showed tassel branch number of plants bordering these hills was not affected. As soon after pollen-shed as possible, tassel branch number was recorded for each plant having an intact tassel. All branches (including the central branch) that contained more than four spikelets were counted.

Means were calculated for all nine generations of each cross and were used for estimating genetic effects as outlined by Gamble (1962). Genetic effects were estimated from a complete model (including effects for F_2 mean, additive and dominance gene action, and three types of first-order epistasis) and from a reduced three-factor model (including F_2 means, plus additive and domi-

Table 1. Mean numbers of tassel branches for several maize inbreds and their F_1 hybrids

Genotype	Mean tassel branch numbers	Midparent value
B75	2.7	
A257	22.4	
F_1	13.0	12.6
B75	2.4	
BSSS-101	19.2	
F_1	21.8	10.8
B75	2.2	
H19	4.7	
F_1	8.7	3.2
B75	2.3	
(M14 \times C103)-1505	5.7	
F_1	7.6	4.0

Table 2. Mean numbers of tassel branches for two inbreds and their reciprocal crosses

Genotype	Mean tassel branch numbers
BSSS-36	11.67 \pm 0.32
BSSS-78	15.17 \pm 0.56
BSSS-36 \times BSSS-78	13.67 \pm 0.95
BSSS-78 \times BSSS-36	18.50 \pm 1.12

nance effects only). Epistatic effects were considered significant only if fitting data for the full model significantly reduced the residual mean square obtained from fitting the reduced model.

Data from individual plants were used to calculate variances among P_1 , P_2 , F_1 , F_2 , B_1 and B_2 plants. Sums of squares for each parent and the F_1 generation for each cross were pooled and divided by appropriate pooled degrees of freedom to obtain an estimate of environmental error. Individual-plant data also were used for estimating variances within F_3 , B_1S and B_2S families. Estimates of variances among F_3 , B_1S and B_2S families were obtained from analyses of variance for plot means. Covariances for tassel branch numbers of F_2 plants with the means of their F_3 progenies also were estimated for all crosses. Genetic variance components were estimated from these variances and covariances according to expectations presented by Mather (1949) and Hallauer (1965).

Mather (1949) proposed a technique for determining the presence of bias introduced into variance-component estimates by linkage. If linkage is present, relative contributions of additive and dominance effects of each locus to the additive and dominance variances are different for the F_2 and F_3 generations. Furthermore, Mather (1949) demonstrated that, with random assortment, the variance among F_2 plants (V_{F_2}) is 2X larger than the variance within F_3 families (\bar{V}_{F_3}). A significant difference between estimates of V_{F_2} and $2\bar{V}_{F_3}$, therefore, suggests that linkage is present.

We used three methods to estimate heritability for tassel branch number. The first was Warner's (1952) method, which uses variance components to obtain a narrow-sense estimate of heritability on a single-plant basis. A broad-sense estimate of heritability on an F_3 -family-mean basis was obtained by using variance among F_3 families as an estimate of σ^2_g . Additionally, heritability was estimated by a standard-unit regression of F_3 family means on F_2 -parent-plant values (Frey and Horner 1957).

Table 3. Estimates of additive and nonadditive components of variance and their standard errors for tassel branch numbers of six maize crosses

Cross	Estimate	
	D	H
A257 × B75	26.76 ± 1.86	-2.72 ± 4.70
(M14 × C103)-1505 × B75	-1.11 ± 0.66	6.93 ± 0.93
BSSS-101 × B75	77.65 ± 1.74	-56.22 ± 4.37
B75 × H19	6.63 ± 0.95	0.11 ± 2.38
BSSS-36 × BSSS-78	23.81 ± 2.00	15.12 ± 5.04
BSSS-78 × BSSS-36	26.95 ± 2.19	-4.69 ± 5.52

Table 4. Estimates of genetic effects and their standard errors for tassel branch number of six maize crosses

Cross	Effect					
	<i>m</i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
A257 × B75	9.24 ± 0.47	10.46 ± 1.25	2.59 ± 1.95	3.80 ± 1.92	1.14 ± 1.49	0.04 ± 4.69
(M14 × C103)-1505 × B75	5.61 ± 0.16	2.36 ± 0.41	4.12 ± 0.64	0.61 ± 0.63	0.72 ± 0.49	-0.35 ± 2.54
BSSS-101 × B75	15.93 ± 0.44	-2.92 ± 1.17	-8.26 ± 1.82	-9.64 ± 1.78	-10.98 ± 1.39	-6.36 ± 4.36
B75 × H19	5.81 ± 0.19	-1.81 ± 0.29	3.19 ± 0.57			
BSSS-36 × BSSS-78	16.92 ± 0.39	0.68 ± 0.61	4.35 ± 0.21			
BSSS-78 × BSSS-36	16.59 ± 0.42	0.33 ± 0.38	4.09 ± 1.32			

Results and Discussion

Results of our study indicated that, although many types of gene action control tassel branch number, additive gene action usually is most important. This generalization is supported by our estimates of genetic variances, genetic effects and heritabilities.

Estimates of genetic variances are presented in Table 3. Additive variance (D) was significant for five of the six crosses studied; it was not significant only for (M14 × C103)-1505 × B75. Tassel branch numbers of (M14 × C103)-1505 and B75 were similar (Table 1). Perhaps these two inbreds possessed identical alleles at many of the loci affecting the trait. Variances due to dominance deviations (H in Table 3) were significant for only two of the crosses [(M14 × C103)-1505 × B75 and BSSS-36 × BSSS-78]. The large, negative estimate of H obtained for BSSS-101 × B75 probably was biased by epistasis. Presence of significant epistasis for this cross is demonstrated by the fact that, although the F_1 mean (9.86 ± 0.29) was not significantly different from the midparent value (9.36), the F_2 mean (18.9 ± 0.43) was nearly twice as large as the mean of the F_1 . The F_3 mean (18.06 ± 0.35) was not different from that of the F_2 . Furthermore, a significant decrease in tassel branch number was observed between B_2 and B_2S (9.87 ± 0.27 and 8.83 ± 0.18 , respectively), but selfing B_1 to produce B_1S resulted in a significant increase in tassel branch number (16.26 ± 0.32 vs. 18.31 ± 0.35). Additionally, $\bar{V}_{B_1} + \bar{V}_{B_2}$ was smaller than V_{F_2} , a phenomenon observed when epistasis is present. Further evidence for presence of epistatic gene action for this cross is given in Table 4. Estimates of effects for *aa*, *ad*, and *dd* were substantially larger than they were for the two other crosses for which the six-factor generation mean analysis was meaningful. Likely, alleles responsible for the epistatic gene action for this cross were inherited from BSSS-101.

Table 4 summarizes estimates of genetic effects obtained from generation mean analyses for all six crosses. Additive effects were significant for four of the six crosses we studied. They were not significant only for the two reciprocal

crosses involving BSSS-36 and BSSS-78, two lines that were closely related since they were developed from Iowa Stiff Stalk Synthetic (BSSS) by single-seed descent. All genetic effects, except dominance \times dominance epistasis (dd), were significant for at least one cross. Daniel (1965b) reported a case in which dd effects for tassel branch number were significant and larger than other genetic effects he estimated. Evidently, all types of gene action can play a role in inheritance of tassel branch number.

Generally, heritability estimates we obtained for tassel branch number were larger than those obtained for other morphological and physiological traits of maize (Bagshaw 1964; Hallauer 1974; Mock 1977; Smith 1977). Estimated on a single-plant basis, narrow-sense heritability ranged from 0.00 for (M14 \times C103)-1505 \times B75 to 1.27 for BSSS-101 \times B75 (Table 5). Additive genetic variance was not significant for the first of these crosses, and variance-component estimates were biased by the presence of epistasis for BSSS-101 \times B75. After elimination of these two extreme heritabilities, the four remaining estimates ranged from 0.54 to 0.64, with a mean of 0.57. Our estimates agreed with those reported by Daniel (1965a) (0.65) and Mock and Schuetz (1974) (0.53). Mean narrow-sense heritability estimated by standard unit regression was 0.66, and estimates ranged from 0.59 to 0.71 [excluding estimates for (M14 \times C103)-1505 \times B75 and BSSS-101 \times B75]. Heritability estimated on an F_3 -family-mean basis (heritability in the broad sense) ranged from 0.93 to 0.98, with a mean of 0.95. Obviously, additive gene action was important, and the environment had little effect on tassel branch number.

Estimates of V_{F_2} and $2\bar{V}_{F_3}$ and their associated standard errors are presented in Table 6. With the exception of the cross, B75 \times H19, estimates of V_{F_2} and $2\bar{V}_{F_3}$ were not significantly different. Bias in variance-component estimates due to linkage, therefore, usually was not detected, suggesting that genes controlling tassel branch number are distributed throughout the entire maize genome.

Our data indicated that, although considerable non-additive gene action was involved in the genetics of tassel branch number, significant additive gene effects and additive genetic variances usually were present. Additionally, both narrow-sense and broad-sense heritability estimates were large. Consequently, mass selection would be most efficient for reducing tassel branch number in maize. This selection scheme could be used to develop small-tasseled breeding populations from which small-tasseled inbreds could be produced by pedigree selection, or, alternatively, pedigree selection for inbreds with reduced tassel branch number and other desirable agronomic traits could be conducted simultaneously in the source populations. According to the formula for expected gain per cycle of selection

presented by Lush (1945), mass selection would reduce tassel size from 0.8 to 7.3 branches per year in populations generated from (M14 \times C103)-1505 \times B75 and BSSS-101 \times B75, respectively. One cycle of mass selection for low tassel branch number could be completed each year; so, within a few years, tassel branch number could be reduced substantially in most maize populations.

Small-tasseled single-cross hybrids must be produced after small-tasseled inbreds are developed if maize breeders are to increase significantly the density tolerance of the U. S. maize crop. The following factors must be considered when selecting inbreds as parents for small-tasseled hybrids: 1) determination of which parent is to be used as the female and which as the male, 2) the tassel size of the parental inbreds and 3) the specific combining ability for tassel size between the two inbreds.

All evidence suggests that choice of a line to be used as a male or female has little bearing on the tassel size of the hybrid progeny. We found no evidence for a reciprocal effect between two crosses involving BSSS-36 and BSSS-78, and mean numbers of tassel branches did not differ significantly for B75 \times H19 (7.35 ± 0.18) and H19 \times B75 (7.74 ± 0.21). Furthermore, Mock and Schuetz (1974) found no evidence for a reciprocal effect for crosses involving BSSS-11 and BSSS-26. Evidently, maize hybrid seed producers do not need to consider tassel branch number when determining which parental inbred to use as the seed parent. Rather, they can use conventional criteria, such as seed yield, seed grade and seed germination.

Table 5. Estimates of heritability for tassel branch number obtained from six maize crosses

Cross	Narrow sense (Single-plant)	Standard unit	Broad sense (F_3 -family)
A257 \times B75	0.60	0.65	0.95
(M14 \times C103)-1505 \times B75	0.00	0.31	0.94
BSSS-101 \times B75	1.27	0.77	0.98
B75 \times H19	0.54	0.59	0.95
BSSS-36 \times BSSS-78	0.56	0.71	0.93
BSSS-78 \times BSSS-36	0.64	0.70	0.94

Table 6. Comparison of estimates of V_{F_2} and $2\bar{V}_{F_3}$ for tassel branch numbers of six maize crosses

Cross	V_{F_2}	$2\bar{V}_{F_3}$
A257 \times B75	21.69 ± 2.04	26.02 ± 0.19
(M14 \times C103)-1505 \times B75	4.39 ± 0.40	4.14 ± 0.22
BSSS-101 \times B75	40.87 ± 3.84	33.96 ± 1.18
B75 \times H19	5.72 ± 0.52	9.62 ± 0.07
BSSS-36 \times BSSS-78	19.77 ± 1.78	22.54 ± 0.16
BSSS-78 \times BSSS-36	19.32 ± 1.78	22.94 ± 0.16

Our data also indicated that two small-tasseled inbreds must be crossed to obtain a small-tasseled hybrid. We obtained F_1 responses varying from overdominance (for [M14 \times C103]-1505 \times B75, BSSS-101 \times B75, B75 \times H19, BSSS-36 \times BSSS-78 and BSSS-78 \times BSSS-36) to partial dominance (i.e., for A257 \times B75) for large number of tassel branches. Dominance of large tassel branch number also was reported by Daniel (1965b) and Mock and Schuetz (1974). The most reliable method for producing small-tasseled hybrids, therefore, would involve crossing small-tasseled inbreds. This scheme, however, may not always result in small-tasseled hybrids. For example, we evaluated two crosses [(M14 \times C103)-1505 \times B75 and B75 \times H19] in which both inbred parents had less than six tassel branches, but their F_1 's had more tassel branches than either parent (7.62 for M14 \times C103-1505 \times B75 and 7.35 for B75 \times H19). Probably, this phenomenon resulted from (M14 \times C103)-1505 and H19 possessing recessive alleles for small tassel branch number at different loci than B75. Consequently, complementation produced an F_1 with more tassel branches than either parent. Furthermore, results from these two crosses suggest that, to obtain a small-tasseled hybrid, the two parents of a cross must, not only be small-tasseled, but also must possess the same set of alleles for tassel branch number.

Finally, there are two crosses for which generation means showed unexpected results (Table 7). A genetic model involving five loci is necessary to partly explain the results for BSSS-101 \times B75. The five loci will be designated A , B , C , X , and Y . A and B act additively, so the substitution of A for a or B for b produces an increase of four tassel branches. For example, $Aabb$ or $aABb$ (genotypes with one dominant allele at either locus) would have five branches, $AaBb$ or $AAbb$ (genotypes with two dominant alleles) would have nine branches, genotypes $AaBB$ or $AABb$ would contain 13 branches and $AABB$ would be characterized by 17 tassel branches. Tassels of the double-recessive genotype ($aabb$) would have only one branch. Locus C displays complete dominance; substituting CC or Cc for cc would add two tassel branches to the genotypic value determined by the genes at the A and B loci. Loci X and Y would interact with the C and B loci, respectively, and any genotype that contains the combination $Xxcc$ or $XXcc$ would have ten more tassel branches than genotypes that lack these combinations of loci. For example, tassels of $Aabbccxx$ plants would have five branches, but tassels on plants of the $AabbccXx$ genotype would have 15 branches because X and c would be interacting. If a dominant allele were present at the C locus, no interlocus interaction would occur. Interaction between genes at the B and Y loci would differ, depending upon the number of Y alleles present in the genotype. No interaction would occur if the genotype were $bbyy$. The $bbYY$ combination

would increase tassel branch number by 12, and the $bbYY$ combination would add 16 branches to the number determined by the A , C and X loci. For example, a plant with the genotype, $Aabbyy$, would have five tassel branches, one with the $AabbYy$ genotype would have 17 and an $AabbYY$ plant would produce tassels with 21 branches. Presence of a dominant allele at the B locus, however, would negate this interaction.

Results in Table 8 were obtained by using this model and demonstrated that observed and expected means were similar. If B75 contained the $aabbCCXXyy$ genotype, it should have three tassel branches (one contributed by $aabb$ and two by CC). The model predicted that BSSS-101 should have 17 tassel branches, all from the A and B loci. The predicted mean for the F_1 was 11 branches; i.e., nine being contributed by the two dominant alleles at the A and B loci and the remaining two resulting from the Cc genotype. Means of the P_1 , P_2 and F_1 generations probably reflect a majority of additive gene action. Our model is consistent with this observation because no epistatic interactions occurred in these three generations.

Expected values for the B_1 , B_2 and F_2 generations are means of several genotypes. The expected and observed means for B_1 and B_2 were similar, but the model underestimated mean tassel branch number of the F_2 . The ob-

Table 7. Mean numbers of tassel branches for nine generations of BSSS-101 \times B75 and BSSS-36 \times BSSS-78

Generation	BSSS-101 (P_1) \times B75 (P_2)	BSSS-36 (P_1) \times BSSS-78 (P_2)
P_1	16.54 \pm 0.31	12.80 \pm 1.98
P_2	2.15 \pm 0.11	14.95 \pm 0.37
F_1	9.86 \pm 0.29	17.69 \pm 0.43
F_2	18.91 \pm 0.43	17.19 \pm 0.28
F_3	18.06 \pm 0.35	15.93 \pm 0.22
B_1	16.26 \pm 0.32	17.70 \pm 0.41
B_2	9.87 \pm 0.27	18.35 \pm 0.34
$B_1 S$	18.31 \pm 0.35	16.54 \pm 0.21
$B_2 S$	8.83 \pm 0.18	15.69 \pm 0.24

Table 8. Observed and expected means obtained with a five-locus model for genetics of tassel branch number of BSSS-101 \times B75

Generations	Genotypes	Means	
		Observed	Expected
BSSS-101 (P_1)	$AABBccxxYY$	16.54 \pm 0.31	17.0
B75 (P_2)	$aabbCCXXyy$	2.15 \pm 0.11	3.0
F_1	$AaBbCcXxYy$	9.86 \pm 0.29	11.0
B_1	Several	16.26 \pm 0.32	15.4
B_2	Several	9.87 \pm 0.27	9.1
F_2	Several	18.91 \pm 0.43	13.3

served minimum and maximum tassel branch numbers in the F_2 generation were 2 and 36. A plant with the genotype *aabbCcxy* would have three tassel branches whereas the genotype *AAbbccXxYY* would have 35 branches (nine resulting from *AA*, 16 from the interaction of *bb* and *YY* and 10 from the interaction of *cc* and *Xx*). Both these genotypes could be obtained in the F_2 if, as evidence suggests, the loci assorted independently. Our proposed model, therefore, adequately explained the observed range of F_2 plants.

Although additive gene action was detected for the cross, BSSS-36 × BSSS-78, we found strong evidence for presence of nonadditive types. Generation mean analysis suggested dominance was the predominant type of non-additive action (Table 4), and a comparison of the F_2 mean and the value midway between the F_1 mean and the midparent value indicated epistasis was important (Table 7). Heterosis component of the analysis of variance was significant, but that for inbreeding depression was not. Compton¹ has suggested a model for two loci that displayed only additive and additive × additive epistatic effects. This model is presented below, using genotypic values obtained in our experiment.

	<i>bb</i>	<i>Bb</i>	<i>BB</i>
<i>aa</i>	4	9.5	15
<i>Aa</i>	8	17.5	27
<i>AA</i>	12	25	38

If a line having genotype *AAbb* (with 12 tassel branches) is crossed with line *aaBB* (with 15 tassel branches), the genotype of the F_1 would be *AaBb*, and the plants would have 17.5 tassel branches. The F_1 , therefore, would exhibit high-parent heterosis. If the F_1 were selfed to homozygosity, equal proportions of *AABB*, *AAbb*, *aaBB* and *aabb* genotypes would be obtained. The mean of the homozygous population would be 17.25 and inbreeding depression would be very small. The model proposed by Compton, therefore, adequately explains 1) the presence of additive and epistatic gene effects and 2) the significant heterosis and nonsignificant inbreeding depression observed for this cross. It does not, however, explain the presence of significant dominance effects detected with the generation mean analysis.

Data in Table 9 show that observed and expected means (calculated from Compton's model) did not differ significantly for the P_1 , P_2 , F_1 , and F_2 generations. The predicted range for the F_2 was from 4 to 38 tassel branches, and the observed range was from 7 to 32. The model slightly underestimated \bar{B}_1 and \bar{B}_2 , indicating there may be other genes controlling tassel branch number of this

Table 9. Observed and expected mean tassel branch numbers obtained by adapting a two-locus model involving only additive and additive × additive gene action to data for generations from BSSS-36 × BSSS-78

Generations	Genotypes	Means	
		Observed	Expected
BSSS-36 (P_1)	<i>AAbb</i>	12.80 ± 1.98	12
BSSS-78 (P_2)	<i>aaBB</i>	14.95 ± 0.37	15
F_1	<i>AaBb</i>	17.69 ± 0.43	17.5
F_2	Several	17.19 ± 0.28	17.37
B_1	Several	17.70 ± 0.41	15.62
B_2	Several	18.35 ± 0.34	17.25

cross. Compton's model, based on additive and additive × additive epistatic gene effects, however, adequately explained much of the variability in tassel branch number observed for BSSS-36 × BSSS-78. As expected, the model also explained results observed for the reciprocal cross (BSSS-78 × BSSS-36) of these two lines.

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Dr. S.H. Schuetz

Dr. J.J. Mock

Agronomy Department

Iowa State University

Ames, Iowa 50011 (USA)