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Title: IDENTIFICATION, INHERITANCE AND ASSOCIATION OF DIFFERENT DWARFING SOURCES AND GIBBERELLIC ACID INSENSITIVITY IN BARLEY (HORDEUM VULGARE L.)

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Three standard height, high yielding cultivars, Larker, Steptoe and Short Wocus and five dwarf cultivars, Minn. 66-102, OR-SS-2, Xv 2334-6R, Apam Dwarf and Indian Dwarf were crossed in a diallel manner. Parents, F_1's, F_2's and F_3 populations were examined. The inheritance of semidwarf plant height and the number of different genes involved were determined. Inheritance to Gibberellin (GA) insensitivity and its relationship to plant height and other important agronomic characteristics was also investigated. Relationships between plant height and yield were examined and each dwarf source was explored for its potential use in a breeding program.

Inheritance of dwarf or semidwarf plant height is controlled by one or two recessive genes, depending on the dwarfing source. In these studies four separate genes were identified. Semidwarf cultivars OR-SS-2 and Minn. 66-102 each have one recessive gene for

short stature. These genes are not allelic and when combined act in an additive manner with the two-gene dwarfs being shorter than either parent. Apam Dwarf, Indian Dwarf and Xv 2334-6R all have the same two recessive genes which respond in an additive manner in governing plant height. Dwarfing genes found in Xv 2334-6R, Apam Dwarf and Indian Dwarf are different from those observed in OR-SS-2 or Minn. 66-102.

Insensitivity to applied GA enables unknown dwarf sources to be characterized quickly without a complete knowledge of the inheritance of semidwarf plant type. Apam Dwarf, Indian Dwarf and Xv 2334-6R are all insensitive to applied GA in the seedling stage. OR-SS-2 and Minn. 66-102 are sensitive to GA.

The inheritance of GA insensitivity appears to be controlled by two recessive genes acting in an additive manner. Plant height and GA insensitivity are closely associated and may be pleiotropic. The close association allows for a seedling selection system which can identify short statured plants in the greenhouse.

Identification, Inheritance and Association of Different Dwarfing Sources and Gibberellic Acid Insensitivity in Barley (*Hordeum vulgare* L.)

by

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Typed by Opal Grossnicklaus for Rollin George Sears

WITH LOVE TO:

Donna, my wife

Stephanie Lynn, my daughter

Mark Christopher, my son

George and Peg, my parents

John and Dagnie, my wife's parents

IN DEDICATION

TO

Dr. Mildred Sears

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The Nature and Inheritance of Gibberellin Insensitivity in Barley.[1]

R. G. Sears, W. E. Kronstad and R. J. Metzger[2]

ABSTRACT

Seedling response to 10 ppm Gibberellic acid (GA) was used to differentiate among different sources of dwarfism in barley. Brachytic mutants were insensitive to GA, while derived semidwarf lines either from the the erectoides mutants or from the 'Jotun' mutant were sensitive to GA.

Insensitivity to GA is strongly associated with reduced plant height in the brachytic mutants and can be used as a screening technique to identify dwarf genotypes in segregating populations, when using this source of dwarfism. Classifying a large number of seedlings 14 days after germination as to their mature plant height would be a major advantage to a breeding program.

Additional index words: Hordeum vulgare L., Gibberellin response, Gibberellin sensitivity, Dwarf, Semidwarf.

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[1]Contribution of the Crop Science Dept., Oregon Agric. Exp. Stn., Corvallis. Part of a thesis submitted by the senior author in partial fulfillment of the requirements for the Ph. D. degree at Oregon State Univ.

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Genetic analysis of F_1 and F_2 generations from the cross Larker x Apam Dwarf suggest that inheritance of GA insensitivity is recessive and controlled by two genes.

Response of barley seedlings to GA provides an effective way to differentiate among different sources of dwarfism and to assist in the identification of dwarfs in genetic studies.

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INTRODUCTION

Grain yield increase in wheat and rice associated with semidwarf plant type has resulted in a search for semidwarf plant types in other major food crops. Dwarf and semidwarf sources of germplasm in barley has been used extensively to develop new cultivars where lodging is reduced and subsequent grain yields increased. Knowledge of the genetics of dwarfism, the number of different genes or sources involved, and how each gene interacts with other genes or agronomic traits would further the development of high yielding semidwarf barley cultivars.

Currently four sources of dwarfing genes are available to barley breeders. Plants with brachytic genes ($\underline{br}_1$ and $\underline{br}_2$) are characterized as having shorter leaves, spikes, awns and internodes. In addition, the $\underline{br}_2$ mutant is reported to have shorter coleoptiles and smaller seeds than tall types (10). Both genes are monofactorial recessive with $\underline{br}_1$ located on chromosome 1 and $\underline{br}_2$ located on chromosome 4 (10). The uz (semi-brachytic) gene is a spontaneous mutant found in many Japanese cultivars. The uz mutant is characterized by having shorter leaves, culms, spikes, seeds and coleoptiles than tall types. A characteristic hook and/or notch at the apex of the coleoptile is characteristic of only the uzu mutant (20). The uz gene, a monofactorial recessive, is located on chromosome 3 (10).

Erectoides mutants (ert) are one of the most numerous mutant types reported in the literature. At least 182 mutants, associated with 26 loci have been described as ert-material (12). Ert-material is easily distinguished from standard height types by having reduced internode and rachis internode length which makes their spikes dense and broad. There is however wide variation for culm length and spike length in the ert-material (12). Many of the high yielding semidwarf barleys have ert-genes in their parentage. Ert-mutants respond to applied GA and their reduced height has been suggested to be caused by a reduction in either biosynthesis or biological activity associated with endogenous GA (17, 18). Ert-genes are monofactorial recessive and randomly distributed throughout six of the seven chromosomes in barley.

The semidwarf germplasm developed at the Minnesota Agricultural Experiment Station traces to a short straw mutant induced by irradiation in the cultivar 'Jotun'. The symbol sdw has been suggested for the recessive gene that controls the semidwarf character (1).

A characteristic of many dwarf plants is their growth response or lack of response to applied GA, in comparison to standard height cultivars. Genetic dwarfs have been reported to display increased growth responses, compared to tall forms in rice (19), wheat (5) and corn (13). Insensitive or decreased response in growth compared

to tall forms have also been reported in the same three species (2, 7, 9). This discrepancy suggests that amounts of endogenous GA in plant tissue is an important regulator of plant height but probably isn't the only factor responsible for dwarfness.

It has been demonstrated in wheat that the Norin 10 and Tom Thumb sources of dwarfism do not respond to GA (6, 7). Semidwarf wheats derived from these backgrounds are not deficient in endogenous GA. A block in the utilization of endogenous GA has been suggested as the mechanism involved in their GA insensitivity (14). The genetic association between plant height and GA insensitivity has been utilized to classify and locate the dwarf and semidwarf genes in wheat (6, 7). This has been especially useful in the genetic analysis of the Norin 10 source of dwarfism. Insensitivity to applied GA has also been reported to be associated with a number of important agronomic traits. The Tom Thumb and Minister Dwarf sources of dwarfism in wheat have been shown to have restricted release of hydrolytic enzymes, especially α-amylase during germination (6). Coleoptile length is also strongly associated with GA insensitivity, and mature plant height (3, 7).

This study was initiated to examine the range of response to GA in commonly used sources of dwarfism in barley breeding programs. The association between GA reaction and plant height may be helpful in developing a better understanding of the inheritance of dwarfing in

barley. Also, the potential to use GA response as a tool for selecting semidwarf types in the seedling stage is investigated.

MATERIALS AND METHODS

Eight barleys (Hordeum vulgare L.) and two wheats (Triticum aestivum L.) were examined for their reaction to GA[1] supplemented in nutrient solution. The barley cultivars consisted of one tall, ('Larker'), two intermediate height ('Steptoe' and 'Short Wocus') and five short ('Minn. 66-102', 'OR-SS-2', 'Apam Dwarf', 'Indian Dwarf' and 'Xv 2334-6R'). The origin, relative heights and dwarfing source of the experimental material are provided in Table 1. The wheat cultivars Maris Huntsmen and Tom Thumb were used as checks in these experiments. Maris Huntsmen, a tall cultivar and Tom Thumb, a dwarf cultivar are sensitive and insensitive to GA respectively.

A modification of the method reported by Gale (6, 7) was used to test for response to GA. Seeds were surface sterilized for one minute in a 10% chlorox solution and rinsed thoroughly with tap water. Kernels were placed crease side down in petri dishes and germinated in the dark at 9°C. When roots were approximately 2-4 mm long, each seed was transferred to a plastic mesh screen and suspended over a 5 liter polyethylene container. Treatment solutions were

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[1] Gibberellin, which contained at least 93% pure GA_3 was supplied by the Van Water & Rodgers Company.

adjusted to allow contact with the screen. Clear plastic wrap was then placed over the top of each tray until the emergence of the first leaf. All experiments were conducted in a growth chamber at 18°C with 12 hours of light (20 Klux).

Each treatment consisted of either a complete nutrient solution as a control (modified Hoagland's), or a complete nutrient solution plus supplemented GA. All seedlings were kept in the control or GA solutions for 14 days. Two independent studies were conducted. In Study I four barley cultivars were used to determine if varying the GA concentrations resulted in different reactions. The four cultivars consisted of Larker, OR-SS-2, Minn. 66-102 and Apam Dwarf. Each cultivar was exposed to solutions composed of 5, 10 and 15 ppm GA and the control nutrient solution. Ten seedlings of each cultivar were measured in each treatment. From these results 10 ppm was selected as the concentration where the clearest difference for GA response was observed between cultivars. The ten cultivars described previously were then tested at GA concentrations of 10 ppm, and the experiment was repeated three times. Response to GA was measured as the difference of the distance between the first and second leaves for the means of ten seedling grown in the control and GA supplemented nutrient solutions. Entries in each replication consisted of ten seedling with mean values used in the statistical analysis. All experiments were analyzed as randomized complete blocks

with three or four replications. In these studies, sensitive cultivars are defined as those that respond to GA treatment as shown by an increase in length between the first and the second leaf. Insensitive cultivars did not respond to GA treatment.

Seedlings of parents, F_1 and F_2 populations were exposed to 10 ppm GA for 14 days to examine the inheritance of GA reaction in study II. Crosses studied were Larker x Apam Dwarf and Minn. 66-102 x OR-SS-2. Each of the three replications consisted of ten seedlings for each parent and F_1 cross. Since effects of replications in previous experiments had not been significant ($P < .05$), F_2 populations were not replicated. Approximately 350 seedling of each F_2 cross were examined for GA reaction.

The significance of the differences between cultivars and crosses for their response to GA was determined by an analysis of variance using mean values. Population distributions and Chi square analysis were used for the genetic interpretation of the GA reaction. Comparison between the same F_2 distributions for the mature plant height and GA response are made. Inheritance of short stature in the barleys used in this experiments has been reported previously (16).

RESULTS AND DISCUSSION

Exposure to GA for 14 days separated the sensitive and insensitive cultivars. Sensitive seedlings were distinctly different from insensitive seedling having an elongated region between the first and second leaves and thinner stems with longer, thinner leaves. Barley cultivars used in this study did not respond to the GA treatment as markedly as the two wheat cultivars tested. In these experiments sensitive wheats had much thinner, weaker stems and longer, thinner leaves than sensitive barley. Insensitive barleys in some experiments respond slightly to GA treatment, having longer leaves than the untreated control. The insensitive wheat Tom Thumb did not show any response to GA.

Different concentrations of GA had a small effect on growth of the cultivars studied (Table 2). Treatments exposed to 5 ppm GA were consistently less responsive across all sensitive cultivars than treatments exposed to 10 and 15 ppm GA. Significant differences between concentrations were only found involving Larker where the concentrations at 10 and 15 ppm caused a greater response than at 5 ppm. The sharpest separation between sensitive and insensitive types was observed at 10 ppm.

All the standard height cultivars in this study were sensitive to GA (Table 3). These results agree with those found in wheat (2, 7).

The cultivar Short Wocus did not appear as sensitive to GA treatment as Steptoe or Larker. However, all three cultivars responded significantly to GA. Furthermore Steptoe and Larker showed a marked response with thinner stems and longer leaves than their respective controls. Leaves and stems of the seedlings of GA treated Short Wocus were similar in appearance to leaves and stems of seedlings grown in control nutrient solutions. The intermediate height attained by Short Wocus has been attributed to minor recessive genes (4).

The semidwarf and dwarf cultivars did not have identical responses to GA treatment (Table 3). Short statured barleys Minn. 66-102 and OR-SS-2 were sensitive to GA treatment. Despite its short stature, OR-SS-2 was significantly more sensitive to GA than the taller cultivars. The semifwarf Xv 2334-6R, derived from the cultivar Indian Dwarf, did not respond to GA treatment. The two dwarf lines Apam Dwarf and Indian Dwarf were both insensitive to GA.

These results indicate that in the barley tested, GA response and short stature are not as closely associated as they appear to be in wheat. Brachytic mutants Apam Dwarf, Indian Dwarf and Xv 2334-6R were all insensitive to GA treatment. The derived ert-type OR-SS-2 was sensitive to GA, this agreeing with results reported for other ert-mutants (17, 18). The Jotun mutant background carried in Minn. 66-102 was also sensitive in these studies which suggests that the short stature attained by these two semidwarfs may be due to a reduction in

either biosynthesis or biological activity of endogenous GA. The Jotun mutant which is not typical of the ert-mutants has normal spike type and weak straw. Although most ert-mutants have dense, compact spikes and stiff straw, they can vary markedly in spike length, culm length and straw strength. Haahr and Wettstein (8) in their studies of the genetics of the short strawed mutants Riso 9265 'Maris Mink', 'Claudia', 'Diamant' and 66/86 a line derived from the Jotun Mutant reported all were alleles from the same locus. Riso 9265, Diamant and 66/86 derived their short stature from independent induced mutations. Maris Mink and Claudia were selected from crosses involving the cultivar Deba, which was derived from the spontaneous ert-mutant Denso (8). Haahr and Wettstein's report and information obtained in this study suggests the two sources of dwarfism, although their morphological appearances differ, are the same in origin. Response to applied GA may be an effective way of classifying the different sources of dwarfism in barley.

To gain a better understanding of the inheritance of GA response in barley, distance between the first and second leaves of seedlings from crosses involving the insensitive Apam Dwarf and three sensitive cultivars, Larker, Minn. 66-102 and OR-SS-2 were determined. All F_1 seedlings tested were sensitive to GA (Table 4), indicating that the gene(s) associated with GA insensitivity are recessive. In other studies involving dwarfing sources in barley the brachytic genes

$\underline{br}_1$ and $\underline{br}_2$ (11, 15), $\underline{uz}$ gene (10) and the $\underline{ert}$-mutants (12) have all been reported as single, recessive genes.

Distributions of the F_2, for the cross Larker x Apam Dwarf indicate that inheritance of GA insensitivity is not clearly associated with one gene. Apam Dwarf carries two recessive genes that differ in degree of expression but act in an additive manner causing dwarfism. F_2 distribution for GA reaction suggests that one recessive gene imparts insensitivity to GA as does the double recessive genotype. The second gene appears to govern partial sensitivity to GA resulting in an intermediate response. Chi square analysis for the ratio 9:3:4 indicates a good fit (p=.94).

Data reported in this study indicate that GA insensitivity is recessive in inheritance. F_2 data suggest that additivity of two recessive genes regulates GA insensitivity. One of the recessive genes in Apam Dwarf may cause insensitivity. Insensitivity appears to be related to a failure to utilize endogenous GA as is the case in insensitive wheats. Double recessive brachytic dwarfs are normal in appearance except for being miniature with respect to morphological traits.

In wheat coleoptile length has been reported to be highly correlated with GA insensitivity (7) and height (3). A similar relationship was found in the barley tested. During the course of these studies it was observed that all the sensitive cultivars had normal coleoptile

lengths, while the insensitive types had shorter coleoptiles. Cultivars with Jotun background have been reported as having normal length coleoptiles (1). The brachytic and uz genes have been reported to have shorter coleoptile lengths than standard height cultivars (15). Coleoptile length in both wheat and barley appears to be associated with GA insensitivity. If this association is consistent, it suggests that the brachytic genes cause an insensitive reaction which is similar to that in wheat (i.e., lack of utilization of endogenous GA). It also indicates that the uz gene, not studied in these experiments, would also be GA insensitive. Although the ert and Jotun types in these studies were semidwarfs, they were sensitive to GA and had long coleoptiles.

The variability for GA reaction, and short stature appear to be very diverse in barley. This offers the plant breeder a large choice in the selection of dwarf sources useful for the breeding of semidwarf cultivars. As improvements are made in agronomic characters and yield it will be important to keep records on the backgrounds of the various dwarf sources utilized. Derived lines with improved agronomic performance are difficult to classify as being originally uz, brachytic or ert-mutants. But the traits associated with short stature, such as GA response, coleoptile lengths and α-amylase activity are very important. The classification of the dwarfing sources utilized in barley programs based on their GA response appears to be an effective way of separating the various

dwarfing sources of barley, especially when plant breeders intercross the different sources of dwarfism. Classification of dwarfing sources of barley into two groups seems appropriate. Semidwarf or dwarf barleys responding to GA can be classified as sensitive and their short stature appears to be due to a lack of endogenous GA. Insensitive dwarf or semidwarf cultivars have shorter coleoptiles than talls and appear to be similar to dwarf wheats in their reaction to GA. The nature of their short stature is different than the sensitive types. Uz and brachytic mutants can be separated based on the characteristic hooked coleoptile in the uz background.

The use of seedling tests for GA reaction can be an effective way of identifying semidwarf individuals if insensitive dwarf sources are utilized. This method could be a useful seedling selection tool for those programs which utilize the greenhouse or growth chambers for single seed descent or other multi-generation breeding schemes. Large numbers of seedlings can be tested and the semidwarf types identified 14 days after germination.

Table 1. Origin, relative height and dwarfing sources of eight barley and two wheat cultivars.

Cultivar	Origin	Height (cm)	Dwarf source
Larker	North Dakota	81[1]	Standard height
Steptoe	Washington	70	Standard height
Short Wocus	Oregon	65	Standard height
Minn. 66-102	Minnesota	55	Jotun derivative
Xv 2334-6R	India	45	Indian Dwarf derivative (brachytic)
Indian Dwarf	India	31	Induced by x-ray mutant (brachytic)
Apam Dwarf	Mexico	33	Cimmyt collection (brachytic)
OR-SS-2	Oregon	43	Tokak mutant (erectoides)
Tom Thumb	Tibet	45[2]	Cimmyt collection
Maris Huntsmen	England	120[2]	Standard height

[1]Grown at Klamath Experimental Station, Klamath Falls, Oregon, 1978.

[2]Grown at Hyslop Experimental Station, Corvallis, Oregon, 1978.

Table 2. Mean response of four barley cultivars, exposed to three concentrations of GA.

Cultivar	GA ppm	Distance between first and second leaves (cm)	Response
Larker	0	4.73	
	5	6.48	1.75**
	10	7.54	2.81**
	15	7.05	2.65**
Minn. 66-102	0	4.47	
	5	6.46	1.99**
	10	7.05	2.58**
	15	5.88	2.41**
OR-SS-2	0	2.83	
	5	5.81	2.98**
	10	6.31	3.48**
	15	6.35	3.52**
Apam Dwarf	0	2.89	
	5	2.66	-.23
	10	2.86	-.03
	15	2.64	-.25
		LSD(.05) .7861	

**Significant at the P(.01) level, paired t-test

Table 3. Mean GA response in eight cultivars of barley and two cultivars of wheat.

Cultivar	Distance between first and second leaves (cm) Control	10 ppm GA	(Response) Diff.
Larker	4.71	6.06	1.35**
Steptoe	3.53	5.23	1.70**
Short Wocus	3.80	4.85	1.05**
Minn. 66-102	4.44	5.62	1.18**
Apam Dwarf	2.89	2.80	-.09
Indian Dwarf	3.49	3.40	-.09
OR-SS-2	3.16	5.72	2.56**
Xv 2334-6R	4.02	4.10	.08
Tom Thumb	.91	.93	.02
Maris Huntsmen	3.24	6.05	2.81**

LSD (.05) = .6479

**Significant at the P(.01) level, paired t-test

Table 4. Mean GA response in four barley cultivars and two F_1 crosses.

Cultivar	Distance between first and second leaves (cm)		Response
	Control	GA	
Larker	4.61	6.79	2.18**
Apam Dwarf	3.57	3.95	0.38
Minn. 66-102	4.21	7.19	2.98**
OR-SS-2	3.54	7.07	3.53**
Larker/Apam Dwarf, F_1	3.75	6.10	2.35**
Minn. 66-102/OR-SS-2, F_1	3.39	7.28	3.89**
		LSD (.05) = .6836	

**Significant at the P(.01) level, paired t-test

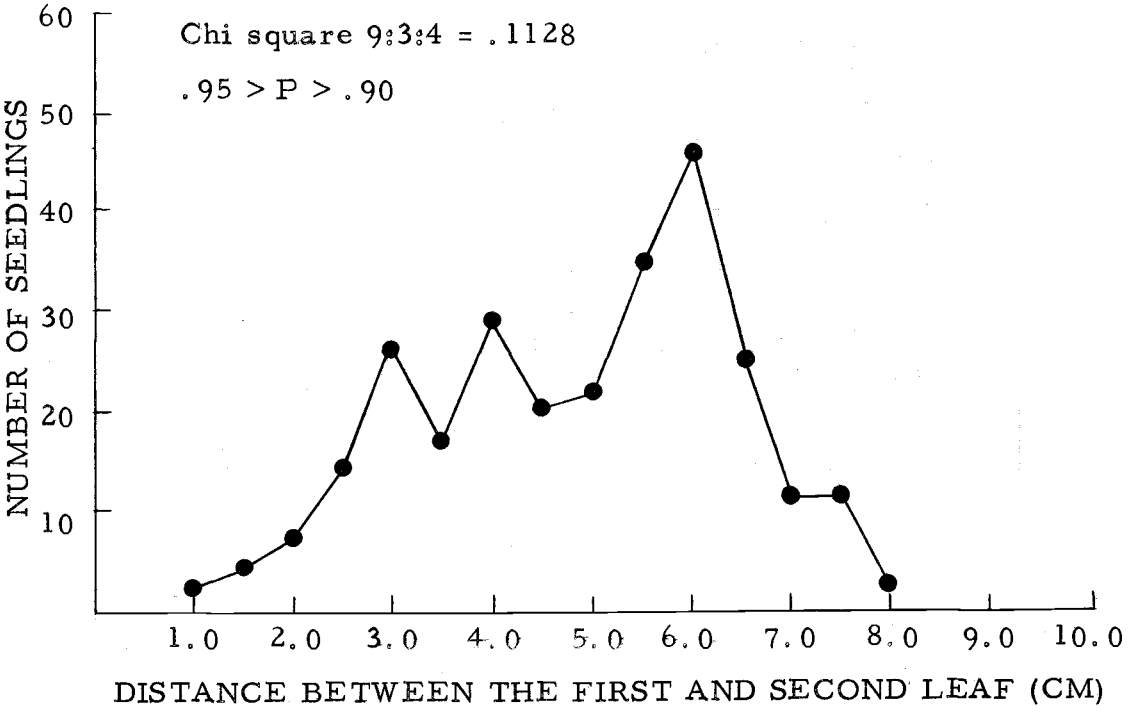

Figure 1. Seedling F_2 distribution of the cross Apam Dwarf x x Larker grown in 10 ppm GA

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Inheritance of Dwarf and Semidwarf plant height in Barley (Hordeum vulgare L.)[1]

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ABSTRACT

Inheritance of dwarfism in barley (Hordeum vulgare L.) was studied in a six parent diallel involving the standard height variety 'Larker' and five short statured lines, 'OR-SS-2', 'Minn. 66-102', 'Indian Dwarf', 'Apam Dwarf' and 'Xv 2334-6R'. Data from F_2 populations and selected F_3 progenies indicated that four gene pairs segregating independently accounted for the differences observed in plant height. Apam Dwarf, Indian Dwarf and Xv 2334-6R appear to

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Additional index words: Dwarf sources, diallel cross, major genes

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[1]Contribution of the Crop Science Dept., Oregon Agric. Exp. Stn., Corvallis. Part of a thesis submitted by the senior author in partial fulfillment of the requirements for the Ph. D. degree at Oregon State University.

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have the same major genes for the inheritance of dwarfness. The reduced plant height in Apam Dwarf is controlled by two recessive gene pairs which act in an additive manner. Minnesota 66-102 and OR-SS-2 each carry single recessive gene pairs for reduced plant height. Crosses among the dwarf sources indicated that Minn. 66-102, OR-SS-2 and Apam Dwarf all have different genes for semidwarf or dwarf plant type. Segregation in F_2 and F_3 generations suggested that all four genes were transmitted independently and semidwarf and dwarf plant types were inherited in an additive manner.

INTRODUCTION

Reduction in plant height has allowed plant breeders to increase the yield potential of many important crops. Because of the increased lodging resistance and high yield potentials of semidwarf barley, breeders are utilizing semidwarf and dwarf germplasm. Currently four sources of dwarf or semidwarf plant type are described in barley; the 'uzu' (3, 6), brachytic (3) and erectoides (4) genotypes and semidwarf lines derived from a short strawed mutant induced in the cultivar 'Jotun' (5). These different sources of semidwarf plant type have been reported as being controlled by single recessive gene pairs (1, 3, 4). More complex dwarfs such as 'Indian Dwarf' have been reported to carry three recessive gene pairs for plant height (2).

The nature of inheritance of dwarfism is not fully understood in many of the dwarf and semidwarf lines utilized in breeding programs. Knowledge of the number of genes involved and their inter and intra allelic interactions is important in selecting parents and predicting desired plant height in segregating populations. How each different dwarfing source affects other characters or interacts with different dwarfing genes may allow a rational choice between the use of one or two genes in a potential variety.

Many sources of dwarf and semidwarf germplasm have been utilized in the Oregon barley improvement program during the past

five years. The objective of this study was to determine if these sources for reduced height possess similar or dissimilar genetic mechanisms and the number of genes involved.

MATERIALS AND METHODS

Inheritance of different dwarfing sources was studied in a six parent diallel of spring barley, involving the standard height cultivar 'Larker' and five short strawed selections. Larker is used as a parent in many breeding programs and is grown commercially throughout the North Central United States. 'Oregon-SS-2' is a line derived from the cross 'Tokak mutant, x 'Steptoe'. Tokak mutant is an induced erectoides mutant originally selected in Turkey. Minnesota 66-102 is a derived line from the induced 'Jotun' mutant. 'Indian Dwarf' is an induced x-ray mutant and 'Xv 2334-6R' is derived from Indian Dwarf. Apam Dwarf was obtained from the International Maize and Wheat Improvement Center (CIMMYT) collection and is similar in phenotype to Indian Dwarf.

Two studies involving one field experiment and a greenhouse study were conducted. The field experiment consisted of parents, F_1 and F_2 populations grown in a randomized block design at the Klamath Falls Experiment Station in 1978. Four replications were sown with each consisting of ten plants for parents and F_1s and 60 F_2 plants. Seeds were space planted on a 30 cm grid, each row was 3.0 m in length. Single rows represented each parent and F_1 while 6 rows were sown for each F_2 population in each replication. Filler plants were planted to maintain uniform competition.

Mature plant height was defined as the average height of the three tallest tillers measured from the base of the culms to the tips of the spikes, excluding awns. Replications were pooled to compute means, variances and population distributions. Chi square values were determined for all populations segregating for plant height. Dominance values were computed by the formula suggested by Romero (1969). Plant height classes were established at 5 cm intervals in all populations studied.

The greenhouse experiment consisted of F_3 progenies grown to verify results obtained from F_2 populations. Crosses included Larker x Apam Dwarf, Minn. 66-102 x Apam Dwarf, Larker x Minn. 66-102 and OR-SS-2 x Minn. 66-102. In the crosses Larker x Apam Dwarf and Minn. 66-102 x Apam Dwarf, 35 F_3 progenies were examined to check F_2 classification. Twenty-four F_3 plants were grown from each F_2 plant selected. Plants were grown in 3.8 liter plastic pots containing a soil mixture consisting of 1/3 peat, 1/3 sand and 1/3 clay loam and fertilized to obtain maximum plant development.

In the crosses Larker x Minn. 66-102 and OR-SS-2 x Minn. 66-102 20 and 23 F_3 progenies, each represented by 18 plants, were grown to verify F_2 classification. In each cross eight replications of both parents were planted to estimate environmental variation associated with the experiment. Variance associated with the parents was used to estimate the environmental variation for each cross

studied.

Mature plant height of each F_3 plant was measured to the nearest centimeter from the base of the tallest culm to the tip of the spike, excluding awns. Plant height classes were established at 5 cm intervals to simplify interpretation of the data. Plant height was uniformly constant across the parents and variances were small. F_3 progeny distributions and chi square analysis were used to verify F_2 classification.

RESULTS AND DISCUSSION

Mean values and standard deviations for plant height of parents, F_1 and F_2 populations are shown (Table 1). The frequency distributions for F_2 plant height are provided in Figures 1-5. In all crosses examined the presence of few major genes conditioning dwarf and semidwarf plant height is suggested.

Dominance values (Table 1) for the crosses involving Larker and the five short lines indicate that the major genes for short plant height are acting in a recessive manner. The large dominance values found in the crosses OR-SS-2 x Apam Dwarf, OR-SS-2 x Minn. 66-102 and Minn. 66-102 x Apam Dwarf indicate that these three cultivars differ genetically for more than one pair of major genes for plant height.

F_2 distributions from the crosses Larker x OR-SS-2 and Larker x Minn. 66-102 (Figure 1) indicate that independent recessive gene pairs govern short stature in each semidwarf parent. Both crosses could be separated into two distinct groups which fit a 3 tall:1 short genetic ratio (Table 2). F_3 data supported the conclusion that Minn. 66-102 carries one gene for semidwarf plant height. Table 3 shows that of 15 tall F_2 plants selected for F_3 progeny testing four did not segregate and were homozygous; 11 plants segregated 3 tall:1 short. The short group representing five F_2 plants was expected to

be homozygous for plant height. As shown by F_3 data however, four plants were homozygous short and one plant, which had been misclassified segregated 3 tall:1 short. This data agrees with other reports (1, 2) that the short stature of Jotun mutant is conditioned by one recessive gene pair.

Crosses among the three dwarf lines, Apam Dwarf, Indian Dwarf and Xv 2334-6R did not differ significantly for culm length. The F_2 height distributions (Figure 2) did not exceed the range of the parents in the cross Indian Dwarf x Xv 2334-6R. This indicates that both Indian Dwarf and Xv 2334-6R probably contain the same major recessive genes for reduced culm length even though they differ in plant height. Crosses involving Apam Dwarf with Indian Dwarf and Xv 2334-6R also lacked variability, although 8% of F_2 plants occurred outside of the range of either parent. The expression for height in these F_1s suggests that Apam Dwarf may have an allelic gene in common with Indian Dwarf and Xv 2334-6R. The lack of variability in the F_2, however, and the similarity in F_2 distributions when these three dwarfs were crossed to the common parent, Larker (Figures 2, 3) suggested that they have the same genetic constitution in relation to plant height. Based on these observations crosses with Indian Dwarf and Xv 2334-6R are not reported in this paper. F_1 plants and F_2 distributions were similar in all respects with crosses involving OR-SS-2 x Apam Dwarf and Minn. 66-102 x Apam Dwarf.

Crosses involving Apam Dwarf, Indian Dwarf and Xv 2334-6R with Larker indicate digenic inheritance. The F_2 distributions for each cross indicated a 9 tall, (A_B_): 3 medium (aa B_) : 3 short (A_bb) : 1 dwarf, (aabb) genetic ratio (Table 2, Figures 2 and 3). F_3 progenies representing F_2 plants selected for each height class of the Larker x Apam Dwarf cross supported the F_2 data that two independent recessive gene pairs dwarf plant type (Table 5). In both F_2 and F_3 generations four distinct height groups were observed. All F_2 plants classified as medium or short were either homozygous or segregated for one gene pair. Both of the recessive genes appear to be additive, are inherited independently and unequal in their effects on plant height. Individually each gene produced shorter plants than the original tall parent Larker.

The extremely high dominance values associated with the cross OR-SS-2 x Minn. 66-102 suggested that semidwarf plant type in these two lines is governed by different independent genes. F_2 distributions for this cross (Figure 3) indicated that two independent gene pairs segregated in a ratio of 9 tall, (C_D_):3 medium (ccD_):3 short, (C_dd):1 dwarf (ccdd) (Table 2). Presence of two independent recessive gene pairs was verified by F_3 data as shown in Table 4. All F_2 plants classified as medium or short were either homozygous or segregated for one gene pair.

Data from the cross Minn. 66-102 x Apam Dwarf indicated that

these two sources of short stature were also different in genetic origin. Large dominance values as well as transgressive segregation for taller types were noted in the F_2 populations. Three distinct height groups (Figure 4) were observed in F_2 distributions suggesting at least two recessive gene pairs controlled dwarfness as noted in previous crosses. However, F_3 progeny tests representing the dwarf F_2 plants were not homozygous, two plants segregated 3 dwarf, (aabbC_):1 triple dwarf (aabbcc) and two plants homozygous for three gene pairs, significantly shorter than Apam Dwarf, were observed (Table 6). The occurrence of a triple dwarf segregant approximately 20-25 cm shorter than Apam Dwarf in greenhouse tests suggests three gene pairs acted to condition plant height. Plant height varied greatly within F_3 progenies grown from F_2 plants representing the intermediate and tall groups. The small number of F_3 plants measured made it difficult to establish genotypes for all classes of plant height observed. Although triple dwarfs were produced when all three recessive genes pairs were present the exact nature of the interaction of the genes could not be determined in this study. It appears, however, that they acted independently and additively to control plant height. Selection of three gene dwarfs as well as two gene dwarfs containing one semidwarf gene from Apam Dwarf and one semidwarf gene from Minn. 66-102 should be possible.

In the cross OR-SS-2 x Apam Dwarf a similar pattern in the

F_2 was observed when compared to the Minn. 66-102 x Apam Dwarf cross (Figure 5). Large numbers of dwarf plants were observed in both crosses. The large dominance value indicated that the two dwarf sources were of different genetic origin. The excessively large number of dwarf plants varying in height in this cross suggested that different combinations of the three gene pairs resulted in the dwarf plants that differed in height. It appears that three gene pairs are involved in the expression of dwarfness in these crosses.

The results reported in this paper indicate that culm length in barley can be conditioned by a number of different dwarfing genes. Minn. 66-102, a Jotun derivative, carries one recessive gene for semidwarf plant type. OR-SS-2 also appears to carry one recessive gene for short stature. Data from the cross OR-SS-2 x Minn. 66-102 indicated that the genes are independent and act in an additive manner to condition plant height. When the genes are combined, plants containing two recessive gene pairs can be recovered that are similar in height to Apam Dwarf, Indian Dwarf and Xv 2334-6R.

Apam Dwarf, Indian Dwarf and Xv 2334-6R appear to have identical or at least similar genes for dwarfness. The dwarf stature of these lines is probably controlled by two recessive genes. Strong evidence was presented suggesting Apam Dwarf carries two recessive major genes for dwarf plant type. Also the genes in Apam Dwarf are different from those contained in Minn. 66-102 and OR-SS-2. F_3

data from the cross Minn. 66-102 x Apam Dwarf suggest that the three recessive gene pairs governed culm length and probably acted independently in an additive manner. Triple dwarfs 20-25 cm shorter than Apam Dwarf, recovered in F_3 lines suggests the presence of three recessive genes.

New recombinations of dwarf and semidwarf genes in barley were developed that can be used to breed new high yielding cultivars. Such recombinations of different genes for dwarfness may be an effective way of breaking up undesirable traits associated with certain dwarf sources, and thus will benefit plant breeding programs.

Table 1. Plant numbers, means and variances of parents, F_1 and F_2 populations and F_1 dominance values.

Populations	Female			Male			F_1			F_2				
	N	$\overline{X}$	S^2	N	$\overline{X}$	S^2	N	$\overline{X}$	S^2	N	X	S^2	D	d
Larker/Jotun	32	81.5	52.9	32	55.0	42.4	32	78.7	47.1	180	75.9	116.7	13.20	1.16
Larker/OR-SS-2	32	81.5	52.9	32	43.1	20.5	32	85.4	46.3	163	73.5	302.6	19.20	1.17
Larker/Apam Dwarf	32	81.5	52.9	32	33.3	9.9	32	73.7	19.9	141	67.3	158.3	24.10	0.82
Larker/Indian Dwarf	32	81.5	52.9	32	31.0	14.2	32	76.5	17.7	159	76.5	240.5	25.20	1.60
Larker/Xv 2334-6R	32	81.5	52.9	32	45.6	29.2	32	85.3	64.4	168	74.0	286.0	17.90	1.17
OR-SS-2/Apam Dwarf	32	43.1	9.9	32	33.3	20.5	32	70.5	44.1	152	59.4	205.4	4.90	8.65
OR-SS-2/Minn. 66-102	32	43.1	20.5	32	55.0	42.4	32	78.0	21.8	172	68.0	301.8	5.95	6.37
Minn. 66-102/Apam Dwarf	32	55.0	42.4	32	33.3	9.9	32	67.2	32.8	154	59.5	217.9	10.80	2.84
Apam Dwarf/Indian Dwarf	32	33.3	9.9	32	31.0	14.2	32	36.3	3.2	160	33.9	42.0	1.15	3.04
Apam Dwarf/Xv 2334-6R	32	33.3	9.9	32	45.6	29.2	32	41.4	25.6	188	43.5	51.6	6.15	1.32
Indian Dwarf/Xv 2334-6R	32	31.0	14.2	32	45.6	29.2	32	33.9	21.9	169	38.4	44.9	7.30	.03

N = number of plants; $\overline{X}$ = mean plant height; S^2 = variance; $D = \overline{TP} - \overline{MP}$; $d = \frac{2(\overline{F}_2 - \overline{MP})}{D}$

Table 2. Height classification for F_2 barley populations and chi square analysis.

	Classification No. of Plants				Ratio tested	P
	Tall	Medium	Short	Dwarf		
Larker x Minn. 66-102	109		37		3:1	.95-.90
Larker x OR-SS-2	111		49		3:1	.50-.25
Larker x Apam Dwarf	75	21	23	8	9:3:3:1	.90-.75
Larker x Indian Dwarf	99	23	27	10	9:3:3:1	.50-.25
Larker x Xv 2334-6R	80	28	34	12	9:3:3:1	.50-.25
OR-SS-2 x Minn. 66-102	105	29	28	18	9:3:3:1	.75-.50

Table 3. Combined F_3 plant height distributions from selected F_2 plants of the cross Larker x Minn. 66-102.

F_2 Classification		F_3 Plant H			
	No. of F_2 Plants	120-150 Tall	85-110 Short	Ratio tested	P
Tall	11	139	60	3:1	.10
	4	72	0		
Short	4	0	72	3:1	.90-.75
	1	14	4		

Table 4. Combined F_3 plant height distributions from selected F_2 plants of the cross OR-SS-2 x Minn. 66-102.

F_2 Classification		F_3 Plant Height (cm)				
	No. of F_2 Plants	60-75 Dwarf	80-110 Intermediate	115-150 Tall	Ratio	P
Dwarf	1	18				
Short	6		108			
	4	19	53		3:1	.90-.75
Med Tall	1	5	13		3:1	.90-.75
	1		4	14	3:1	.90-.75
Tall	3		12	42	3:1	.23
	3			54		
	3	2	9/10	34	9:6:1	.50-.25

Table 5. Combined F_3 plant height distributions from selected F_2 plants of the cross Larker x Apam Dwarf.

F_2 Classification		F_3 Plant Height					
	No. of F_2 Plants	60-75 Dwarf	80-110 Short	105-120 Med Tall	115-140 Tall	Ratio tested	P
Dwarf	5	118	0	0	0		
Short	2	0	47	0	0		
Med Tall	5	35	85			3:1	.75-.50
	4	22		74		3:1	.90-.75
Tall	8	36		127		3:1	.75-.50
	5	9	23	27	58	9:3:3:1	.50-.25
	3	0	0	0	72		

Table 6. Combined F_3 plant height distributions from selected F_2 plants of the cross Minn. 66-102 x Apam Dwarf.

F_2 Classification	No. of F_2 Plants	Plant Height (cm) and No. of F_3 Plants observed for each class					Ratio tested	P
		35-55	55-70	71-95	95-115	115-140		
Dwarf	2	48						
	3		72					
	2	17	31				3:1	.10
Intermediate	1		24				3:1	.90
	2	12	36				3:1	.10
	2							
	2	2	8	6	10	26		
Tall	13	16	15	54	95	129		
	4		25		71		3:1	.90-.75
	1			5		19	3:1	.90-.75
	3					72		

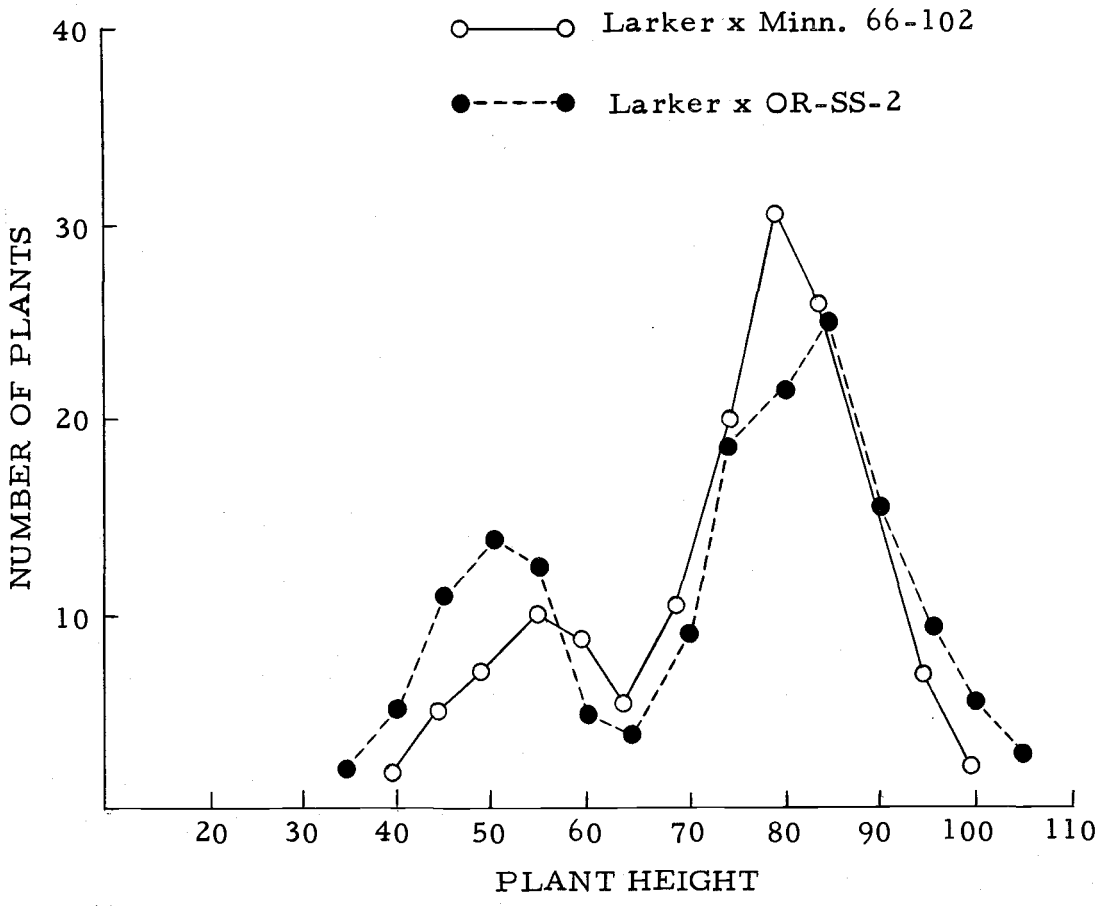

Figure 1. Plant height (cm) F_2 distributions of the crosses Larker x Minn. 66-102 and Larker x OR-SS-2

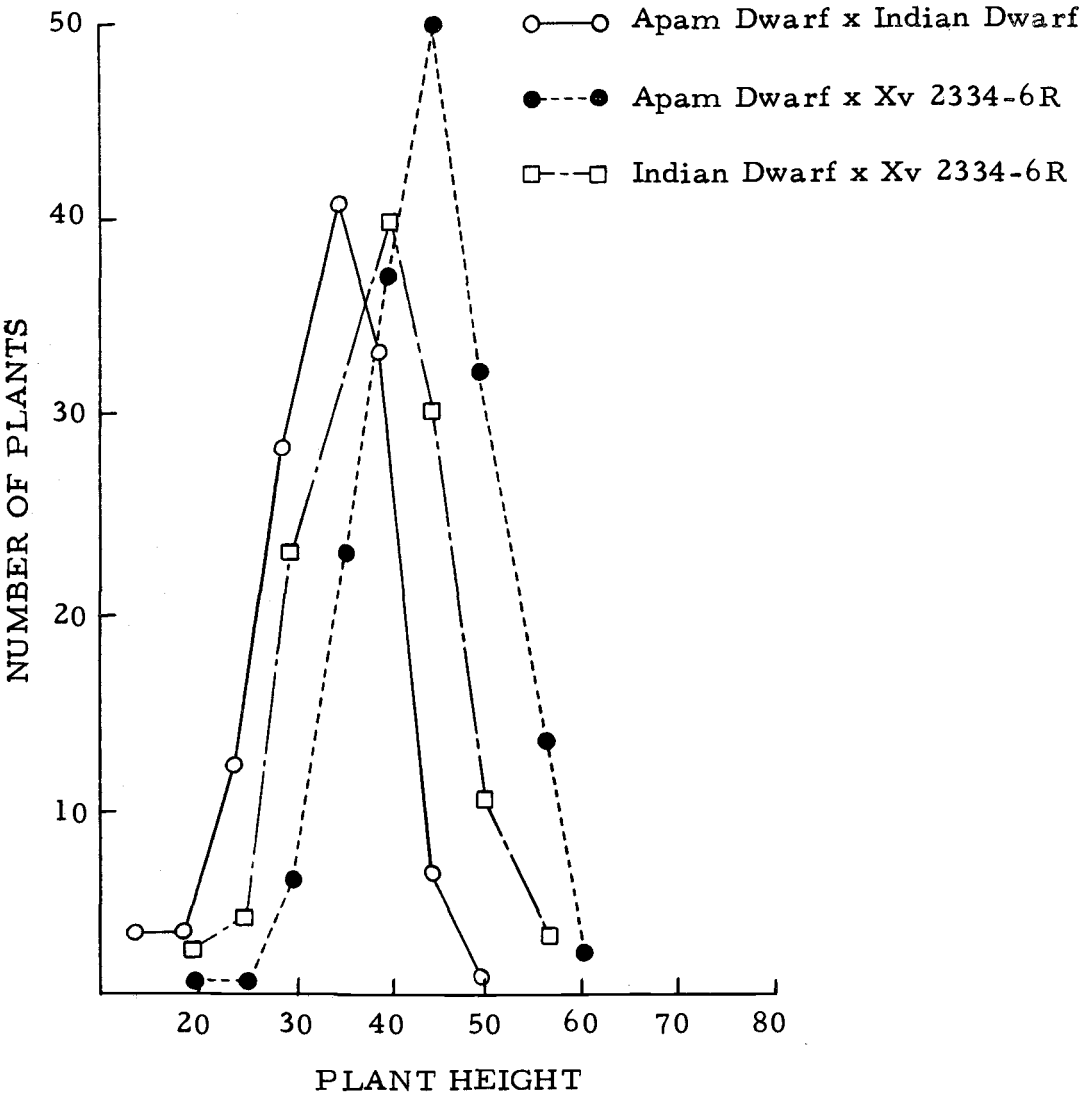

Figure 2. Plant height (cm) distributions of F_2 plants of the crosses Apam Dwarf x Xv 2334-6R, Apam Dwarf x Indian Dwarf and Indian Dwarf x Xv 2334-6R

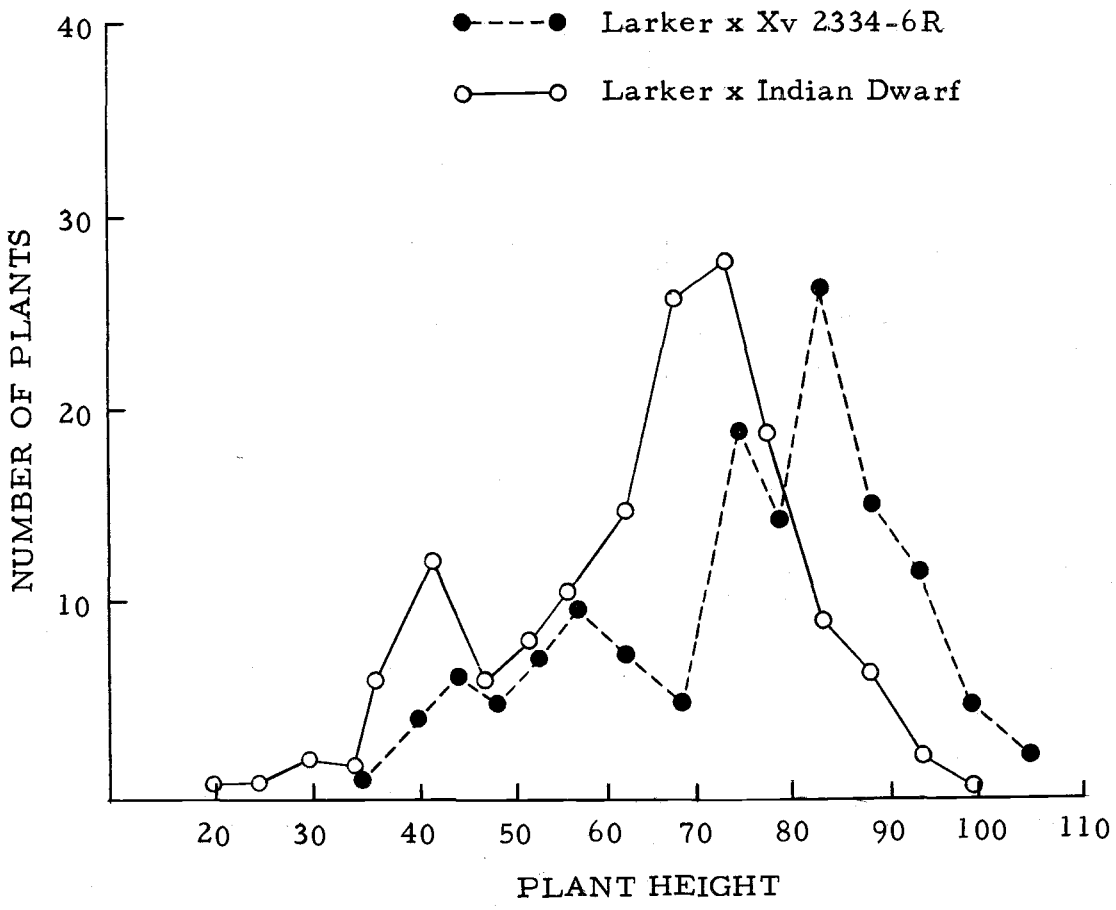

Figure 3. Plant height (cm) F_2 distributions of the crosses Larker x Xv 2334-6R and Larker x Indian Dwarf

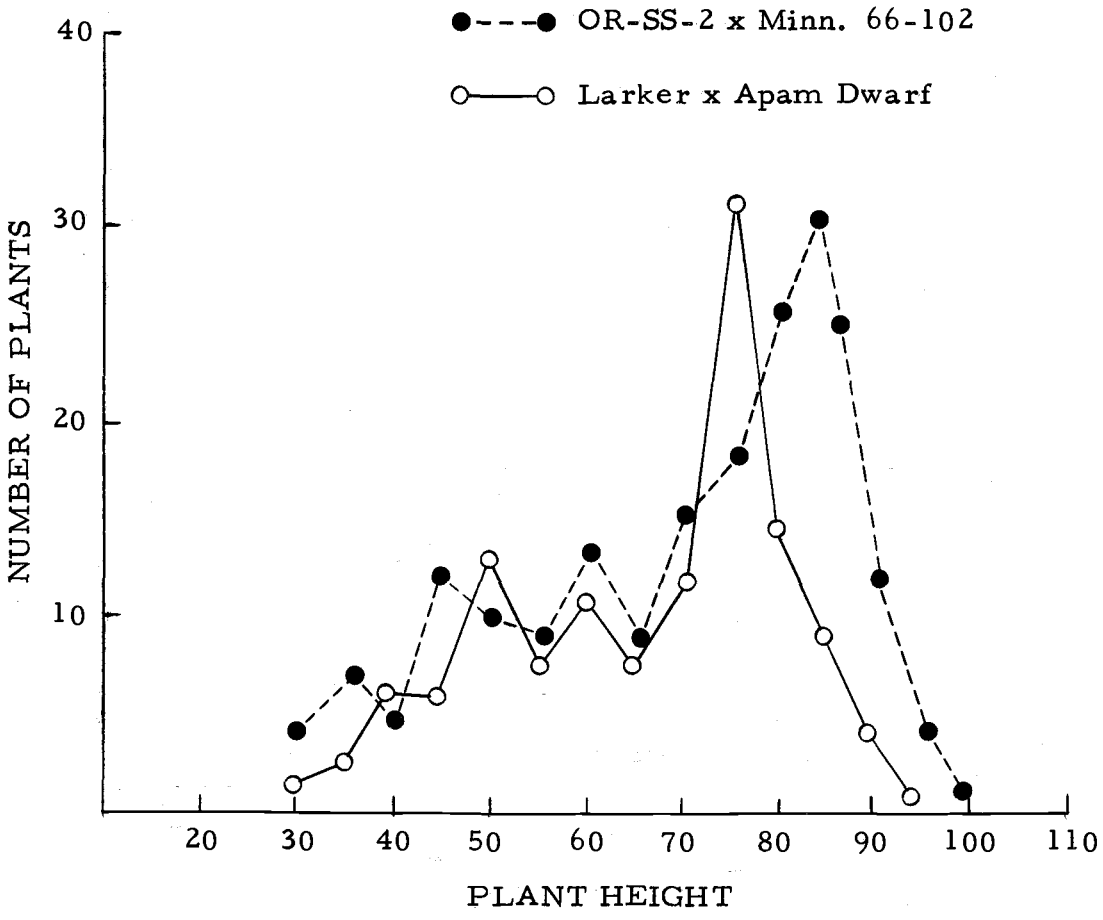

Figure 4. Plant height (cm) F_2 distributions of the crosses Larker x Apam Dwarf and OR-SS-2 x Minn. 66-102

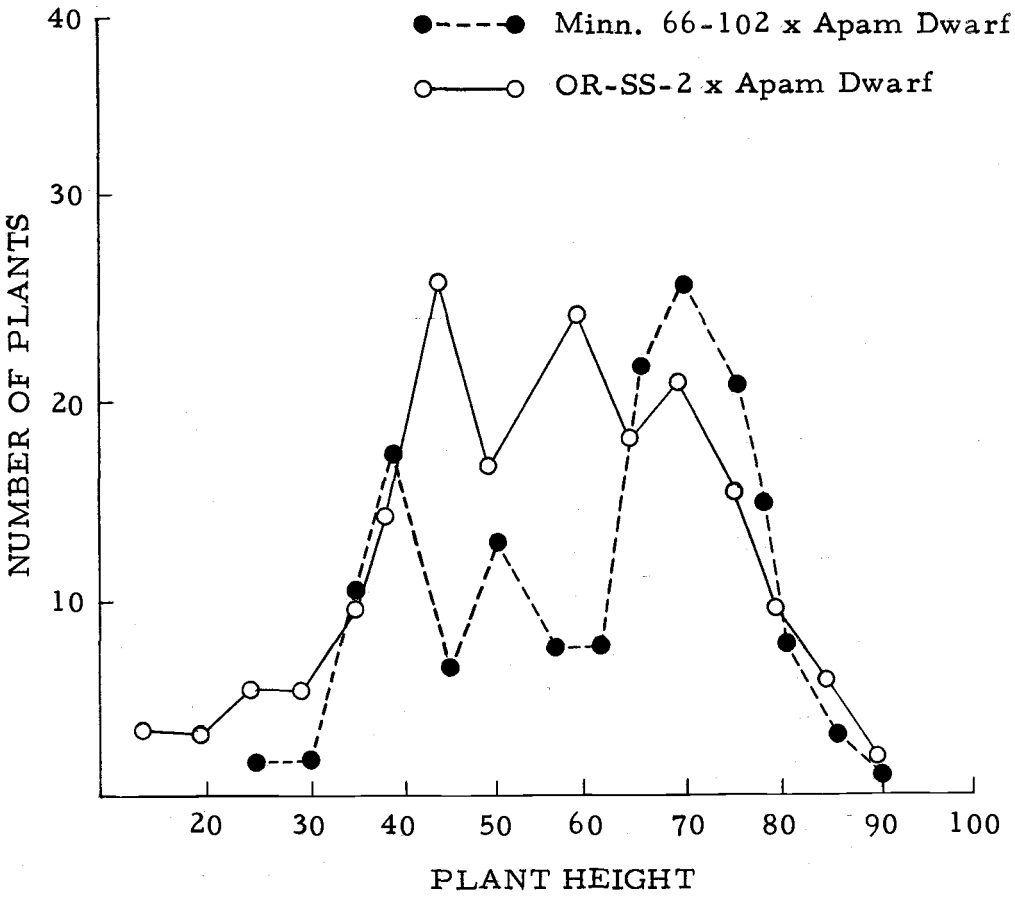

Figure 5. Plant height (cm) F_2 distributions of the crosses Minn. 66-102 x Apam Dwarf and OR-SS-2 x Apam Dwarf

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