# GENES FOR DWARFNESS IN WHEAT, *TRITICUM AESTIVUM* L.[1]

G. N. FICK[2] AND C. O. QUALSET

*Department of Agronomy and Range Science, University of California, Davis, California 95616*

## ABSTRACT

The genetic control of plant height was studied in crosses of four spring wheats involving the standard height variety Ramona 50 and short-statured selections Olesen, D6301, and D6899. Data from parent, $F_1$, $F_2$, and $F_3$ populations indicated that four independently segregating loci account for most of the differences among the four varieties. Two major genes of a highly recessive nature condition reduced height in Olesen and the Norin 10 derivative D6301. Olesen also carries a third dwarfing gene which is partially dominant in its effects over genes for tallness. This gene, or a gene that acts in a similar manner, is also present in the standard height variety Ramona 50. Dwarfing in D6899, a derivative of Tom Thumb, is controlled primarily by a single gene with mainly additive effects which is not present in any of the other three varieties.

Genetic components estimated from generation means (parental, $F_1$, $F_2$, $F_3$, and backcross) indicated that additive gene effects were the major component of variation in four of the six crosses, and of similar magnitude to dominance effects in another cross. The primary source of genetic variation in the cross Olesen × D6899 was due to epistasis with both additive × additive and dominance × dominance effects of major importance. The results of the generation mean analyses were consistent with the models for major-gene control of plant height based on segregation patterns.

A S a result of increased lodging resistance and high yield potential of semi-dwarf wheat varieties, most wheat improvement programs now utilize semidwarf germplasm. Three sources of reduced height that have been used extensively include the Japanese semidwarf variety Norin 10 (CI 12699) and its derivatives, the Olesen dwarf (CI 14497), and the variety Tom Thumb (CI 13563) from Tibet. Semidwarfing in Norin 10 is believed to be controlled by two major independent recessive genes (ALLAN, VOGEL and PETERSON 1968; BRIGGLE and VOGEL 1968). The Olesen dwarf is less recessive than Norin 10 in crosses with taller varieties (CIMMYT Report 1966–67), and control by two genes has been suggested (ANAND and AULAKH 1971; OZSABUNCU 1971). $F_1$ hybrids with Tom Thumb are shorter than the tall parent (CIMMYT Report 1966–67; PIECH 1968) and genetic analysis reveals a single semi-dominant gene for short plant height (MORRIS, SCHMIDT and JOHNSON 1972). Whether different genes for

dwarfing are represented in these three varieties is not known nor is the type of gene action primarily responsible for the reduced height. This paper reports on the interrelationships of dwarfing genes in Olesen and derivatives of Norin 10 and Tom Thumb, and on the relative importance of additive, dominant, and epistatic gene effects for plant height in crosses involving these varieties.

<div align="center">MATERIALS AND METHODS</div>

The genetic control of plant height was studied in a four-parent diallel cross of wheat involving the standard height variety Ramona 50 and three short-strawed selections designated Olesen, D6301, and D6899. All varieties have spring growth habit. Ramona 50 is adapted to California. The Olesen dwarf was developed in Rhodesia from a combination of crosses involving short-strawed selections Norin 10, Mara, and Angolian line X2–50 (I. B. EDWARDS, personal communication). D6301 and D6899 are experimental lines from CIMMYT from the crosses Mayo 54 × Norin 10-Brevor and Tom Thumb-Sonora 64 × Tacuari, respectively. Norin 10 and Tom Thumb have winter growth habit and do not grow well in the field at Davis. The spring habit derivatives, D6301 and D6899, are believed to have the same genes for short stature as Norin 10 and Tom Thumb, respectively. Three lines of evidence support this assumption: (1) their nature plant heights are comparable to those of the respective parents; (2) no segregation for height was observed in the $F_2$ generation of the crosses D6301 ×Norin 10 (FICK 1971) and D6899 × Tom Thumb (unpublished); and (3) when the original parents and derivatives are crossed to a common parent, similar frequency distributions are found in the $F_2$ generation (FICK 1971).

Three field experiments were conducted. The first consisted of parent, $F_1$, and $F_2$ populations grown in a randomized block design at Davis, California in 1970 (December 1969 to June 1970). Five replicates of each parent and $F_2$ population, and two replicates of each $F_1$ were grown. A replicate consisted of two 5-m rows of each $F_2$ population and one row of each parent and $F_1$ with seeds hand-spaced 15 cm apart in rows spaced 30 cm apart. Ten seeds were sown in the $F_1$ rows and, to maintain uniform competition, the remainder of the row was planted to a dwarf durum wheat.
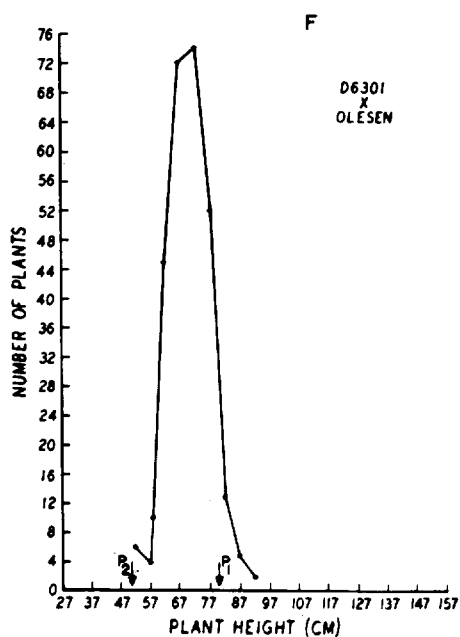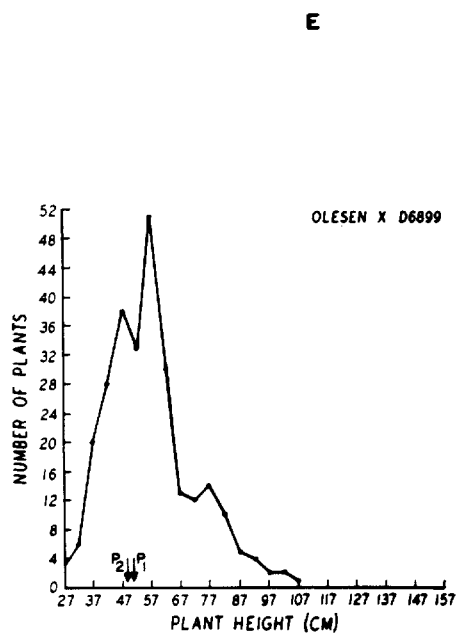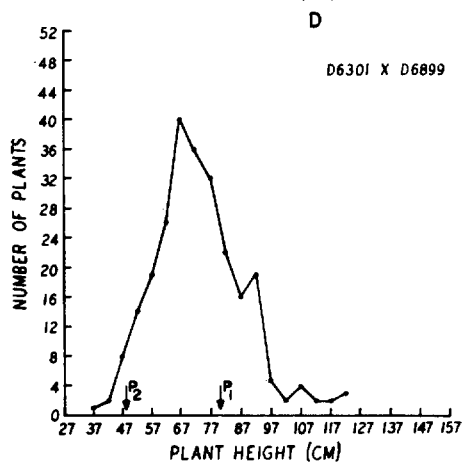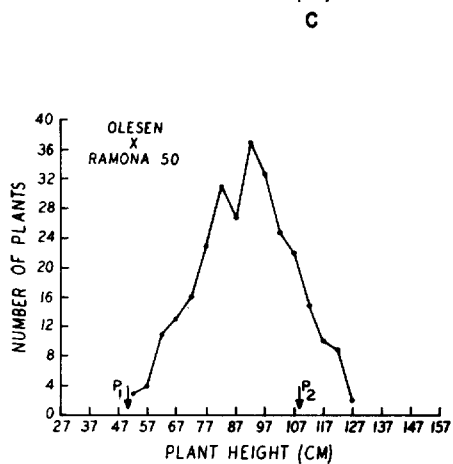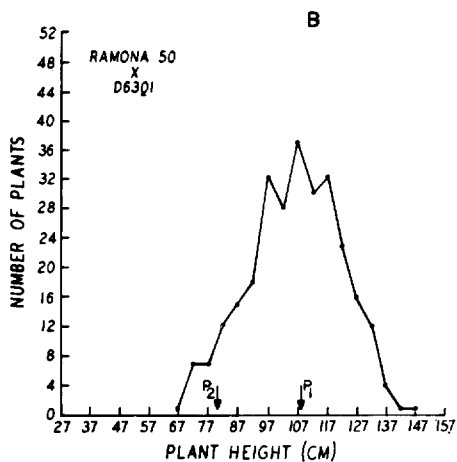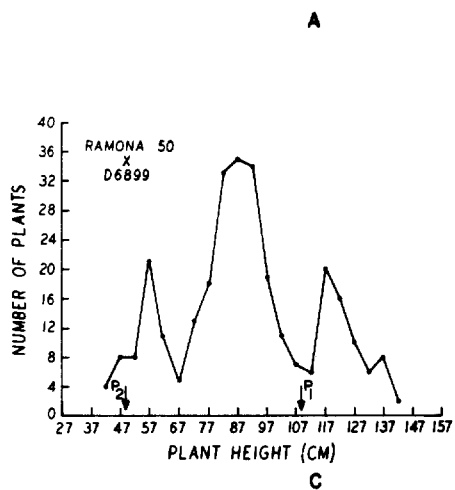
Height was measured on all competitive plants from the base of the culm to the tip of the spike, not including awns, of the longest tiller on each plant before harvest and recorded to the nearest centimeter. Analyses of variance for height indicated no significant replication differences for any of the populations represented. Hence, data from all replications were pooled in computing means and variances. Plant height classes were established at 5-cm intervals for all populations. In the frequency distributions (Figures 1A to 1F) the class values shown represent the upper limit of height for each class.

In the second study, parent, $F_2$, and $F_3$ populations from the six hybrid combinations were grown in an off-season summer nursery (July to October) at Davis during 1970. Each cross was handled as a separate experiment and planted in a randomized block design with two blocks. Each block consisted of four rows of each parent and $F_2$ and two rows of each of 100 $F_3$ lines. Seed for each $F_3$ line was derived from random individual $F_2$ plants. The experiment was machine-planted at the rate of 33 seeds per 2.5-m row, with rows spaced 75 cm apart. Heights of individual plants for the crosses of Ramona 50 with Olesen and D6301 were measured as described in the first experiment. In the crosses involving Olesen × D6301 and Ramona 50, Olesen and D6301 with D6899, individual $F_3$ rows were scored for the presence or absence of short, intermediate, and tall plants. The following scale was used: 2, approximately the same height as D6301 (45 cm); 1, distinctly shorter than 2; and 3, distinctly taller than 2. Thus each row was scored as either 1, 2, or 3, or any combinations of 1, 2, and 3.

The third experiment, grown in 1971 (December 1970 to June 1971), consisted of parent, $F_1$, $F_2$, $F_3$, and both backcross $F_1$ populations from each of the six crosses with each cross in a randomized block design with two replicates. Two 5-m rows of each $F_2$ and $F_3$ and one row each of the backcross and parental populations were included in a single replicate. Seeds were sown 15 cm apart in rows spaced 30 cm apart. Each $F_3$ population was derived from compositing equal

TABLE 1

*Number of plants, means, and variances for plant height for parent, F₁, and F₂ generations for six wheat crosses grown in 1969–70*

| $P_1 \times P_2$ | $P_1$ | | | $P_2$ | | | $F_1$ | | | $F_2$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | x̄ | $s^2$ | n | x̄ | $s^2$ | n | x̄ | $s^2$ | n | x̄ | $s^2$ |
| Ramona 50 × D5899 | 134 | 108.1 | 41.7 | 130 | 48.6 | 18.1 | 20 | 85.5 | 13.2 | 296 | 89.1 | 572.2 |
| D5301 × Ramona 50 | 132 | 79.8 | 21.5 | 134 | 108.1 | 41.7 | 20 | 110.6 | 11.0 | 277 | 104.5 | 256.0 |
| Olesen × Ramona 50 | 115 | 50.4 | 11.1 | 134 | 108.1 | 41.7 | 17 | 92.2 | 30.9 | 281 | 88.7 | 267.7 |
| D5301 × D6899 | 132 | 79.8 | 21.5 | 130 | 48.6 | 18.1 | 11 | 68.0 | 9.6 | 255 | 71.3 | 228.7 |
| Olesen × D6899 | 115 | 50.4 | 11.1 | 130 | 48.6 | 18.1 | 13 | 55.2 | 6.0 | 273 | 55.7 | 225.2 |
| D5301 × Olesen | 132 | 79.8 | 21.5 | 115 | 50.4 | 11.1 | 18 | 68.1 | 21.8 | 265 | 69.2 | 49.0 |

A — RAMONA 50 X D6899

B — RAMONA 50 X D6301

C — OLESEN X RAMONA 50

D — D6301 X D6899

E — OLESEN X D6899

F — D6301 X OLESEN

amounts of seed from 50 random $F_2$ plants. Individual plant heights were recorded and used to calculate generation means and variances. HAYMAN's (1958) weighted least squares analysis was used to estimate the relative contributions of gene effects attributable to additive $(d)$, dominance $(h)$, and epistatic effects additive by additive $(i)$, additive by dominance $(j)$, and dominance by dominance $(l)$.

<div align="center">RESULTS AND DISCUSSION</div>

The means and variances for plant height of parent, $F_1$, and $F_2$ populations are shown in Table 1 and the frequency distribution curves for $F_2$ plant height of the six crosses in Figure 1. The presence of relatively few genes with major effects is suggested for most crosses. In the cross Ramona 50 × D6899 (Figure 1A) three major height classes in the relative proportions of 1 short : 2 intermediate : 1 tall are indicated. This suggests that the difference in height between D6899 and Ramona 50 is controlled mainly by a single gene with additive effects. This hypothesis was supported by classification of $F_3$ lines. The 100 $F_3$ lines, derived from random $F_2$ plants, segregated 21 short to 56 short, intermediate, and tall to 23 tall ($x^2 = 1.52$, $.45 < P < .50$). Comparison of $F_3$ line behavior with $F_2$ plants showed that all short-statured $F_3$ lines were derived from $F_2$ plants less than 70 cm in height. Segregating $F_3$ lines were progenies from $F_2$ plants ranging in height from 68 to 104 cm. $F_3$ lines classified as tall were progenies of $F_2$ plants taller than 100 cm.

Figures 1B and 1C, respectively, show the $F_2$ distributions for plant height in the crosses Ramona 50 × D6301 and Ramona 50 × Olesen. Distinct groupings are apparent but the degree of overlapping precludes a precise estimate of the number of genes involved or their mode of action. To estimate the number of major genes conditioning height in these crosses, comparisons were made between the variabilities of parents and of $F_3$ lines derived from random individual $F_2$ plants. The mean variance in height among plants within parent rows was 30.6 and 33.4 cm² in the crosses Ramona 50 × D6301 and Ramona 50 × Olesen, respectively. Assuming that these values represented the maximum variation that would be expected in homozygous $F_3$ lines, 12 of 100 $F_3$ lines in the cross Ramona 50 × D6301 and 19 of 100 $F_3$ lines in the cross Ramona 50 × Olesen were classified as homozygous. These proportions are suggestive of a three-gene segregation in the former cross and intermediate to those expected for a two- and three-gene distributions in the latter cross.

Ramona 50 is a relatively short standard height variety and it is likely that it also has a gene(s) that results in the expression of reduced height in the crosses with D6301 and Olesen. In the cross Ramona 50 × D6301 numerous $F_2$ plants were taller than Ramona 50 and it is assumed they are segregates that lack the effects of dwarfing genes in either parent. If the effects of the different dwarfing genes are cumulative, then homozygous genotypes shorter than D6301 would also be expected. Homozygous lines ranging in height from 55 to 140 cm have been extracted from the Ramona 50 × D6301 cross (unpublished results). It is

FIGURE 1.—$F_2$ frequency distributions for plant height in six wheat crosses. Mean height of parents indicated by arrows, $P_1$ and $P_2$ are the first and second parents listed for each cross.

likely that three genes govern the expression of height in this cross, and it is suggested that two dwarfing genes are present in D6301 (originally from Norin 10) and one in Ramona 50.

Crosses among the three short-strawed varieties suggest that the gene for reduced height in D6899 is not present in D6301 and Olesen. The $F_2$ segregation in D6899 × D6301 and D6899 × Olesen (Figure 1D and 1E) gave plants that were considerably taller than either parent and represented by discrete groups with heights greater than 87 and 72 cm in the D6301 and Olesen crosses, respectively. The proportions exceeding these heights are about 3/16 of their total populations and suggestive of two genes with complementary or other non-allelic interactions. A possible explanation for the segregation is that the parents differ, not only for the D6899 dwarfing gene, but also for a dominant or semidominant gene for tallness with the effects of this gene being suppressed by the dwarfing gene from D6899. The results obtained on the $F_3$ generation were 21:45:24 ($x^2 = 0.20$; .90 < P < .95) and 31:48:21 ($x^2 = 2.16$; .30 < P < .40) for segregation of the dwarfing gene based on an expected 1:2:1 ratio and 21:(14:31): (3:16:5) ($x^2 = 4.30$; .50 < P < .60) and 31:(13:35):(8:11:2) ($x^2 = 5.35$; .30 < P < .40) for segregation based on the two-gene model with an expected ratio of 4:(2:6):(1:2:1) in the crosses D6301 × D6899 and Olesen × D6899, respectively.

The $F_2$ distribution for the cross D6301 × Olesen (Figure 1F) showed variation that occurred largely within the range of the parental varieties. In addition, general similarities are noted for the crosses D6301 and Olesen with Ramona 50 and D6899 (Figure 1B, 1C, 1D, and 1E). Norin 10 occurs in the pedigrees of both D6301 and Olesen and crosses of these varieties with Norin 10 show little variability (FICK 1971). It is likely that both D6301 and Olesen have the two major dwarfing genes present in Norin 10. Because Olesen is 20 to 30 cm shorter than Norin 10 and D6301, an additional gene(s) for reduced height in Olesen is likely. When crossed with Big Club 60, an extremely tall variety not possessing any known genes for dwarfing, an $F_2$ population of 336 plants showed 7 plants were recovered in the height range of Olesen and 8 plants in the height range of Big Club 60 (data not presented). The proportions each represent about 1/64 of the total population, indicative of a three-gene distribution.

The presence of a third dwarfing gene in Olesen is also suggested by the fact that the dwarfing effect of Olesen in crosses is less recessive than that of either D6301 or Norin 10 (CIMMYT Report 1966–67; FICK 1971). Assuming that two genes are present from the Norin 10 source, the effect of the third dwarfing gene in Olesen must involve gene action other than recessivity to genes for tallness. Genes that condition the grass-dwarf phenotype and presumed to be dominant or epistatic over genes for tallness have been identified in Olesen and Ramona 50 (FICK and QUALSET 1973) and it is likely that the grass-dwarfing genes contribute to the segregation patterns observed for the cross of Ramona 50 × Olesen.

Observed generation means and among-replicate variances for plant height for the six crosses grown in 1970–71 are presented in Table 2. Although the plants were shorter than in 1969–70, the relative values were similar in the two years.

## TABLE 2

Observed generation means and variances for plant height (centimeters) for six wheat crosses grown in 1970-71

| $P_1 \times P_2$ | $P_1$ | | $P_2$ | | $F_1$ | | $F_2$ | | $F_3$ | | $B_1$ | | $B_2$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ | $\bar{x}$ | $s^2$ |
| D6899 × Ramona 50 | 42.38 | 0.120 | 95.56 | 0.911 | 67.57 | 18.318 | 72.67 | 5.260 | 76.03 | 6.867 | 60.48 | 4.666 | 82.71 | 6.864 |
| D6301 × Ramona 50 | 71.94 | 1.203 | 95.56 | 0.911 | 92.79 | 9.060 | 91.76 | 3.525 | 85.87 | 8.085 | 83.85 | 0.096 | 97.98 | 0.297 |
| Olesen × Ramona 50 | 44.05 | 0.219 | 95.56 | 0.911 | 78.52 | 11.390 | 74.56 | 8.401 | 72.20 | 12.909 | 58.33 | 0.416 | 90.57 | 0.240 |
| D6301 × D6899 | 71.94 | 1.203 | 42.38 | 0.120 | 61.72 | 0.181 | 59.85 | 1.420 | 57.10 | 0.127 | 68.10 | 0.221 | 51.09 | 2.190 |
| Olesen × D6899 | 44.05 | 0.219 | 42.38 | 0.120 | 51.50 | 0.109 | 48.88 | 2.782 | 54.41 | 4.559 | 46.67 | 0.534* | 45.28 | 0.534* |
| Olesen × D6301 | 44.05 | 0.219 | 71.94 | 1.203 | 60.92 | 0.106 | 57.87 | 1.910 | 57.54 | 0.894 | 49.36 | 0.381* | 67.43 | 0.381* |
| Number of replicates | 6 | | 6 | | 2 | | 4 | | 4 | | 2 | | 2 | |

* Weighted estimate because the variances of $B_1$ and $B_2$ were greatly different.

## TABLE 3

Estimates of parameters with standard errors and $\chi^2$-values for goodness of fit to three- and six-parameter models for plant height for six wheat crosses grown in 1970-71

| $P_1 \times P_2$ | Mean m | Additive d | Dominance h | Add. × Add. i | Add. × Dom. j | Dom. × Dom. l | $\chi^2(4)$ | $\chi^2(1)$ |
|---|---|---|---|---|---|---|---|---|
| D6899 × Ramona 50 | 71.66 ± 1.12 | −26.64 ± 0.50 | 5.13 ± 2.39 | — | — | — | 9.09 | — |
| D6301 × Ramona 50 | 90.59 ± 0.29 | −13.08 ± 0.47 | 13.60 ± 1.51 | — | — | — | 8.95 | — |
| Olesen × Ramona 50 | 74.49 ± 1.42 | −32.24 ± 0.81 | 8.62 ± 6.31 | 0.17 ± 5.69 | −6.48 ± 0.97 | −0.83 ± 9.56 | 44.86** | 0.00 |
| D6301 × D6899 | 59.16 ± 0.50 | 16.68 ± 1.47 | 7.13 ± 1.22 | 2.54 ± 1.24 | 1.93 ± 1.59 | −4.00 ± 4.06 | 17.62** | 0.41 |
| Olesen × D6899 | 50.06 ± 0.87 | 1.39 ± 1.03 | −8.41 ± 3.47 | −16.69 ± 3.46 | 0.55 ± 1.07 | 22.55 ± 4.58 | 26.15** | 0.68 |
| Olesen × D6301 | 58.18 ± 0.49 | −18.07 ± 0.87 | 3.69 ± 1.77 | 0.78 ± 1.78 | −4.12 ± 1.06 | 3.57 ± 3.07 | 25.52** | 0.05 |

** P < .01.

Estimates of the genetic parameters with their standard errors are shown in Table 3. For two of the crosses, D6899 × Ramona 50 and D6301 × Ramona 50, the three-parameter model provided a satisfactory fit of observed-to-expected generation means. The six-parameter model, indicative of significant epistatic effects, was required to explain adequately the genetic variation in the remaining four crosses. Additive gene effects were the major component of variation in the crosses of Olesen and D6899 with Ramona 50 and D6301 and were of similar magnitude to dominance effects in the cross D6301 × Ramona 50. Epistasis was the primary source of genetic variation in the cross Olesen × D6899 with both additive × additive and dominance × dominance effects of major importance.

The data from the generation mean analysis are in general agreement with the results provided by the $F_2$ and $F_3$ distribution data. The major contribution of additive gene effects to the crosses of Olesen and D6899 with Ramona 50 and D6301 was indicated by the fact that $F_2$ means and distributions occurred largely within the range of the parental varieties. Similarly, the relatively large dominance component for tallness for the cross D6301 × Ramona 50 was expected because the $F_2$ mean and distribution more nearly approximated the tall parent. The marked epistatic effects noted for the cross Olesen × D6899, and to a lesser degree for D6301 × D6899, were expected because of the tall transgressive segregates which accounted for approximately 3/16 of the $F_2$ populations.

The results of this paper are in agreement with data obtained by POWELL and SCHLEHUBER (1967), by ALLAN, VOGEL and PETERSON (1968), and by JOHNSON et al. (1966) which indicate that plant height is governed by a few genes with major effects. That additive gene effects are relatively more important than dominance and epistatic effects is consistent with the results of several authors (AMAYA, BUSCH and LEBSOCK 1972; BHATT 1972; CHAPMAN and McNEAL 1971; JOHNSON et al. 1966; POWELL and SCHLEHUBER 1967). However, the major contribution of epistatic effects in one cross and significant epistatic gene action in four of the six crosses suggests that epistasis contributes to genetic variation in plant height more than previously realized. The occurrence of the grass-dwarf phenotype in wheat is controlled by genetic effects involving epistasis (HERMSEN 1967; MOORE 1969) and limited evidence suggests that grass-dwarfing genes may also contribute to the expression of semidwarf plant height (FICK and QUALSET 1973). Additional studies are required to determine the relationship of grass-dwarfing genes, such as present in Ramona 50, D6301, and Olesen (FICK and QUALSET 1973), with those carried by the semidwarf varieties.

## LITERATURE CITED

ALLAN, R. E., O. A. VOGEL and C. J. PETERSON, JR., 1968   Inheritance and differentiation of semidwarf culm length of wheat. Crop Sci. **8**: 701–704.

AMAYA, A. ARNOLDO, R. H. BUSCH and K. L. LEBSOCK, 1972   Estimates of genetic effects of heading date, plant height, and grain yield in durum wheat. Crop Sci. **12**: 478–481.

ANAND, S. C. and H. S. AULAKH, 1971   Inheritance of dwarfness in Olesen's dwarf (*T. aestivum* L.). Wheat Information Service **32**: 14–17.

BHATT, G. M., 1972 Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. Crop Sci. **12**: 95–98.

BRIGGLE, L. W. and O. A. VOGEL, 1968 Breeding short-stature, disease-resistant wheats in the United States. Euphytica **17** (Suppl. No. 1): 107–130.

CHAPMAN, S. R. and F. H. McNEAL, 1971 Gene action for yield components and plant height in a spring wheat cross. Crop Sci. **11**: 384–386.

CIMMYT Report, 1966–67 Dwarfness in hybrids. p. 78. Intern, Maize and Wheat Improvement Center, Mexico.

FICK, G. N., 1971 Genetic control of plant height and coleoptile length and associations with gibberellic acid response and amylase activity in short-statured wheats. Unpublished Ph.D. dissertation. University of California, Davis, California.

FICK, G. N. and C. O. QUALSET, 1973 Inheritance and distribution of grass-dwarfing genes in short-statured wheats. Crop Sci. **13**: 31–33.

HAYMAN, B. I., 1958 The separation of epistatic from additive and dominance variation in generation means. Heredity **12**: 371–390.

HERMSEN, J. G. TH., 1967 Hybrid dwarfness in wheat. Euphytica **16**: 134–162.

JOHNSON, V. A., K. J. BIEVER, A. HAUNOLD and J. W. SCHMIDT, 1966 Inheritance of plant height, yield of grain and other plant and seed characteristics in a cross of hard red winter wheat, *Triticum aestivum* L. Crop Sci. **6**: 336–338.

MOORE, K., 1969 The genetical control of the grass-dwarf phenotype in *Triticum aestivum* L. Euphytica **18**: 190–203.

MORRIS, ROSALIND, J. W. SCHMIDT and V. A. JOHNSON, 1972 Chromosomal location of a dwarfing gene in 'Tom Thumb' wheat derivative by monosomic analysis. Crop Sci. **12**: 247–249.

OZSABUNCU, N. S., 1971 Inheritance of plant height and necrosis in wheat crosses involving the Olesen dwarf variety. Unpublished M.S. thesis, University of California, Davis, California.

PIECH, J., 1968 Monosomic and conventional analyses of semidwarfism and grass-clump dwarfism in common wheat. Emphytica **17** (Suppl. No. 1): 153–170.

POWELL, J. B. and A. M. SCHLEHUBER, 1967 Components of height inheritance of the semi-dwarf straw character in wheat, *Triticum aestivum* L. Crop Sci. **7**: 511–516.

Corresponding editor: R. W. ALLARD