

AN ABSTRACT OF THE THESIS OF

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Title: Evaluating Grain Yield as Influenced by Biological Yield and  
Harvest Index in Four Winter Wheat (*Triticum aestivum*)  
Crosses Involving Near-Isogenic Lines

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Crosses between four near isogenic lines for height reducing genes  $Rht_1$  and  $Rht_2$  and one agronomically superior dwarf line, including generations through  $F_3$  with reciprocal backcrosses constituted the experimental materials. Mean, range and standard deviation values for eleven traits pertaining to the different generations were obtained. Heterosis and inbreeding depression along with broad and narrow sense heritability estimates for the traits provided information regarding nature of gene action. Possible relationship between selected traits were also determined.

The amount of genetic diversity between crosses depended upon the number and specific dwarfing genes involved. A limited number of traits were different in crosses involving either  $Rht_1$  or  $Rht_2$  isolines. This may have resulted since 'Yamhill Dwarf' also carries the  $Rht_1$  allele. For generations, differences were detected for all eleven traits

measured. The cross involving the standard height isoline ( $rht_1rht_2$ ) and Yamhill Dwarf registered the highest mean values for plant height, grain yield, 300-kernel weight and biological yield; but had the lowest value for harvest index. Increased grain yield was more a function of higher "biological yield" than "harvest index" in all crosses and populations examined.

Consistent and positive associations were also found between grain yield and biological yield; however the same was not true for grain yield with harvest index where little or no associations were detected for any of the crosses.

Heterosis estimates were high for most traits in  $rht_1Rht_2$ /Yamhill Dwarf cross and low in the cross  $Rht_1rht_2$ /Yamhill Dwarf.

Inconsistent broad and narrow sense heritability estimates were observed in several crosses for most traits measured. The one exception was for 300-kernel weight, being relatively high and consistent in all crosses except  $Rht_1Rht_2$ /Yamhill Dwarf. In some instances, negative narrow sense heritability estimates were realized. This was particularly true for the cross between the standard height isoline ( $rht_1rht_2$ ) and Yamhill Dwarf. Also, depending on the cross and trait measured, larger narrow sense heritability estimates were obtained when compared to the broad sense estimates. This could reflect some sampling error or a large genotype X environmental interaction which was observed.

EVALUATING GRAIN YIELD AS INFLUENCED BY BIOLOGICAL YIELD AND  
HARVEST INDEX IN FOUR WINTER WHEAT (Triticum aestivum)  
CROSSES INVOLVING NEAR-ISOGENIC LINES

by

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**EVALUATING GRAIN YIELD AS INFLUENCED BY BIOLOGICAL YIELD AND  
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**INTRODUCTION**

During the last few decades, wheat breeders have endeavoured to produce short, stiff-strawed cultivars that are compatible with heavy applications of nitrogen fertilizer. The introduction of semi-dwarfing genes,  $Rht_1$  and  $Rht_2$  from 'Norin 10' has largely been responsible for modern semidwarf cultivars replacing the traditional tall wheats. The cultivar 'Norin 10', released in 1935 in Japan, was introduced in the United States by Dr.S.C.Salmon in 1948. It has been extensively used in crosses, first by O.A. Vogel, and now in many wheat breeding programs. The cultivar 'Gaines' released in 1961 was the first high yielding semidwarf where  $Rht$  genes were used. Following O.A. Vogel's work, Dr. N.E. Borlaug, the pioneer of the so called "Green Revolution" incorporated the 'Norin 10' dwarfing gene(s) in Mexican wheats along with daylength insensitivity. Today many of the present-day semidwarf wheats are derivatives of the 'Norin 10' dwarfing gene(s).

Several approaches have been attempted in the past to explain the cause of higher grain yield due to the use of 'Norin 10' genes. These include: stiffer straw accounting for resistance to lodging, greater physiological ability in dry matter partitioning to parts of economic yield, less biomass and more grain yield determining higher harvest index, increased tillering capacity, high spikelet fertility, and

pleiotropic/linkage effect of the dwarfing genes with yield and yield traits.

However, no concrete decision has been reached so far. It therefore poses questions to the wheat breeders as to which role the dwarfing genes play in effecting grain yield. To produce more information a different approach has been undertaken in this investigation, which encompassed a detailed study of the progenies through  $F_3$  including backcrosses using crosses involving  $Rht_1$  and  $Rht_2$  dwarfing genes.

By employing different combinations of the  $Rht$  dwarfing alleles, it may be possible to determine the optimum biological yield to maximize grain yield. Also the nature of gene action influencing the traits measured can be determined by heritability estimates to identify which dwarfing genes resulted in the greatest genetic diversity. Also concerns regarding possible association between different dwarfing genes and specific agronomic traits must be evaluated.

Keeping these in view, the  $F_1$ ,  $F_2$ ,  $F_3$  and backcrosses resulting from crosses between an agronomically superior cultivar and four isogenic lines with different combinations of  $Rht_1$  and  $Rht_2$  dwarfing genes were evaluated in the present study. Of primary interest was to see the effect of plant height on grain yield and different yield traits including harvest index and biological yield. Secondary objectives of this study were to determine possible association between selected traits and finding the nature of gene action governing different traits.

## REVIEW OF LITERATURE

Semidwarf height genes,  $Rht_1$  and  $Rht_2$  in 'Norin 10' came originally from a two-phase cross, 'Fultz' X 'Daruma', and 'Fultz-Daruma' X 'Turkey Red'. The Fultz and Turkey Red were from United States (US) while Daruma was of Japanese origin. Following the last cross made in 1924, one of the selections, Tohoku No.34 later named 'Norin 10', was released in Japan in 1935. Salmon brought this semidwarf source to the US in 1948 ( Reitz and Salmon, 1968). Subsequently, the dwarfing alleles were incorporated into a number of selections, including 'Norin 10 X Brevor 14' (Vogel et al, 1956).

Norin 10/Brevor 14 germplasm has been used extensively throughout the world in the past few decades to develop high yielding semidwarf winter and spring wheats. In the Pacific Northwest region of the United States, these semidwarf cultivars account for approximately 90% of the winter and spring wheat production, respectively (Allan, 1983). Austin (1978) reported that the yield of wheat in the United Kingdom has increased by an average of almost 70 kg/ha/year over the last thirty years, or by about 80% as a result of the use of semidwarf wheats.

### SEMIDWARFISM AND ASSOCIATED EFFECTS

#### Multi-Approaches to Explain the Higher Yield of Norin 10-Based

##### Semidwarf Wheats:

There are conflicting reports in the literature concerning the effect of semidwarfism on yield and yield components of wheat.

According to Gale et al (1981), the international success of the Norin 10 semidwarf bread wheats is not only due to the height reductions caused by Gai/Rht alleles, but also to their beneficial pleiotropic or linked effects with other beneficial traits. As reported by Rawson and Evans (1971), the semidwarf wheats provide greater resistance to lodging and reduced competition for assimilates between stem and grain. They also noted other features relating to the pleiotropic effects of the dwarfing genes, specifically increased spikelet and tiller number. An increased harvest index has also been suggested as the reason for higher grain yields in case of semi-dwarf wheats when compared to taller types (Vogel et al, 1963; Thorne et al, 1969; Syme, 1970). Simpson (1968) ascribed the grain yield advantage of the short statured cultivars of wheat largely to their greater capacity for tillering. Rawson (1971) found more spike bearing tillers in Norin 10 derived semidwarf lines than taller cultivars. Borojevic et al (1980) noted that semidwarf wheat cultivars do produce the same number of spikelets per spike as the tall cultivars, but differ only in a greater number of kernels per spikelet and therefore a greater number of kernels per spike. Borlaug (1968) and Clements et al (1974) concluded that the dwarfing genes do have significant effects on number of grains per spike and grain yield per spike. Pepe and Heiner (1975) compared dwarf, semidwarf and tall  $F_5$  lines from a cross between two parents possessing different semidwarfing genes. They found no significant association between plant height and grain yield in hexaploid wheat. No significant differences in grain yield were observed by Busch and Chamberlain (1981) when comparing semidwarf and tall  $F_6$  lines across four locations from a cross between 'Justin', a tall daylength-sensitive and 'Ciano

67', a semidwarf daylength-insensitive cultivar. Rather, Busch and Chamberlain (1981) observed a significant increase in grain yield associated with the tall lines over the semidwarf lines at two locations.

#### Morphological and Physiological Basis of Higher Yield in Norin 10-Based Semi Dwarf Wheats:

There is no denying the fact that high yielding cultivars bearing 'Norin 10' gene owe their superior productivity in part to their dwarf stature. In addition to short straw, these cultivars also have stiffer straw which tends to avoid lodging under conditions of high fertility and irrigation. However, according to Jain and Kulshrestha (1976), factors other than height and stiff straw, play roles in determining yielding capacity of the dwarf plants. Bingham (1972) suggested that in the dwarf genotypes, the reduction in stem growth may reduce competition with the spike and this may be related to their higher yield of grain. Fisher (1973) considered that Norin 10 derived semi dwarf wheats were high yielding because they had a markedly different pattern of spike development. He suggested that stronger apical dominance in the spike and individual spikelets of Norin 10 derivatives allowed for a greater number of spikelets and florets to be formed.

A number of effects associated with Norin 10 genes on yield and several yield parameters was observed by Gale (1978) while studying the parents and F<sub>3</sub> lines of Chinese Spring(gai/rht<sub>2</sub>) X Hobbit S(Gai/Rht<sub>2</sub>) and Capelle Desprez (gai/rht<sub>2</sub>) X Hobbit S crosses. He found plant height to be a highly heritable trait and that the Gai/Rht<sub>2</sub> locus

accounted for at least two-thirds of the heritable variation for plant height. Grain number/spike and 100-grain weight were the 2nd and 3rd highest heritable traits respectively, following plant height. The gene, *Gai/Rht<sub>2</sub>* was associated with increased tiller number in both crosses. The most striking effect he obtained was the increase in grain number/spike due to *Gai/Rht<sub>2</sub>* allele where he found a 20% increase over the tall segregates. He also noticed that the increase in grain number i.e., spikelet fertility, was accompanied by a decrease in grain size in both crosses. In light of these findings, the author suggested that wheat breeders should exploit both *Rht<sub>1</sub>* and *Rht<sub>2</sub>* alleles in order to find "tall dwarfs" that can produce the best yield by maximizing larger grain size and higher grain number.

In a detailed study of four lines homozygous for *Gai/Rht<sub>2</sub>* and *gai/rht<sub>2</sub>* from a cross between 'Capelle-Desprez' (*gai/rht<sub>2</sub>*) and 'Hobbit S' (*Gai/Rht<sub>2</sub>*), Brooking and Kirby (1981) found no consistent differences in shoot apex morphogenesis. In general, they observed that a similar number of spikelets and floret primordia were initiated in both *gai/rht<sub>2</sub>* and *Gai/Rht<sub>2</sub>* genotypes, but different numbers of potentially fertile florets were present at anthesis. The contrasts between the genotypes were related to the differences in the way in which assimilates were partitioned to the developing spike and stem prior to anthesis. Such an association was more consistent with the presence of the dwarfing gene rather than height per se. Homozygous lines with *Gai/Rht<sub>2</sub>* gene partitioned more dry matter to the spike during its development and less to the stem. As a result, differences were created in the number of floret primordia that were developed into potentially grain-bearing florets in contrast to those which were

aborted. This process occurred in the 12-15 days period prior to anthesis. Partitioning of more dry matter was reflected later in greater spike weight, more fertile florets and grains per spikelet, higher harvest index and higher grain yield than the gai/rht<sub>2</sub> genotypes. They concluded that the association between assimilate partitioning and genes for dwarfness might provide some physiological basis for the "tall dwarf" model for high grain yield.

Using F<sub>6</sub> progenies of crosses involving several wheat parents, Kulshrestha et al (1978) found that grain yield per plant and yield per plot increased with the reduction in plant height up to 76-90cm level. The same situation existed for the number of grains per main tiller. They concluded that the 76-90cm height was the most efficient in utilization of soil resources available to the plant. They further observed that an increase in the number of grains per main tiller contributed to the differences in yielding capacity of various height groups. The number of tillers and number of spikelets per main tiller did not show any change among different height classes.

Brandle and Knott (1986) in a study of 64 F<sub>4</sub> lines derived from F<sub>2</sub> population from a cross between semidwarf and tall wheat cultivars noted that the semidwarf lines (tested through their response to GA<sub>3</sub>) outyielded the tall lines by 13.1% in a 1982 rainfed test and by 4.1% in the 1983 irrigated trial. However, the semidwarf lines yielded 2.7% less than the tall lines in the 1983 irrigated test when a hot dry period at the end of the growing season forced early maturity. They mentioned that where the semidwarfs were higher yielding, the spikes/m<sup>2</sup> and the kernels/spike were greater than with taller types, but the kernel weight was less. It appeared that it was the balance among the



three components that determines whether the semidwarfs would outyield the taller lines.

Influence of  $Rht_1$  gene from four sources of durum wheat when crossed to a conventional height cultivar was studied by McClung et al (1986). Semidwarf and tall height classes were selected from the  $F_2$  generation following GA-sensitivity test. The semidwarfs produced significantly greater yield, tiller number, kernels/spike than the tall height class. The latter however, gave taller plants and more number of kernels/spike than the former. They reported a significant negative correlation between plant height and grain yield within the tall height class ( $r=-0.61$ ), and a nonsignificant positive correlation ( $r=0.07$ ) in the semidwarf height class. This indicated that grain yield levels could be increased by using the  $Rht_1$  gene in durum wheats.

#### COMPARISON OF HOMOZYGOUS LINES AT $Rht$ LOCI

Allan (1983) conducted an experiment with nine backcross-derived populations; each carrying zero, one or two alleles of  $Rht_1$  and  $Rht_2$  representing three height classes- tall, medium and short. He obtained highest yield from lines carrying a single  $Rht$  allele, which gave 11 and 16% higher yield than double and zero- allelic doses, respectively. The one- $Rht$  phenotype also showed wider yield potential across diverse environments and in most genetic backgrounds. In three populations higher yields were recorded when  $Rht_1$  and  $Rht_2$  were both present as compared to the standard height class.

In a further study, Allan (1986) worked with five near-isogenic lines of wheat. Two lines had both  $Rht_1$  and  $Rht_2$  alleles from two

different sources (Norin 10/Brevor 14 and Suwon 92), two lines had one of the alleles (either  $Rht_1$  or  $Rht_2$ ) from the same two sources, and one line involved the  $Rht_3$  allele from the 'Tom Thumb' source. All were backcrossed to a common background using the cultivar 'Burt', as standard height parent. He found that plants with both  $Rht_1$  and  $Rht_2$  attained a shorter height than lines carrying single dose of either allele. Furthermore, when considering single dose, the semidwarfing allele from the Norin 10 source gave shorter statured plants than those using Suwon 92 source. Plants carrying the  $Rht_3$  allele from the Tom Thumb had the shortest height. The  $Rht_3$  lines also had the lowest grain yield of 3.3 t/ha. Lines with both  $Rht_1$  and  $Rht_2$  alleles from Suwon 92 were superior in grain yield than Norin 10 source, although both were outyielded by Burt. They yielded also significantly less than semidwarf lines with both sources. Semidwarf sources from Suwon 92 yielded the highest (4.9 t/ha) and were followed by Burt (4.4 t/ha). Kernels from a single  $Rht$  allele from Norin 10 and Suwon 92 dwarfing sources were 20 and 5% lighter, respectively than Burt. Lines with both  $Rht_1$  and  $Rht_2$  from Norin 10 and Suwon 92 sources produced 27 and 24% lighter kernels, respectively when compared to Burt. Again, lines with both dwarfing genes had about 12% fewer kernels/spike than Burt. Those with either  $Rht_1$  or  $Rht_2$  alleles were similar in kernels/spike to Burt.

Pinthus and Levy (1983) conducted a study with  $F_5$  and  $F_6$  generations obtained from three crosses involving four parents differing in  $Rht$  alleles. Two of the parents had  $Rht_2$  and a high grain weight. The two parents with  $Rht_1$  had a lower grain weight. They classified the segregates into tall, semidwarf and dwarf height levels based on the GA-sensitivity test. They observed that the dwarf lines ( $Rht_1Rht_2$ )

yielded significantly less than either of the semidwarf lines ( $Rht_1rht_2$  or  $rht_1Rht_2$ ). In most cases, both semidwarf lines yielded less than the tall genotype ( $rht_1rht_2$ ). The lines with the  $Rht_1rht_2$  genotype were significantly higher yielding than  $rht_1Rht_2$ . They pointed out that the yield difference among the three height groups was primarily attributed to grain weight rather than number of grains/spike. The yield superiority of the tall lines over the semidwarf lines indicated that the  $rht$  alleles may have favourable effects on grain yield. The authors concluded that whether these effects were due to these alleles per se (through pleiotropy or close linkage with favourable genes) or physiological factors associated with culm length or with GA sensitivity remains to be investigated. They suggested that tall genotypes in a wheat breeding program should not be discarded. In another study, Pinthus and Levy (1984) found that the genotype  $Rht_1rht_2$  and  $rht_1Rht_2$  did not produce any significant difference in grain weight, although both were exceeded by the tall genotype,  $rht_1rht_2$ . Of course, the semidwarf lines had higher grain weight when compared to the double dwarf ( $Rht_1Rht_2$ ).

In crosses between tall and dwarf wheat cultivars, followed by selection for homozygous tall and homozygous dwarf in  $F_3$  and  $F_4$  generations, Sharma et al (1983) observed that the tall parents and homozygous tall lines were statistically superior in grain yield per plant when compared to the short statured plants. Although under plot testing, the  $Rht_1$  and  $Rht_2$  semidwarfs yielded more than the tall and the  $Rht_3$  dwarfs. They interpreted this situation as an indicative of association with a higher number of spike-bearing tillers/ $m^2$  in case of semidwarf plants. The authors suggested that the "tall dwarfs", were

better yielders in plot tests than the tall and dwarfs. They found a significant increase in number of spikes/plant using  $Rht_1$  and  $Rht_3$ , while  $Rht_2$  gave a significant increase in number of grains/spike.

Joppa (1973) while studying several tall and semidwarf near-isogenic lines of durum wheat possessing Norin 10  $Rht$  alleles, observed that the semidwarf lines almost always headed one day later than their tall counterparts. Also, they produced more seed bearing culms which tended to be compensated for by their decreased kernel weight. The tall lines had higher test weight and kernel weights than the semidwarfs. Correlations between plant height, and test weight and kernel weight were positive for both semidwarf and tall lines. He noticed that the taller semidwarfs produced significantly higher yields indicating a positive correlation between plant height and grain yield in the semidwarfs. In the tall group, height and grain yield were negatively associated.

In an investigation of homozygous  $F_3$  lines for  $Rht_1$  and  $rht_1$  from two tall X semidwarf tetraploid wheat crosses, Gale et al (1981) observed that the  $Rht_1$  lines on average were 40 cm shorter than the  $rht_1$  counterparts. The semidwarfs produced lower kernel yields due mainly to reduced grain weight, but had a higher tiller number than the taller genotypes. There were significant positive correlations between plant height and grain yield, kernel weight, and kernel number. This suggested that that selection for "tall dwarfs" might give an overall increase in yield by increasing both grain weight and grain number per spike in tetraploid wheats.

Grain weight of the tall  $F_6$  line from a cross between a semidwarf and a tall cultivar was significantly higher than the

corresponding semidwarf lines. Also, the number of grains per spike and grain yield of primary tillers were significantly lowered in the semidwarf plants. However, no significant difference in grain yield was obtained between the F<sub>6</sub> progenies of semidwarf and tall plants as reported by Pinthus (1983). Apart from reducing plant height itself, the Rht alleles caused an increase in spikelet fertility of 20 percent and a decrease in grain size of about the same magnitude when compared to their rht counterpart, as reported by Gale and Youssefian (1983). In this study on isolines developed with either Rht or rht alleles, they also obtained an increased tiller number due to Rht genes. However, they mentioned that environmental factors can modify the grain yield and yield related traits while using 'Norin 10' sources.

#### RELATIONSHIP BETWEEN GRAIN YIELD, HARVEST INDEX AND BIOLOGICAL YIELD

Harvest index (HI), the ratio of grain yield to biological yield, has received renewed attention in cereal breeding. Donald (1968) stated that "higher wheat grain yields can be achieved only by either increasing biological yield with a sustained harvest index, or by increasing harvest index alone". Wallace et al (1972) contended that "harvest index is an important aspect of differential partitioning of photosynthate and that improved HI represented an increased physiological capacity of the crop to mobilize photosynthate and translocate it to the organs of economic value".

Donald and Hamblin (1976) proposed the following mathematical formula for grain yield, harvest index and biological yield.

$$(a+b) \times a/(a+b) = a$$

$$Y_{\text{bio}} \times \text{H.I.} = Y_{\text{gr.}}$$

where, 'a' is the grain yield; and 'b' is the yield of vegetative parts. According to the authors, "it is more frequent to find stronger positive correlation between grain yield and biological yield than that between grain yield and harvest index in a segregating population". The authors postulated that "reduction in plant height, appears to lead an increased harvest index through a reduction in the weight of vegetative parts and through a direct contribution to the grain production. However, breeding for higher harvest index is not always a useful approach to higher grain yields, rather higher biological yield should be combined with higher harvest index to maximize grain yield".

Jain and Kulshrestha (1976) worked with four groups of wheat (tall, T; semidwarf, D<sub>1</sub>; dwarf, D<sub>2</sub>; and very dwarf, D<sub>3</sub>) using Norin 10 dwarfing sources. The tall cultivars, as a group, differed from the three dwarf groups in respect of HI, number of effective tillers and grain weight. There was a continued increase in HI with the decrease in plant height, with exception of insignificant difference between D<sub>1</sub> and D<sub>2</sub> classes. The dwarf groups of cultivars showed higher HI values than the tall type indicating that the Norin 10 genes are better able to partition the dry matter in a more favourable direction in respect of grain yield. This suggests that the Norin 10 genes are physiologically more efficient from the standpoint of crop production. In general, they obtained positive correlations between grain yield and HI, number of effective tillers, and number of grains per primary spike. Plant height was significantly and positively correlated with grain yield. There was also a positive association between HI and number of effective tillers.

Since grain yield is the product of biological yield and HI, the authors suggested that the strategy for higher grain yield in wheat should be to select for greater dry matter production, while maintaining the high HI value.

Allan (1983) studied seven near-isogenic lines, developed following backcrossing to six different normal height cultivars. Each isogenic line represented three distinct culm height phenotypes referred to short (two-gene semidwarf), medium (one-gene semidwarf) and tall (no semidwarf gene). He found that the mean values for HI, when calculated across 11 tests locations and nine populations, for the two-gene semidwarf, one-gene semidwarf and normal height lines were 41.4, 38.0 and 31.6, respectively. The two and one-gene semidwarf doses increased HI by 31 and 20% respectively over the tall height class. He obtained a positive correlation between grain yield and HI and a negative relationship between HI and culm length. Based on simple correlations, the use of HI as a selection criteria for grain yield appeared to be more feasible among the taller parents than for the semidwarf types. Although the author obtained highest HI value in a two-gene semidwarf level, he pointed out that most two-gene semidwarfs have lower biological yield, and therefore it is difficult to combine high HI with higher biological yields, as suggested by Donald and Hamblin (1976). Finally, Allan (1983) mentioned that populations with relatively tall backgrounds and low HI were proportionately more benefited for HI by inclusion of one or two doses of semidwarfing genes than populations derived from shorter height backgrounds and relatively high HI values.

In a study of  $F_2$  and  $F_3$  lines from crosses involving two

parents with low (34-35%) and two parents with high (42-45%) HI values, Bhatt (1977) obtained a larger positive correlation between grain yield and HI in  $F_3$  than in the  $F_2$  generation. Also, selection for low HI in the  $F_2$  gave plants with low HI in the  $F_3$ . Those plants selected for high HI in  $F_2$  segregated for high and medium HI in the  $F_3$ . Based on these results, he suggested more selection pressure be applied for high HI and reject the low HI segregates in the  $F_2$ . He further pointed out that selection for yield indirectly through HI was better than direct selection for grain yield per se. The correlation coefficient between plant height and grain yield was positive and highly significant in both  $F_2$  and  $F_3$  generations. Associations between plant weight and HI were always negative and highly significant in all but few cases. Relationships between grain yield and HI were positive in both  $F_2$  and  $F_3$  generations.

Bhatt and Derera (1978) studied 15 near-homozygous lines ( $F_5$ - $F_7$ ) selected from 46 spring wheat crosses. The lines selected for grain yield based on high, medium and low harvest indexes, performed similarly during 1976. The ranking closely reflected the grain yield performance as well. There were significant positive correlations between grain yield and HI within and over years.

Snape and Parker (1984) conducted a trial with  $Rht_2$  and  $rht_2$  alleles. They observed that  $Rht_2$  gene reduced plant height and the vegetative yield thereby raising the HI value. This however, did not make a significant difference in the yielding ability of the two groups. They noticed that  $Rht_2$  gene increased the number of grains per spike, but this was offset by a corresponding decrease in grain weight. Thus,  $Rht_2$  gene reduced the nonproductive and not the productive



component of biomass. As a consequence, HI increases were realized without a change in grain yield. They found high positive correlations between biological yield and plant height, and spike number/plant and grain yield /plant for both dwarf and tall height groups, separately. Harvest index showed a negative correlation with biomass, particularly in case of *rht<sub>2</sub>*-allele bearing tall plants; although in neither case was it significant. They obtained correlation coefficients of 0.92 and 0.83 between grain and vegetative yield for *Rht<sub>2</sub>* and *rht<sub>2</sub>* lines, respectively, indicating that larger plants have higher grain and vegetative yield. This suggests that selection for increased biomass will also increase grain yield potential.

A significant negative association between plant height and HI was obtained by Sapiro and Hughes (1977) while studying 17 triticale, three wheat and three rye lines. Also they noticed that HI was positively correlated with 1000-kernel weight, grain yield and seed set percentage, but resulted in a negative association with biological yield. Moreover, they found a positive correlation between grain yield and plant dry weight, indicating that selection based on grain yield alone would also retain lines with a high biological yield.

Syme (1970) conducted a trial with nine wheat cultivars across five locations. The trial included six Australian, one German (Opal), one Mexican (Mexico 120), and a semidwarf selection (WW15) from Norin 10/Brevor 14 from Mexico. The cultivar WW15 was 67cm in height compared to Mexico 120 which was 50cm. All others ranged from 73 to 98cm. WW15 gave the highest yield/ha with a HI value of 0.39. Mexico 120 was the second highest cultivar both in respects of grain yield and HI, and was followed by Wren, a Australian cultivar with a height of 73cm giving

the third highest yield. For all cultivars, the mean grain yield was highly correlated with mean HI value. Association between HI and grain yield accounted for 92% of the variation in grain yield. Grain yield was negatively correlated with culm length, 1000-kernel weight and date of spike emergence in all cultivars.

Singh and Stoskopf (1971) conducted a study with 100 winter wheat lines along with two check cultivars ('Genesee' and 'Talbot'), and found a wide range of variation in HI. The presence of genetic variability and a positive correlation between HI and grain yield suggested the possibility of improving the HI genetically and thereby increasing grain yield. Also, a negative correlation between plant height and HI in winter wheat indicated that HI can be improved by reducing plant height. They mentioned that reduced plant height lowered the dry weight of the vegetative parts of plants thereby giving low straw yield which was reflected in an increased HI. The dwarf lines of winter wheat therefore had a higher HI value (0.42) than the taller lines (0.38) and checks (0.36). The dwarf lines (58 cm) had 45% less dry stem weight and a 18% higher HI than the checks (113 cm); and the taller lines (86 cm) had 21% less dry stem weight and a 7% higher HI value than the checks.

In a study with  $F_1$  and  $F_2$  generations of eight wheat crosses, Bhatt (1976) found that the  $F_1$  mean values were closer to the high HI parent suggesting partial dominance in the expression of HI values. The  $F_2$  means were between the midparent and high HI parent confirming the partial dominance nature of the gene action for high HI. Based on high broad sense heritability estimates together with high genetic coefficient of variation, the author noted that large gains from

selection could be made by selecting plants with high HI values in two out of the eight crosses.

Inheritance of HI was studied by Gill et al (1980) in parental, F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub> and F<sub>4</sub> populations of three wheat crosses involving five parents of varying HI values. An additive-dominance model was suggested as the mode of inheritance for HI. A strong positive correlation between HI and grain yield was obtained by the authors, who commented that HI should be given more emphasis as a selection criteria than the yield alone.

Loffler and Busch (1982) provided results which showed that harvest index and biological yield were positively correlated with grain yield. Moreover, biological yield was highly correlated with days to heading and days to maturity thereby giving an indication that selection for higher biological yield to improve grain yield would result in lengthening the duration of the crop cycle.

Austin et al (1980) found greater biomass weights in four old cultivars having no Rht<sub>2</sub> allele compared to four modern wheat cultivars with the Rht<sub>2</sub> allele. The authors noted that one reason for high yield in semidwarf wheats was the increase in the number of grains/spikelet (3.18), compared to the older cultivars (2.50). Moreover, a reduction in stem height by 50% was accompanied by a reduction in stem weight by about one-third. Harvest index showed positive and negative correlations with yield and plant height, respectively. The HI values in case of semidwarf wheats were higher (48-51%) when compared to the non-semidwarfs (34-36%). Straw yields were negatively correlated with grain yield.

Different explanations have been put forward by different authors regarding effects of Norin 10 dwarfing genes on yield and yield traits. Many authors reported higher harvest index associated with the semi- and more truly with the double dwarfing genes, but they did not obtain any increase in biological yield. However, grain yield was more often related with harvest index. In the present investigation, an approach was taken to relate plant height as exhibited through harvest index and biological yield influencing grain yield.

## MATERIALS AND METHODS

The parental lines for this investigation consisted of four near-isogenic lines from the cross 'Itana'/3/'Norin 10'/'Brevor'14//\*Itana and Yamhill Dwarf. The latter is a soft white winter wheat selection from the cross Alba/Heines VII. In addition, the  $F_1$ ,  $F_2$ ,  $F_3$ , and reciprocal backcross populations resulting from the Yamhill Dwarf crossed to each of the isolines were obtained. The four isolines represent three height classes. These consisted of the standard height ( $rht_1rht_2$ ), two semidwarfs ( $rht_1Rht_2$  and  $Rht_1rht_2$ ), and the double dwarf ( $Rht_1Rht_2$ ). A more detailed description of the parental materials is presented in Appendix Table 1.

The experimental populations were planted in a complete randomized split plot design with three replications during the 1985-86 season. Main plots were represented by the four crosses, and the seven generations were treated as subplots. In the cross Yamhill Dwarf/ $rht_1rht_2$ , the  $F_1$  was omitted due to lack of seed. The experimental subplots comprised of single row(s) for the parent(s) and  $F_1$ 's, five rows for the  $F_2$ 's, ten rows for the  $F_3$ 's, and two rows each for backcrosses. Ten kernels were planted per row. A space of 25 cm was used between rows and between plants. To avoid a border effect, each block was surrounded by barley plants. Missing plants within the experimental plots were resown with Yamhill Dwarf in order to maintain uniform competition.

The experiment was conducted at the Hyslop Agronomy Farm which is located 11 km northeast of Corvallis, Oregon. The farm is located at latitude  $44^{\circ} 30'N$  and longitude  $123^{\circ} 30'W$  with an elevation of 68 m

above the sea level. The soil type is a fine, silty mixed mesic aquultic argixeroll. Urea-sul (40N-0P-0K-6S) was applied 15 days before planting at the rate of 60 kg/ha of Nitrogen and 7.5 kg/ha of sulfur. The same fertilizer and rate were topdressed on March 21, 1986 to increase the fertility status of the soil.

The experimental materials were planted on October 19, 1985. The F<sub>1</sub>'s were transplanted on January 2nd, 1986 from the greenhouse. To control leaf rust (*Puccinia recondita*) and septoria leaf blotch (*Septoria tritici*), Propiconazole, 1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1H-1,2,4-triazole was sprayed twice in the spring. Plots were hand-weeded during the season. Plants were harvested on July 25, 1986.

Data were obtained on a per plant basis for the following traits: Heading Date was obtained by recording the number of days from planting to the date when the spike of the main tiller was 50% beyond the auricles of the flag leaf.

Flowering Date was noted when more than 50% of the anthers from the spike of the main tiller were visible.

Maturity Date was recorded when the spike and the peduncle of the main tiller had reached physiological maturity as evidenced by their loss of green color.

Biological Yield was obtained by cutting at base of the plant and included the weight of the grain and straw.

Plant Height was obtained by measuring (in cm) from the base of the crown to the base of the spike-bearing first primary tiller.

Tiller Number was counted as the number of productive tillers i.e., culms bearing fertile spikes.

Spikelets Per Spike were obtained from five randomly selected spikes from individual plants, followed by counting the total number of spikelets and dividing by five.

Grains Per Spikelet were obtained from the randomly selected five spikes which were threshed using a single-head thresher. The total number of grains obtained was divided by the number of spikelets counted in the five spikes.

300-Grain Weight was determined by weighing a random sampling of 300 grains from individual plants. Counting was done by the Seed Counter and weight was obtained by an Electric Balance.

Grain Yield was the total weight in grams of the cleaned seed from each plant.

Harvest Index expressed as percentage, was calculated as the ratio of the grain yield per plant to the weight of the whole plant excluding roots.

Due to the lack of  $F_1$  seed for one cross, two analyses of variance were used. The first analysis involved all generations omitting one cross. While the second included all four crosses but excluding the  $F_1$  populations. First analysis (called 'Type-B') had three crosses and seven generations, and the latter (called 'Type-A') had four crosses and six generations. Orthogonal contrasts were conducted for five traits, which were significant for crosses. For generations, mean, range and standard deviation values were calculated for all eleven traits measured in the four crosses.

Heterosis and Inbreeding Depression values (in percentage) were obtained using mid parent (MP),  $F_1$  and  $F_2$  mean for all the eleven characters studied. The formulae, as outlined by Fehr (1986), are given

below.

$$\text{Heterosis} = \frac{F_1 - MP}{MP} \times 100$$

(for any specific trait and a specific cross)

$$\text{Inbreeding Depression} = \frac{F_1 - F_2}{F_1} \times 100$$

(for any specific trait and a specific cross)

Broad- and Narrow-sense heritability estimates were computed using methods as described by Weber and Moorthy (1952), and Warner (1952).

$$H_{B.S.} = \frac{V_{F_2} - V_E}{V_{F_2}} \times 100$$

$$= \frac{V_{F_2} - \frac{V_{P_1} + V_{P_2} + V_{F_1}}{3}}{V_{F_2}} \times 100$$

Where, 1)  $V_{F_2}$  is the total  $F_2$  variance for a character, X; and  $V_{F_2}$  for any given trait =  $V_G + V_E$ ; when

2)  $V_G$  and  $V_E$  are the variances due to genotypic and environmental portions respectively, for the expression of the character, X;

3)  $V_E$ , the environmental variance was calculated from the parental and  $F_1$  values.



$$\begin{aligned}
 H_{N.S.} &= \frac{V_{F_2} - \frac{V_{F_1P_1} + V_{F_1P_2}}{2}}{V_{F_2}} \times 100 \\
 &= \frac{D}{V_{F_2}} \times 100
 \end{aligned}$$

Where, 1)  $V_{F_2}$  is the total  $F_2$  variance for the character,  $X$ ; and

2) 'D' is the additive genetic component of variance calculated by subtracting the total within variance of the backcrosses of  $F_1$  to both parents from the total  $F_2$  variance for the character in study.

Phenotypic correlations ( $r$ ) among traits were computed for the parents. Coefficients of determination ( $R^2$ ) were calculated for the crosses for some of the selected traits.

## RESULTS

The results of this investigation will be divided into three sections. Information gained from the analysis of variance including means, ranges and standard deviations for the eleven traits studied will be provided for crosses and generations. Estimates of the nature of gene action controlling the traits will then be presented followed by an examination of the possible associations between selected traits.

### Analysis of Variance

The results from the analysis of variance where the  $F_1$  generations were excluded for crosses and generations are presented in Table 1. For crosses, differences were observed for days to heading and maturity, plant height, 300-kernel weight and spikelets per spike. Differences were noted for all eleven traits when generations are considered. A cross X generation interaction was observed for all traits except tiller number, grain yield and kernels per spikelet.

When all populations are considered, including the  $F_1$ 's for three crosses, differences were found only for plant height and spikelets per spike; however differences for generations were detected for all eleven traits measured (Table 2). A cross X generation interaction was detected for all traits except grain yield, biological yield, spikelets per spike and kernels per spikelet.

In both analyses, the coefficient of variation values were high for grain yield, biological yield and tiller number and low for the

Table 1. Mean Squares from 'Type-A' ANOVA for 11 traits involving parental, F<sub>2</sub>, F<sub>3</sub> and backcross populations of crosses between Yamhill Dwarf and four isolines for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Sources	df	Days to heading	Days to flowering	Days to maturity	Plant Height (cm)	Tiller Number	Grain Yield (g)	300-Kernel Weight (g)	Biological Yield (g)	Spikelet per Spike	Kernel per Spikelet	Harvest Index (%)
Cross	3	9.35*	0.72	32.84**	1286.30**	3.14	79.70	2.33*	1487.99	16.64**	0.06	26.33
Error (A)	6	1.44	1.76	3.49	34.83	25.33	115.86	0.42	592.36	0.33	0.03	6.81
Generation	5	11.03**	3.99**	86.94**	1359.68**	109.29**	313.66**	12.88**	787.68*	20.34**	0.17**	62.52**
Cross X Gener.	15	2.57**	1.32**	12.00**	341.76**	3.44	51.21	0.54**	484.94	1.71**	0.02	7.93**
Error (B)	40	0.39	0.43	2.08	9.43	5.13	62.55	0.16	320.67	0.56	0.02	2.25
CV (%)		0.40	0.41	0.74	3.30	10.94	15.10	3.30	13.76	3.32	4.20	3.73

\*, \*\* = Significant at 0.05 and 0.01 levels, respectively.

'Type-A' ANOVA was conducted with four crosses and six generations in split-plot design.

Table 2. Mean Squares from 'Type-B' ANOVA for 11 traits involving parental, F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub> and backcross populations of crosses between Yamhill Dwarf and four isolines for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Sources	df	Days to heading	Days to flowering	Days to maturity	Plant Height (g)	Tiller Number	Grain Yield (g)	300-Kernel Weight (g)	Biological Yield (g)	Spikelets per Spike	Kernels per Spikelet	Harvest Index (%)
Cross	2	2.16	0.70	32.82	611.14**	19.68	10.80	0.45	316.82	14.94**	0.13	13.37
Error (A)	4	2.74	0.81	6.19	45.68	16.82	76.18	0.36	486.67	0.21	0.04	7.47
Generation	6	5.41**	2.43**	36.21**	493.83**	83.98**	235.32**	9.09**	660.19*	8.97**	0.10**	30.63**
Cross X Gener.	12	3.04**	1.62**	9.53**	230.85**	9.62*	41.17	0.55**	413.45	1.23	0.02	6.71**
Error (B)	36	0.40	0.44	2.37	8.71	4.55	59.20	0.16	281.53	0.63	0.02	2.62
CV (%)		0.40	0.41	0.79	3.26	10.17	14.73	3.39	13.21	3.48	4.24	3.95

\*, \*\* = Significant at 0.05 and 0.01 levels, respectively.

'Type-B' ANOVA was conducted with three crosses and seven generations in split-plot design.

other traits.

#### Orthogonal Contrasts for Crosses

Orthogonal contrasts between different combinations of the four crosses for five traits are found in Table 3. Days to maturity differed between cross II and cross III. Differences were also noted for days to maturity, plant height and spikelets per spike when cross II and cross III are contrasted with cross I involving the double dwarf. When cross IV is contrasted with the other three crosses (cross I/cross II/cross III), differences were observed for all five traits. Similar results are reflected also in the Appendix Table 3 where the mean values are provided for the eleven traits involving all four crosses.

#### Mean values, Ranges and Standard Deviations

With the exception of the  $F_1$  generation for cross IV and the parents, the mean values, ranges and standard deviations for the eleven traits measured for crosses and generations can be observed in Tables 4-14.

For both heading, flowering and maturity dates, significant interactions between crosses and generations were observed (Table 1). Such interactions are also apparent in Tables 4, 5 and 6, respectively for these traits. In general, the greatest variability as noted from the ranges can be seen in the  $F_2$  and  $F_3$  generations.

Since the different isolines differed in their dwarfing genes, plant height is of special interest. Differences for crosses, generations and interaction between crosses and generations were

Table 3. Orthogonal contrasts showing sum of squares for five traits from crosses involving four isolines and Yamhill Dwarf for the experiment conducted at the Hyslop Agronomy Farm during 1985-86 1/

Contrasting Crosses <u>2/</u>	Days to heading	Days to maturity	Plant height (cm)	300-kernel weight (g)	Spikelets per spike
1. C-II Vs. C-III	1.18	8.43*	3.50	0.01	3.38
2. C-II/C-III Vs.C-I	0.22	47.28**	1069.67**	0.88	14.60**
3. C-IV Vs. C-II/ C-III/C-I	26.66**	42.80**	2785.72**	6.09*	31.93**

1/ = Taken from 'Type-A' ANOVA, where 5 traits were significant.

\*, \*\* = Significant at 0.05 and 0.01 levels, respectively.

2/ Cross I =  $Rht_1Rht_2$ /Yamhill Dwarf ( $Rht_1$ )  
 Cross II =  $Rht_1rht_2$ /Yamhill Dwarf ( $Rht_1$ )  
 Cross III =  $rht_1Rht_2$ /Yamhill Dwarf ( $Rht_1$ )  
 Cross IV =  $rht_1rht_2$ /Yamhill Dwarf ( $Rht_1$ )

Table 4. Mean, range and standard deviation for Days to Heading in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	156.61	156.27	154.88	
	R	153.00-160.00	151.00-160.00	151.00-158.00	
	S.D.	1.77	2.31	1.92	
$F_2$	M	156.19	156.84	155.95	154.45
	R	151.00-167.00	149.00-169.00	151.00-168.00	145.00-167.00
	S.D.	3.05	3.55	3.40	3.27
$F_3$	M	157.02	157.82	155.95	156.21
	R	150.00-169.00	149.00-169.00	148.00-168.00	147.00-165.00
	S.D.	3.62	3.44	3.40	3.21
$F_1P_1$	M	155.90	156.13	155.73	154.30
	R	152.00-162.00	151.00-161.00	151.00-164.00	148.00-161.00
	S.D.	2.38	2.72	2.87	2.61
$F_1P_2$	M	156.59	156.55	159.36	156.04
	R	152.00-161.00	150.00-170.00	153.00-168.00	152.00-160.00
	S.D.	2.38	3.04	4.19	2.33

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub>= 156.73; Rht<sub>1</sub>rht<sub>2</sub>= 155.52; rht<sub>1</sub>Rht<sub>2</sub>= 154.71; rht<sub>1</sub>rht<sub>2</sub>= 153.38; and Yamhill Dwarf= 158.00(cross I); 158.03(cross II); 156.48(cross III); 157.17(crossIV).

Table 5. Mean, range and standard deviation for Days to Flowering in F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub> and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
F <sub>1</sub>	M	161.08	161.00	160.08	
	R	157.00-163.00	157.00-163.00	156.00-164.00	
	S.D.	1.67	1.83	2.16	
F <sub>2</sub>	M	160.60	161.21	160.70	160.34
	R	156.00-168.00	152.00-169.00	156.00-168.00	153.00-169.00
	S.D.	2.30	2.85	3.07	2.64
F <sub>3</sub>	M	161.38	161.54	160.90	161.09
	R	155.00-175.00	156.00-171.00	153.00-171.00	154.00-169.00
	S.D.	2.98	2.35	3.22	2.80
F <sub>1</sub> P <sub>1</sub>	M	160.56	160.63	160.15	159.83
	R	157.00-164.00	155.00-167.00	156.00-166.00	155.00-166.00
	S.D.	1.94	2.20	2.44	2.79
F <sub>1</sub> P <sub>2</sub>	M	160.74	161.32	163.32	161.07
	R	156.00-164.00	156.00-168.00	158.00-168.00	157.00-164.00
	S.D.	1.86	2.63	2.36	1.77

M = mean; R = range; S.D. = standard deviation; F<sub>1</sub>P<sub>1</sub> = backcross to isoline parent and F<sub>1</sub>P<sub>2</sub> = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub>= 160.70; Rht<sub>1</sub>rht<sub>2</sub>= 160.59; rht<sub>1</sub>Rht<sub>2</sub>= 159.92; rht<sub>1</sub>rht<sub>2</sub>= 160.00; and Yamhill Dwarf= 161.81(cross I); 161.64(cross II); 160.32(cross III); 161.70(cross IV).



Table 6. Mean, range and standard deviation for Days to Maturity in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	197.08	194.27	196.44	
	R	183.00-203.00	189.00-199.00	194.00-202.00	
	S.D.	3.78	2.91	1.94	
$F_2$	M	194.84	193.37	195.46	192.59
	R	184.00-208.00	164.00-203.00	185.00-205.00	182.00-203.00
	S.D.	5.22	6.13	4.31	5.35
$F_3$	M	194.96	196.02	194.55	195.27
	R	183.00-207.00	185.00-204.00	182.00-207.00	181.00-206.00
	S.D.	5.35	4.44	4.68	5.20
$F_1P_1$	M	196.24	192.94	195.03	190.91
	R	189.00-203.00	186.00-202.00	184.00-200.00	183.00-201.00
	S.D.	3.36	3.92	3.42	4.41
$F_1P_2$	M	196.19	194.00	197.92	196.38
	R	186.00-203.00	184.00-200.00	195.00-205.00	187.00-203.00
	S.D.	3.64	4.35	2.12	3.78

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub>= 196.50; Rht<sub>1</sub>rht<sub>2</sub>= 188.93; rht<sub>1</sub>Rht<sub>2</sub>= 188.93; rht<sub>1</sub>rht<sub>2</sub>= 186.00; and Yamhill Dwarf= 199.21(cross I); 197.52(cross II); 197.24(cross III); 198.20(cross-IV).

detected (Table 1). In Table 7, it can be observed that the greatest variation was observed for the  $F_2$  and  $F_3$  populations involving cross II. This is surprising since this cross involved the isoline  $Rht_1rht_2$  and Yamhill Dwarf. The latter cultivar is thought to also carry the  $Rht_1$  dwarfing gene. Thus it would be anticipated that less variability for plant height would be found in segregating populations for this cross. A similar situation was noted in the backcross population  $F_1P_2$  where Yamhill Dwarf was the recurrent parent.

In Table 8, a comparison for crosses and generations is made for tiller number. Since no differences were detected for crosses (Table 1), only generations are considered. As can be seen in the backcross population  $F_1P_2$ , where Yamhill Dwarf was the recurrent parent, the mean values and the ranges were small suggesting that the low tiller number capacity of the Yamhill Dwarf was passed on to the progeny. No consistent trends for this trait can be observed between other generations.

Differences for grain yield were noted only between generations (Table 1). When the generations were compared, the  $F_2$  generation resulting from the cross I and the backcross generation  $F_1P_2$  in cross IV had the highest mean values and the greatest ranges. In contrast, the backcross generation,  $F_1P_1$  constantly had lower mean values and a smaller range of grain yield (Table 9).

For 300-kernel weight, differences were noted for both crosses, generations and the interaction (Table 1). In Table 10, cross IV consistently had the highest mean values for kernel weight. When generations are noted, the backcross generation  $F_1P_2$  had the highest

Table 7. Mean, range and standard deviation for Plant Height (cm) in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	90.96	96.91	101.80	
	R	73.00-110.00	87.00-106.00	76.00-120.00	
	S.D.	9.11	5.38	12.3	
$F_2$	M	91.03	91.49	94.51	101.63
	R	45.00-137.00	50.00-124.00	59.00-123.00	68.00-131.00
	S.D.	17.40	17.14	13.32	13.12
$F_3$	M	89.30	82.90	97.17	96.32
	R	49.00-127.00	47.00-130.00	69.00-130.00	58.00-131.00
	S.D.	16.86	18.85	12.00	14.56
$F_1P_1$	M	84.50	99.57	99.15	117.32
	R	55.00-156.00	68.00-127.00	83.00-114.00	43.00-139.00
	S.D.	15.73	13.70	7.34	15.59
$F_1P_2$	M	86.00	96.70	81.52	93.00
	R	61.00-112.00	62.00-125.00	71.00-97.00	75.00-115.00
	S.D.	11.12	15.42	6.82	11.18

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 73.37; Rht<sub>1</sub>rht<sub>2</sub> = 110.48; rht<sub>1</sub>Rht<sub>2</sub> = 109.68; rht<sub>1</sub>rht<sub>2</sub> = 138.11; Yamhill Dwarf = 75.71 (cross I); 75.17 (cross II); 76.83 (cross III); 77.80 (cross IV).

Table 8. Mean, range and standard deviation for Tiller Number in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	20.46	20.18	28.00	
	R	7.00-41.00	10.00-31.00	12.00-39.00	
	S.D.	7.38	5.53	7.06	
$F_2$	M	23.36	21.80	23.60	21.44
	R	7.00-51.00	5.00-43.00	6.00-53.00	9.00-56.00
	S.D.	8.45	7.43	8.59	8.42
$F_3$	M	19.28	20.02	21.98	21.14
	R	4.00-48.00	6.00-43.00	6.00-47.00	9.00-52.00
	S.D.	6.95	5.85	7.30	6.79
$F_1P_1$	M	24.20	23.32	23.68	23.15
	R	10.00-41.00	8.00-39.00	9.00-43.00	9.00-45.00
	S.D.	7.09	6.14	7.70	8.25
$F_1P_2$	M	16.38	17.60	20.32	19.07
	R	7.00-32.00	5.00-29.00	8.00-34.00	5.00-39.00
	S.D.	5.71	5.54	7.72	9.26

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isolate parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 22.80; Rht<sub>1</sub>rht<sub>2</sub> = 24.00; rht<sub>1</sub>Rht<sub>2</sub> = 21.71; rht<sub>1</sub>rht<sub>2</sub> = 23.92; and Yamhill Dwarf = 16.04 (cross I); 15.45 (cross II); 15.65 (cross III); 16.50 (cross IV).

Table 9. Mean, range and standard deviation for Grain Yield (gm) in F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub> and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
F <sub>1</sub>	M	56.52	55.47	59.37	
	R	22.00-122.00	27.10-77.80	17.60-84.00	
	S.D.	24.34	15.00	18.55	
F <sub>2</sub>	M	61.66	51.78	58.12	59.08
	R	15.30-145.00	16.60-107.00	15.30-134.50	14.80-126.70
	S.D.	27.71	21.76	26.86	25.51
F <sub>3</sub>	M	49.24	49.20	54.52	50.94
	R	15.40-136.00	14.80-104.00	15.00-126.00	15.30-113.70
	S.D.	20.20	18.70	23.15	18.31
F <sub>1</sub> P <sub>1</sub>	M	47.77	49.30	49.30	45.53
	R	14.70-85.00	16.30-88.90	23.40-121.90	18.30-99.50
	S.D.	17.08	17.28	21.07	19.19
F <sub>1</sub> P <sub>2</sub>	M	55.30	58.68	61.00	63.77
	R	19.70-118.00	18.10-105.00	15.90-109.60	14.60-142.00
	S.D.	22.13	21.39	30.05	32.17

M = mean; R = range; S.D. = standard deviation; F<sub>1</sub>P<sub>1</sub> = backcross to isoline parent and F<sub>1</sub>P<sub>2</sub> = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub>= 40.09; Rht<sub>1</sub>rht<sub>2</sub>= 48.01; rht<sub>1</sub>Rht<sub>2</sub>= 47.34; rht<sub>1</sub>rht<sub>2</sub>= 53.00; and Yamhill Dwarf= 52.68(cross I); 48.47(cross II); 45.53(cross III); 58.26(cross IV).

Table 10. Mean, range and standard deviation for 300-Kernel Weight (gm) in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	12.60	12.68	12.82	
	R	11.00-13.90	11.70-14.20	9.40-14.10	
	S.D.	0.93	0.59	0.88	
$F_2$	M	11.80	11.59	12.34	13.08
	R	7.70-14.70	7.80-14.90	8.40-14.30	9.60-16.20
	S.D.	1.38	1.42	1.21	1.31
$F_3$	M	11.90	11.46	12.24	12.25
	R	7.30-16.90	8.00-15.40	8.00-16.00	7.40-16.80
	S.D.	1.51	1.40	1.28	1.28
$F_1P_1$	M	10.90	11.27	11.78	12.26
	R	7.70-13.60	8.90-13.20	10.50-13.30	10.50-15.20
	S.D.	1.20	0.95	0.78	0.94
$F_1P_2$	M	13.40	13.69	13.02	14.08
	R	9.10-16.70	11.60-16.30	10.10-14.30	11.50-16.70
	S.D.	1.45	1.13	1.11	1.15

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 9.52; Rht<sub>1</sub>rht<sub>2</sub> = 10.84; rht<sub>1</sub>Rht<sub>2</sub> = 10.56; rht<sub>1</sub>rht<sub>2</sub> = 10.94; Yamhill Dwarf = 12.79(cross I); 12.95(cross II); 12.25(cross III); 12.81(cross IV).

mean yields across all crosses. The greatest ranges were observed for the  $F_3$  generation.

As noted in Table 1, differences in biological yield were detected only for generations. Even though there is considerable variability for the values presented for biological yield, the  $F_2$  and  $F_1P_2$  generations tended to have higher mean values, greater ranges and higher standard deviations (Table 11).

Spikelets per spike were found to be different among crosses, generations and for the interaction (Table 1). With the exception of the  $F_3$  populations, the mean values associated with cross I were the highest (Table 12). For generations, the backcross population  $F_1P_2$  tended to have higher mean values. In general, the  $F_2$  generation had greater ranges and higher standard deviations.

Differences for kernels per spikelet were observed only for generations (Table 1). As presented in Table 13, considerable variability exists between generations for this trait, however the backcross population  $F_1P_2$  tended to have higher mean values when compared to other segregating generations. In three of the crosses, a greater range can be observed for the  $F_3$  generation for kernels per spikelet than in other generations.

Harvest index differences were detected for generations and a significant interaction between crosses and generations was also observed (Table 1). In Table 14, the interaction between crosses and generations is quite apparent. With the exception of the  $F_1$  for cross I, the backcross generation  $F_1P_2$  had the highest mean values. The greatest ranges were found for the  $F_3$  generations in crosses III and IV

Table 11. Mean, range and standard deviation for Biological Yield (gm) in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	128.61	127.00	145.88	
	R	45.00-240.00	67.00-176.00	42.00-238.00	
	S.D.	52.41	33.00	45.41	
$F_2$	M	152.23	126.37	138.70	146.03
	R	39.00-339.00	34.00-246.00	42.00-297.00	43.00-296.00
	S.D.	63.29	48.98	62.09	58.69
$F_3$	M	123.53	118.74	140.18	133.66
	R	33.00-330.00	40.00-262.00	39.00-286.0	47.00-270.00
	S.D.	47.16	43.89	51.03	43.61
$F_1P_1$	M	114.58	126.45	124.91	122.80
	R	37.00-195.00	35.00-210.00	58.00-295.00	49.00-230.00
	S.D.	38.59	41.68	54.82	46.32
$F_1P_2$	M	127.26	131.55	141.68	153.04
	R	47.00-273.00	39.00-229.00	46.00-250.00	34.00-308.00
	S.D.	46.72	46.35	64.72	70.19

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub>= 98.07; Rht<sub>1</sub>rht<sub>2</sub>= 132.67; rht<sub>1</sub>Rht<sub>2</sub>= 127.18; rht<sub>1</sub>rht<sub>2</sub>= 162.19; and Yamhill Dwarf= 124.36(cross I); 115.17(cross II); 108.21(cross III); 137.30(cross IV).



Table 12. Mean, range and standard deviation for Spikelets/Spike (number) in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	23.56	22.83	20.18	
	R	19.00-27.20	17.40-27.80	15.40-26.00	
	S.D.	1.83	2.54	2.51	
$F_2$	M	23.17	22.08	21.86	21.42
	R	13.00-28.20	11.80-28.40	11.80-27.00	14.20-27.30
	S.D.	2.56	3.22	3.43	2.30
$F_3$	M	23.34	23.59	22.55	21.98
	R	12.00-30.60	13.60-30.60	12.80-29.40	13.20-28.30
	S.D.	2.75	2.65	3.05	2.50
$F_1P_1$	M	22.19	21.78	21.37	19.00
	R	15.00-26.60	15.20-27.20	14.20-26.20	14.20-24.40
	S.D.	2.73	2.83	3.10	2.31
$F_1P_2$	M	25.41	23.41	22.68	22.15
	R	19.00-30.00	18.20-29.30	16.00-27.00	17.60-24.80
	S.D.	2.36	2.30	3.08	1.89

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 22.85; Rht<sub>1</sub>rht<sub>2</sub> = 21.67; rht<sub>1</sub>Rht<sub>2</sub> = 21.55; rht<sub>1</sub>rht<sub>2</sub> = 19.02; and Yamhill Dwarf = 24.92(cross I); 24.64(cross II); 23.74(cross III); 24.81(cross IV).

Table 13. Mean, range and standard deviation for Kernels/Spikelet (number) in F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub> and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
F <sub>1</sub>	M	3.40	3.30	2.99	
	R	2.80-3.90	2.80-3.90	2.00-3.50	
	S.D.	0.25	0.30	0.30	
F <sub>2</sub>	M	3.23	3.02	2.98	3.28
	R	1.90-4.20	2.00-4.00	2.00-4.10	1.70-4.40
	S.D.	0.49	0.38	0.38	0.46
F <sub>3</sub>	M	3.15	3.11	3.02	3.03
	R	1.30-4.40	1.90-4.30	1.30-4.20	1.60-4.30
	S.D.	0.51	0.43	0.56	0.41
F <sub>1</sub> P <sub>1</sub>	M	3.15	3.19	3.04	3.08
	R	2.10-4.00	2.10-4.00	2.30-3.80	1.90-4.20
	S.D.	0.43	0.39	0.31	0.40
F <sub>1</sub> P <sub>2</sub>	M	3.25	3.20	3.16	3.21
	R	1.00-4.10	1.60-4.20	2.50-3.70	2.50-3.80
	S <sup>2</sup>	0.55	0.46	0.39	0.29

M = mean; R = range; S.D. = standard deviation; F<sub>1</sub>P<sub>1</sub> = backcross to isoline parent and F<sub>1</sub>P<sub>2</sub> = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 2.96; Rht<sub>1</sub>rht<sub>2</sub> = 3.10; rht<sub>1</sub>Rht<sub>2</sub> = 3.06; rht<sub>1</sub>rht<sub>2</sub> = 3.16; and Yamhill Dwarf = 3.40(cross I); 3.36(cross II); 3.27(cross III); 3.51(cross IV).

Table 14. Mean, range and standard deviation for Harvest Index (percent) in  $F_1$ ,  $F_2$ ,  $F_3$  and backcross populations of four crosses involving five parents, conducted at the Hyslop Agronomy Farm during 1985-86

Generation/ Parameter		Cross-I	Cross-II	Cross-III	Cross-IV
		Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
$F_1$	M	44.00	43.53	40.63	
	R	36.78-52.18	40.24-49.12	29.83-45.10	
	S.D.	4.46	2.28	3.73	
$F_2$	M	40.17	40.81	41.84	40.11
	R	21.85-49.64	29.89-52.63	28.94-53.33	28.70-53.33
	S.D.	4.57	4.82	4.92	4.57
$F_3$	M	39.70	41.41	38.34	38.05
	R	23.89-54.88	24.82-53.26	21.17-52.64	22.64-54.54
	S.D.	5.13	5.13	5.80	5.39
$F_1P_1$	M	41.61	38.95	39.95	36.97
	R	27.27-52.20	28.39-48.09	26.86-48.07	20.32-47.81
	S.D.	4.82	4.46	4.03	5.47
$F_1P_2$	M	42.99	44.71	42.26	41.27
	R	24.62-50.64	38.77-57.20	27.98-57.42	34.16-47.21
	S.D.	4.66	4.04	5.95	3.73

M = mean; R = range; S.D. = standard deviation;  $F_1P_1$  = backcross to isoline parent and  $F_1P_2$  = backcross to Yamhill Dwarf parent. Mean values for the parents were, Rht<sub>1</sub>Rht<sub>2</sub> = 40.70; Rht<sub>1</sub>rht<sub>2</sub> = 36.19; rht<sub>1</sub>Rht<sub>2</sub> = 37.30; rht<sub>1</sub>rht<sub>2</sub> = 32.41; and Yamhill Dwarf = 42.87(cross I); 42.48(cross II); 42.21(cross III); 42.69(cross IV).

and the backcrosses  $F_1P_2$  in cross III.

### Nature of Gene Action

When estimates of heterosis and inbreeding depression are considered for cross I, several observations are possible (Table 15). The highest estimates of heterosis were noted for plant height, grain yield, 300-kernel weight and biological yield. When similar comparisons are made in the  $F_2$  for plant height, grain yield, biological yield and tiller number, even higher values resulted. This resulted in negative values for inbreeding depression which is unrealistic. The greatest inbreeding depression was observed for harvest index, 300-kernel weight and grains per spikelet. Estimates of heterosis for grain yield (14.98) and harvest index (10.66) were the highest in the  $F_1$  generation of cross II (Table 16). In the  $F_2$ , the values were lower for most traits with the exception of tiller number which exceeded the  $F_1$  heterosis estimate. Relatively high inbreeding depressions were found for 300-kernel weight, grains per spikelet, grain yield, harvest index and plant height.

As observed in Table 17, high heterosis values for tiller number, grain yield and biological yield in both  $F_1$  and  $F_2$  generations of cross III. The values were intermediate for plant height and 300-kernel weight in the  $F_1$  generation. The largest inbreeding depression was observed for tiller number followed by plant height.

Broad and narrow sense heritability estimates for the 11 traits for each cross can be found in Table 18. Considerable variability existed for the estimates depending on the specific trait and cross. In general, relatively high broad sense estimates were observed for days

Table 15. Heterosis and Inbreeding Depression in percentage for all 11 traits in Cross-I involving Rht<sub>1</sub>Rht<sub>2</sub> and Yamhill Dwarf parents, conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Heterosis(%)		Inbreeding Depression (%)
	F <sub>1</sub>	F <sub>2</sub>	
Days to heading	-0.45	-0.74	0.27
Days to flowering	-0.11	-0.50	0.30
Days to maturity	-0.39	-1.52	1.14
Plant height (cm)	22.03	22.12	-0.08
Tiller number	5.36	20.29	-14.17
Grain yield (g)	21.85	32.94	-9.09
300-kernel weight (g)	12.94	5.73	6.35
Biological yield (g)	15.65	36.88	-18.36
Spikelets per spike	-1.84	-2.97	1.19
Grains per spikelet	6.92	1.57	5.00
Harvest index (%)	5.31	-3.85	8.70

Table 16. Heterosis and Inbreeding Depression in percentage for all traits in Cross-II involving Rht<sub>1</sub>rht<sub>2</sub> and Yamhill Dwarf parents, conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Heterosis(%)		Inbreeding Depression (%)
	F <sub>1</sub>	F <sub>2</sub>	
Days to heading	-0.32	-0.04	-0.36
Days to flowering	-0.07	0.06	-0.13
Days to maturity	0.40	0.08	0.32
Plant height (cm)	4.40	-1.43	5.59
Tiller number	2.31	10.55	-8.03
Grain yield (g)	14.98	7.34	6.65
300-kernel weight (g)	6.60	-2.52	8.60
Biological yield (g)	2.48	1.97	0.50
Spikelets per spike	-1.40	-4.62	3.28
Grains per spikelet	2.17	-6.50	8.48
Harvest index (%)	10.66	3.76	6.25

Table 17. Heterosis and Inbreeding Depression in percentage for all 11 traits in Cross-III involving  $rht_1Rht_2$  and Yamhill Dwarf parents, conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Heterosis(%)		Inbreeding Depression (%)
	F <sub>1</sub>	F <sub>2</sub>	
Days to heading	-0.46	0.23	-0.69
Days to flowering	-0.02	0.36	-0.39
Days to maturity	1.74	1.23	0.50
Plant height (cm)	9.16	1.35	7.16
Tiller number	49.89	26.34	15.71
Grain yield (g)	27.87	25.18	2.11
300-kernel weight (g)	12.41	8.24	3.74
Biological yield (g)	23.95	17.85	4.92
Spikelets per spike	-10.89	-3.40	-8.32
Kernels per spikelet	-5.54	-5.70	0.33
Harvest index (%)	2.20	5.26	-2.98

to heading, flowering and maturity dates and plant height. Intermediate values were noted for tiller number, grain yield, 300-kernel weight, biological yield, spikelets per spike and kernels per spike. However, for these latter traits some variation in the estimates existed depending on the cross. For example, for tiller number the estimates varied from 65.92 for cross IV to 23.94 in cross II. This was also true for harvest index where in cross IV a value of 62.37 was recorded in contrast to 27.12 in cross I.

For narrow sense heritability estimates, relatively high values were observed for days to heading (except cross III), days to maturity, tiller number (except cross III) and 300-kernel weight (except cross I). Lower estimates can be noted for spikelets per spike, kernels per spikelet and harvest index. In several instances, negative values were detected suggesting large experimental error. No one cross consistently produced high heritability estimates for all traits. The only trait where both high broad and narrow sense heritability estimates were realized was for days to maturity.

### Associations Between Selected Traits

Correlations between the eleven traits are provided for the four isolines and Yamhill Dwarf in Table 19. For plant height and days to maturity, a negative value was found with the Yamhill Dwarf. Significant correlation values can be observed for tiller number, grain yield and biological yield when associated with plant height in the four isolines. The one exception is for the association between plant height and tiller number for the isolate  $rht_1rht_2$ . Plant height was



Table 18. Broad and narrow sense heritability estimates for eleven traits from the parental, F<sub>1</sub> and F<sub>2</sub> generations in all four crosses involving four isolines and Yamhill Dwarf as parents in the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Cross-I		Cross-II		Cross-III		Cross-IV <sup>Ⓢ</sup> <sub>1</sub>	
	B.S	N.S	B.S	N.S	B.S	N.S	B.S	N.S
Days to heading	66.92	40.14	61.67	33.74	77.06	-11.92	80.00	42.66
Days to flowering	56.94	31.62	60.72	27.67	64.44	38.82	81.62	21.34
Days to maturity	72.14	55.00	76.98	54.33	53.41	56.42	82.91	40.93
Plant height	81.35	38.67	89.33	27.63	56.66	28.30	80.26	-6.85
Tiller number	32.07	41.96	23.94	37.95	49.73	19.51	65.92	-8.35
Grain yield	50.08	49.14	47.34	20.20	69.43	6.62	53.96	-7.80
300-kernel weight	38.18	7.15	53.35	46.05	44.44	37.39	71.83	35.54
Biological yield	50.87	54.17	35.60	19.02	65.35	6.71	42.83	-2.66
Spikelet per spike	62.68	0.63	64.72	36.03	67.86	18.43	66.09	16.25
Kernels per spikelet	47.62	-1.45	45.27	-21.28	21.92	14.38	67.70	41.48
Harvest index	27.12	-7.91	52.78	22.09	38.07	-6.76	62.37	-4.96

B.S and N.S = Broad and Narrow sense heritability estimates, respectively, in percentage. <sup>Ⓢ</sup><sub>1</sub> = Environmental variation in the cross IV included the parental sources only, unlike in cases of the other three crosses where both parental and F<sub>1</sub> sources were used for the estimate.

also found to be associated with spikelets per spike.

Grain yield was positively associated with days to heading in isoline  $rht_1Rht_2$ , days to flowering in isolines  $Rht_1Rht_2$  and  $rht_1Rht_2$ , grain weight in  $Rht_1rht_2$ , grains per spikelet in  $Rht_1Rht_2$  and harvest index for isolines  $Rht_1Rht_2$  and  $rht_1rht_2$ . For tiller number, biological yield and spikelets per spike, positive correlations were obtained with grain yield. The one exception was in isoline  $Rht_1Rht_2$  for spikelets per spike.

The only association between biological yield and harvest index was noted for isoline  $rht_1rht_2$ .

When the coefficients of determination are considered for the crosses involving generations in Tables 20 and 21, the values were low especially for associations with plant height. For grain yield, high  $R^2$  values were found with biological yield and to a lesser extent with tiller number.

Table 19. Correlation coefficients (r) between plant height and grain yield with ten and nine traits respectively and biological yield and harvest index for the five parents of the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Characters Compared	Isogenic Lines				Yamhill Dwarf
	Rht <sub>1</sub> Rht <sub>2</sub>	Rht <sub>1</sub> rht <sub>2</sub>	rht <sub>1</sub> Rht <sub>2</sub>	rht <sub>1</sub> rht <sub>2</sub>	
Plant height and					
Days to heading	-0.24	-0.03	0.16	-0.17	-0.08
Days to flowering	0.19	-0.13	0.11	-0.37	0.21
Days to maturity	-0.23	-0.13	0.04	-0.23	-0.47**
Tiller number	0.39*	0.44*	0.49**	0.10	0.31
Grain yield	0.42**	0.46**	0.50**	0.40*	0.14
Grain weight	-0.02	0.12	-0.20	0.18	0.34
Biological yield	0.41**	0.51**	0.51**	0.44*	0.16
Spikelet per spike	-0.23	0.37*	0.35	0.07	-0.30
Grain per spikelet	0.29	-0.29	0.03	0.28	-0.29
Harvest index	0.26	0.36	-0.05	0.06	-0.16
Grain Yield and					
Days to heading	0.12	-0.02	0.37*	0.04	-0.31
Days to flowering	0.37*	-0.17	0.37*	-0.26	-0.28
Days to maturity	0.04	0.23	0.04	0.36	-0.20
Tiller number	0.76**	0.93**	0.64**	0.71**	0.86**
Grain weight	0.03	0.41*	-0.05	0.28	-0.18
Biological yield	0.97**	0.99**	0.98**	0.98**	0.97**
Spikelet per spike	0.17	0.66**	0.49**	0.48**	0.50**
Grain per spikelet	0.51**	0.25	0.22	0.26	0.30
Harvest index	0.41*	0.13	0.07	0.58**	-0.22
Biological Yield and					
Harvest index	0.19	-0.01	-0.14	0.42*	-0.27

Data were taken from number of plants for isogenic lines, Rht<sub>1</sub>Rht<sub>2</sub>= 30; Rht<sub>1</sub>rht<sub>2</sub>= 27; rht<sub>1</sub>Rht<sub>2</sub>= 28; rht<sub>1</sub>rht<sub>2</sub>= 26; and for Yamhill Dwarf=30

Table 20. Coefficients of Determination ( $R^2$ ) between plant height and ten other traits in all four crosses across generations for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Characters Compared	Cross-I	Cross-II	Cross-III	Cross-IV
	Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
Plant height and				
Days to heading	0.05	0.11	0.08	0.11
Days to flowering	0.00	0.01	0.02	0.04
Days to maturity	0.08	0.23	0.10	0.26
Tiller number	0.00	0.04	0.05	0.07
Grain yield	0.12	0.09	0.07	0.01
300-kernel weight	0.16	0.07	0.01	0.00
Biological yield	0.18	0.18	0.12	0.06
Spikelets per spike	0.00	0.00	0.00	0.10
Grains per spikelet	0.02	0.00	0.00	0.02
Harvest index	0.01	0.07	0.01	0.11

Number of Plants in Cross-I= 504; Cross-II= 502; Cross-III= 420; Cross-IV= 427

Table 21. Coefficients of Determination ( $R^2$ ) between grain yield and harvest index and biological yield for all four crosses across generations for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Characters Compared	Cross-I	Cross-II	Cross-III	Cross-IV
	Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf

#### Grain Yield and

Days to heading	0.03	0.01	0.04	0.01
Days to flowering	0.02	0.00	0.05	0.04
Days to maturity	0.00	0.01	0.00	0.00
Tiller number	0.42	0.33	0.37	0.45
300-kernel weight	0.10	0.19	0.09	0.05
Biological yield	0.92	0.88	0.90	0.87
Spikelets per spike	0.07	0.11	0.18	0.11
Grains per spikelet	0.15	0.17	0.19	0.11
Harvest index	0.11	0.10	0.17	0.15

#### Harvest Index and

Biological yield	0.00	0.00	0.02	0.00
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Number of Plants in Cross-I= 505; Cross-II= 502; Cross-III= 416; Cross-IV= 427

## DISCUSSION

Dramatic increases in world wheat production have occurred during the past two decades. This has been due in part to the widespread adoption of stiff-strawed, semidwarf cultivars. The dwarfing genes which have received the greatest attention are  $Rht_1$  and  $Rht_2$ . These so called 'Daruma' genes are found in the cultivars Norin 10 and Suwon 92 obtained from Japan and Korea, respectively.

Several approaches have been employed to elucidate the effects of these dwarfing genes on agronomic, morphological and physiological traits. Particular interest has been given to how these genes have influenced grain yield and the components of yield. Nevertheless, the possible association of the dwarfing genes and subsequent grain yield increases are not fully understood. To provide additional information on the role of dwarfing genes, a different approach to the problem was taken in this investigation. The  $F_1$ ,  $F_2$ ,  $F_3$  and reciprocal backcrosses were evaluated from crosses between a soft white winter wheat selection with good agronomic performance and four isolines involving various combinations of the  $Rht_1$  and  $Rht_2$  dwarfing genes. Unfortunately due to limited  $F_1$  seed in one cross, this generation had to be eliminated from some of the statistical analyses.

Of special interest was how plant stature, namely biological yield and harvest index influenced grain yield. Unfortunately no differences were obtained between crosses for these two traits at the five percent level of significance. However, differences were noted for both biological yield and harvest index when different generations were considered. There were also cross X generation interactions associated

with both traits.

For the eleven traits measured, differences between crosses were observed only for days to heading, days to maturity, plant height, 300-kernel weight and spikelets per spike. Subsequent research by the Oregon State University cereal research group has confirmed that the agronomically superior common parent "Yamhill Dwarf" also carries one of the dwarfing genes ( $Rht_1$ ). This may have contributed to the limited number of differences observed between the crosses for the different traits.

Evidence for this assumption is also provided when the orthogonal contrasts between specific crosses are considered. When Yamhill Dwarf was crossed to the two semidwarf isolines ( $Rht_1rht_2$  and  $rht_1Rht_2$ ), for only one trait, days to maturity, was a difference noted. When crosses involving the semidwarfs were compared to the double dwarf isolate ( $Rht_1Rht_2$ ) with Yamhill Dwarf, differences were detected for days to maturity, plant height and spikelets per spike. When dwarf and semidwarf crosses were compared to the standard height isolate, in addition to differences previously noted, days to heading and 300-kernel weight were also significantly different. Thus it would appear that greater genetic diversity for several traits did occur depending on the number of dwarfing genes present. Also since Yamhill Dwarf was carrying one of the dwarfing genes in common with one of the semidwarf isolines, less genetic variability resulted in these crosses involving only  $Rht_1$  or  $Rht_2$ .

It is interesting to note that Yamhill Dwarf, which was similar in plant height to the double dwarf isolate, had the highest mean value for harvest index and was similar to the standard height isolate for

grain yield. The latter cultivar had the lowest mean value for harvest index, but the highest values for grain yield and biological yield. When the mean values for all six generations are considered, the cross involving the standard height isoline with Yamhill Dwarf resulted in the highest values for plant height, grain yield, 300-kernel weight and biological yield; but the lowest value for harvest index. These findings support the conclusion by Pinthus and Levy (1984), Gale et al (1981), Busch and Chamberlain (1981) and Sharma et al (1983) that to increase grain yield, plant breeders should select taller semidwarfs. It does question the importance of harvest index as a major component of grain yield in contrast to total biological yield.

When generations are considered, differences were observed for all eleven traits. For days to heading, flowering and maturity, the mean values were similar to the mid parent values. As would be expected, the ranges and standard deviations were generally high in the F<sub>2</sub> and F<sub>3</sub> generations where maximum genetic segregation occurred. Based on relatively high heritability estimates, selection in early generations (F<sub>2</sub> and F<sub>3</sub>) should be effective for these traits within the limits of the genetic variability available. A similar situation exists for plant height, with greater variability observed in the F<sub>2</sub> and F<sub>3</sub> generations. The mean values also tended to be intermediate between the parental values. With the exception of the backcross population to the semidwarf isoline Rht<sub>1</sub>rht<sub>2</sub>, the highest mean values for plant height were associated with the standard height isoline/Yamhill Dwarf cross. Again, based on relatively high heritable estimates, selection in early generations for a wide array of plant heights would be available in progeny of this cross.



With the exception of the backcrosses to the Yamhill Dwarf, mean values for most generations tended to favor the higher tillering isoline parents. This tendency is also apparent in the populations derived from backcrosses to the isolines. A conflict observed in these results was that the mean values of the  $F_2$  were consistently higher than the  $F_1$  in three of the crosses for tiller number. Thus instead of an inbreeding depression as would be expected based on the  $F_1$  performance when compared to the parental means, there was a positive response in the  $F_2$ . This is also apparent when the broad and narrow sense heritability estimates are considered. In two crosses narrow sense estimates were higher than the broad sense values, and in one case a negative narrow sense estimate was noted. The overall performance of the generations and the inconsistencies of the heritability estimates suggest that it might be difficult to effectively select in early generations for increased tiller number in these experimental populations.

Grain yield was of special interest. With the exception of cross II ( $Rht_1rht_2$  X Yamhill Dwarf), the mean grain yields of the  $F_1$  and  $F_2$  generations and the backcrosses to Yamhill Dwarf were higher than the parental means. The highest mean value and the greatest variability observed for yield was noted with the backcross population to Yamhill Dwarf involving cross IV or the standard height isoline ( $rht_1rht_2$ ).

For all crosses relatively high estimates of broad sense heritabilities were realized for grain yield; however it is of interest that the fewer dwarfing genes present the lower the narrow sense heritability estimate. With the standard height isoline ( $rht_1rht_2$ ), a negative estimate was realized. Higher inbreeding depression was noted

in the cross involving the double dwarf isoline ( $Rht_1Rht_2$ ). Thus for grain yield there are several conflicting results. It does appear that there is considerable nonadditive gene action controlling this trait and selection would have to be delayed until the  $F_4$  or  $F_5$  generation when a high degree of homozygosity is attained. At this point most of the nonadditive genetic variability would be lost and the true genetic differences between lines could be estimated.

The reciprocal backcrosses had the greatest mean values and the most variability for plant height; especially for the standard height isoline ( $rht_1rht_2$ ) and Yamhill Dwarf. A negative narrow sense heritability was noted for this same cross. It would appear however that despite this heritability estimate, selection for discrete height levels would be possible in the early generation. As would be expected with the greater variability, the cross involving the standard height isoline ( $rht_1rht_2$ ) and Yamhill Dwarf would offer the most promise in selecting different height levels. With the higher grain yield also associated with this cross, it would again support the results of others that taller, semidwarf wheats offer the greatest opportunity to increase grain yield.

For 300-kernel weight, a major component of grain yield, the  $F_1$  generation for the three crosses favored the Yamhill parent as reflected in the higher mean values. There did appear to be some inbreeding depression as both the mean values of the  $F_2$  and  $F_3$  generations were less than the  $F_1$ . Based on the mean values and the apparent variability, the backcross populations to Yamhill Dwarf would be the most promising from which selections might be made in order to increase 300-kernel weight. However, even though the mean values were

low, considerable variation in all crosses was noted in the  $F_3$  generation. Care must be taken as suggested by the  $F_1$  performance which reflected partial to full dominance. This indicates that considerable nonadditive gene action may be present making successful early generation selection difficult.

To increase biological yield in these populations based on both mean values and the apparent variability present, the backcross populations to the Yamhill Dwarf parent for crosses III and IV involving  $rht_1Rht_2$  and  $rht_1rht_2$  isolines respectively, would appear the most promising. These isolines therefore appear to either carry a different dwarfing gene than Yamhill Dwarf or where no dwarfing genes are present as with the isolate  $rht_1rht_2$ .

For spikelets per spike, other than the crosses where the isolines were the recurrent parents, most generation mean values favor the higher Yamhill Dwarf parent. When compared to the  $F_1$  means, the  $F_2$  and  $F_3$  populations did not reflect any inbreeding depressions. They also had more variability than the  $F_1$  populations as noted by the range and standard deviation values. This evidence, plus the response noted toward increased spikelets per spike in the backcross populations to Yamhill Dwarf and especially in the cross involving the double dwarf isolate  $Rht_1Rht_2$ , suggest that early generation selection would be effective for this trait.

Grains per spikelet is considered to be an important component of grain yield. When the  $F_1$  mean values are compared with subsequent generations, there does appear to be some inbreeding depression for crosses involving isolines  $Rht_1Rht_2$  and  $Rht_1rht_2$ . With the exception of the  $F_3$  in cross III ( $rht_1Rht_2$  X Yamhill Dwarf), it would appear based

on mean values and the variability across generations that the double dwarf isoline  $Rht_1Rht_2$  would offer the greatest opportunity for selection; however there does appear to be some nonadditive gene action controlling this trait making early generation selection questionable.

Harvest index frequently has been cited as the trait most influenced with the development of semidwarf wheat cultivars. In three of the crosses of this study, the  $F_1$  mean values exceeded both the parents and the  $F_2$  and  $F_3$  values. Also there was considerable inbreeding depression when the  $F_1$  and  $F_2$  mean values are considered in three of the crosses. This is strong evidence that considerable nonadditive gene action is involved in controlling this trait. Based on the performance of the backcross progeny where Yamhill Dwarf was the recurrent parent, a backcrossing program using double or semidwarf lines might be the best breeding approach. Otherwise it may be necessary to delay selection until later generations, such as  $F_4$  or  $F_5$ , when the additive portion of the total genetic variability becomes fixed.

### Nature of Gene Action

When three crosses are contrasted as to the amount of heterosis or inbreeding depression, the largest values were noted for the 300-kernel weight, kernels per spikelet and harvest index. This was true for the crosses involving the double dwarf  $Rht_1Rht_2$  and the semidwarf  $Rht_1rht_2$ . However, for cross III involving the semidwarf  $rht_1Rht_2$ , the higher values for heterosis and inbreeding depression were observed for tiller number, 300-kernel weight and biological yield. With the common parent Yamhill Dwarf also carrying the  $Rht_1$  dwarfing gene, it would appear

that the similarities in dwarfing genes did influence the nature of gene action. Thus in the first two crosses, I and II,  $Rht_1$  was a common dwarfing gene and the same three traits (300-kernel weight, kernels per spikelet and harvest index) reflected inbreeding depression. While in cross III, Yamhill Dwarf ( $Rht_1rht_2$ ) and the isoline ( $rht_1Rht_2$ ) with different dwarfing genes, 300-kernel weight, plant height, tiller number and biological yield all exhibited heterosis and inbreeding depression.

To further determine the nature of gene action controlling the eleven traits measured, broad and narrow sense heritability estimates were calculated. The significant genetic X environmental interaction may have contributed to lack of consistency observed between crosses and the fact that in some instances narrow sense heritabilities were higher than the broad sense. Also, negative values were encountered for several of the narrow sense estimates. Since the narrow sense heritabilities are regarded as estimates of additive gene action, they are the most important to the breeders of the self pollinated crops like wheat. In general, high narrow sense heritability estimates have been reported for qualitatively inherited traits like days to heading, flowering and maturity, and plant height. In this study, similar findings were noted suggesting that much of the genetic variability associated with these traits was due to genes responding in added manner. Since specific dwarfing genes were involved, it would have been anticipated that high narrow sense estimates would have been realized. This was the situation except for the cross between standard height isoline ( $rht_1rht_2$ ) and Yamhill Dwarf ( $Rht_1rht_2$ ) where a negative value was found. In fact, as previously noted, negative estimates involving

this cross were observed for tiller number, grain yield, biological yield and harvest index. When the mean values and variability associated with generation means were evaluated, this particular cross appeared to be the most promising and especially for the improvement of grain yield. In general, the narrow sense heritability estimates were low for grain yield in all four crosses. This was also true for harvest index.

Based on the inconsistencies observed, and perhaps due to the generation X environmental interaction, no meaningful exacting interpretation of these heritability estimates should be made.

#### Possible Associations

A more realistic estimate of the possible association between traits is to evaluate the coefficients of determination for the various components of grain yield. When such comparisons were made in this study with plant height and the ten other traits measured, the  $R^2$  values were low for all comparisons. This suggests that despite the fact that the various isolines carried different dwarf genes, plant height per se did not account for much of the variabilities involving the other traits. However, when the coefficients of determination were obtained for grain yield and nine traits, several interesting comparisons emerged. High and consistent  $R^2$  values were observed between grain yield and biological yield in all four crosses. This might be considered as suggesting that a critical mass for photosynthetic activity is required to develop an adequate sink-source relationship to support grain yield. It further indicates that plant height per se is not necessarily responsible for biological yield, but

as evidenced by the intermediate  $R^2$  values between grain yield and tiller number, the latter may also contribute to the total biomass.

In general the results of this study, employing isoline for plant height, support results obtained by other investigators using different approaches. To increase grain yield the taller semidwarf plants appear more promising. Results of this study further suggest that the breeder should consider biological yield as a major component influencing the final grain yield of a plant. In contrast, harvest index did not appear to be a major factor influencing grain yield.

## SUMMARY AND CONCLUSIONS

Four near isogenic lines were crossed to a common parent with parents and generations through the  $F_3$ , including reciprocal backcrosses constituting the experimental material. The objectives of this study were : (1) to evaluate the influence of plant height on grain yield and different yield parameters, (2) to determine how harvest index and biological yield are influenced by plant height, (3) to ascertain possible relationships between plant height and grain yield with different yield components, and (4) to provide information on the nature of gene action governing selected traits. The experiment was conducted using split plot design with crosses being main plots and generations the subplots and grown on the Hyslop Agronomy Farm during 1985-86. Observations were taken for eleven agronomic traits on an individual plant basis. Based on the results, the following conclusions are made.

1. Differences were observed between crosses for certain traits depending on the number and specific dwarfing genes present.
2. In crosses with the standard height isoline ( $rht_1rht_2$ ), differences were noted for five traits in contrast to only one trait being different in crosses involving the two semidwarf isolines  $Rht_1rht_2$  and  $rht_1Rht_2$ . This might have been resulted due to the fact that Yamhill Dwarf, the common parent, also carries  $Rht_1$ .
3. Differences were detected for all eleven traits when generations were considered within crosses.
4. The crosses involving the standard height isoline ( $rht_1rht_2$ ) resulted in the tallest plants and the highest mean values for both



grain yield and biological yield; however this cross had the lowest mean value for harvest index.

5. To maximize grain yield, the results of this study indicate that the tall semidwarf plants would be more promising than the extreme dwarf phenotypes.

6. The consistent and positive associations obtained between grain yield and biological yield suggest the need to maintain an adequate amount of photosynthetic area to support an acceptable sink-source relationship.

7. Heterosis was more pronounced in the cross 'rht<sub>1</sub>Rht<sub>2</sub>/Yamhill Dwarf' for most traits suggesting that more nonadditive gene action may be involved, thus making selection in early generations difficult within this cross.

8. Both broad and narrow sense heritability estimates varied greatly between crosses. In the standard height isolate (rht<sub>1</sub>rht<sub>2</sub>) and Yamhill Dwarf cross, narrow sense heritability estimates were negative for several traits. In other crosses, the narrow sense estimates were greater than broad sense estimates for certain traits. Thus very little value can be placed on these estimates in identifying the nature of gene action for any of the traits.

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## APPENDICES

Appendix Table 1. Pedigree and description of the parents of different crosses used in the experiment conducted at the Hyslop Agronomy Farm during 1985-86

1. Yamhill Dwarf : Resulted from the cross of Alba/Heines VII. This selection is late maturing, high yielding with large fertile spikes and medium to large kernels. It is a soft white winter wheat. It possesses Rht<sub>1</sub> as a dwarfing source allele.

Sl. No.	Germ-plasm Reg.No.	Selection No.	CI No.	Dwarfing Loci	Pedigree
2.	GP181	77255	17864	Rht <sub>1</sub> Rht <sub>1</sub> Rht <sub>2</sub> Rht <sub>2</sub>	'Itana'/3/'Norin 10'/ 'Brevor' 14//6* Itana
3.	GP184	77260	17867	Rht <sub>1</sub> Rht <sub>1</sub> rht <sub>2</sub> rht <sub>2</sub>	"
4.	GP189	77266	17872	rht <sub>1</sub> rht <sub>1</sub> Rht <sub>2</sub> Rht <sub>2</sub>	"
5.	GP192	77269	17875	rht <sub>1</sub> rht <sub>1</sub> rht <sub>2</sub> rht <sub>2</sub>	"

All these isolines (from Sl.No.2-5) are hard red winter wheat. Their agronomic characteristics very much conform to the 'Itana' background parent. They are white stemmed with mid-dense spikes that have brown to brown-black glumes. The kernels are red, short, ovate and hard. Taken from Allan and Pritchett (1982).

Appendix Table 2. Mean values of 11 different agronomic traits for the isolines and the Yamhill Dwarf as parents of the four crosses for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Parents				Yamhill Dwarf
	Isolines				
	Rht <sub>1</sub> Rht <sub>2</sub>	Rht <sub>1</sub> rht <sub>2</sub>	rht <sub>1</sub> Rht <sub>2</sub>	rht <sub>1</sub> rht <sub>2</sub>	
Days to heading	156.73	155.52	154.71	153.38	157.42
Days to flowering	160.70	160.59	159.92	160.00	161.19
Days to maturity	196.50	188.93	188.93	186.00	198.04
Plant height(cm)	73.37	110.48	109.68	138.11	76.36
Tiller number	22.8	24.00	21.71	23.92	15.91
Grain yield(g)	40.09	48.01	47.34	53.00	51.23
300-kernel weight(g)	9.52	10.84	10.56	10.94	12.70
Biological yield(g)	98.07	132.67	127.18	162.19	121.26
Spikelets spike	22.85	21.67	21.55	19.02	24.53
Kernels per spikelet	2.96	3.10	3.06	3.16	3.38
Harvest index(%)	40.70	36.19	37.30	32.41	42.56

Number of plants in cases of Rht<sub>1</sub>Rht<sub>2</sub>= 30; Rht<sub>1</sub>rht<sub>2</sub>= 27; rht<sub>1</sub>Rht<sub>2</sub>= 28 and Yamhill Dwarf= 115



Appendix Table 3. Mean values of 11 different agronomic characters of the four crosses across six generations for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Traits	Cross-I	Cross-II	Cross-III	Cross-IV
	Rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	Rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> Rht <sub>2</sub> X Yamhill Dwarf	rht <sub>1</sub> rht <sub>2</sub> X Yamhill Dwarf
Days to heading	156.74	156.78	156.42	155.24
Days to flowering	160.96	161.14	160.92	160.66
Days to maturity	196.32	193.85	194.82	193.22
Plant height(cm)	83.30	92.43	93.05	103.96
Tiller number	20.31	20.35	21.07	21.04
Grain yield(g)	51.18	50.83	51.99	55.43
300-kernel weight(g)	11.71	11.96	12.00	12.56
Biological yield(g)	123.35	124.74	129.07	143.24
Spikelets per spike	23.66	22.86	22.25	21.39
Kernels per spikelet	3.19	3.17	3.08	3.21
Harvest index(%)	41.39	40.82	40.14	38.59

Number of plants in Cross-I= 514; Cross-II= 512; Cross-III= 426; and Cross-IV= 435

Appendix Table 4. Coefficients of Orthogonal Contrasts while comparing within crosses in 'Type-A' analysis for the experiment conducted at the Hyslop Agronomy Farm during 1985-86

Cotrasting Crosses	Cross-I	Cross-II	Cross-III	Cross-IV
1. C-II Vs. C-III	0	+1	-1	0
2. C-II/C-III Vs. C-I	+2	-1	-1	0
3. C-IV Vs. C-II/C-III/C-I	-1	-1	-1	+3

Appendix Table 5. Summary of the meteorological data for Corvallis, Oregon for the period from September, 1985 to August, 1986

Months	Average Temperature ( $^{\circ}\text{C}$ )			Average Precipitation		Relative Humidity (%)
	Max.	Min.	Mean	Monthly	Total	
				rate(cm)	days	
September	22.0	7.6	14.8	1.98	12	45.53
October	17.6	4.7	11.1	9.88	14	51.48
November	7.1	-0.2	3.4	11.91	16	67.66
December	4.5	-3.6	0.4	9.45	9	70.77
January	9.7	2.1	5.9	16.59	26	77.00
February	10.0	3.0	6.5	25.15	20	73.62
March	15.6	5.3	10.4	7.72	17	58.12
April	15.1	4.1	9.6	4.67	16	51.53
May	18.7	6.9	12.8	6.35	13	52.58
June	25.2	10.6	17.9	0.79	4	49.13
July	24.6	10.0	17.3	2.92	6	48.87
August	30.6	11.3	20.9	0.00	0	41.72

Note: Observations were taken from Hyslop Agronomy Farm, Corvallis, Oregon.