NOTES AND COMMENTS

THE CHROMOSOMAL LOCATION OF A MAJOR DWARFING GENE FROM NORIN 10 IN NEW BRITISH SEMI-DWARF WHEATS

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SUMMARY

A gene for gibberellic acid sensitivity, *Gai*₂, present in British semi-dwarf wheats and derived from the variety Norin 10, was located on chromosome 4D. This gene was associated with the semi-dwarf habit indicating that the gene, *Rht*₂, for reduced height was also located on this chromosome.

1. INTRODUCTION AND RESULTS

THE increased yields of the common bread wheat, *Triticum aestivum* ($2n = 6x = 42$), over the past half-century have been accompanied by steady decreases in straw length. These shorter wheats are compatible with higher fertiliser levels while remaining resistant to "lodging" during inclement weather before harvest.

The most recent British short-strawed varieties have derived their semi-dwarf habit from genes transferred from the Japanese variety Norin 10. This variety has been the basis of most successful semi-dwarf wheats, including the "green revolution" varieties from Mexico (Borlaug, 1968).

Many attempts have been made to characterise the genetic system controlling height in Norin 10 and its semi-dwarf derivatives. Estimations of the number of "major genes" involved and their chromosomal locations have been hampered by the quantitative nature of height variation. The presence of modifying genes tends to obscure segregation into the discrete height classes necessary for conventional Mendelian analysis.

The chromosomal location of these genes has usually been attempted by monosomic analysis (Sears, 1953). Unfortunately, the removal of single chromosomes as in monosomics ($2n - 1 = 41$) can have a large effect on final plant height (Law and Worland, 1972), so that it is not possible using monosomic analysis to distinguish between effects due to chromosome dosage from those due to allelic differences.

The number of major factors in Norin 10 has been suggested as two. These genes, to which the symbols *Rht*₁ and *Rht*₂ have been assigned, are reported to be recessive (Fick and Qualset, 1973) or partly recessive (Allan and Vogel, 1963). Chromosomes 2A, 2B, 2D, 3D and 4B have been suggested as possible locations for these genes by Allan and Vogel (1963), whereas 2A and 4D (Jha and Swaminathan, 1969), 6D (Jha and Swaminathan, 1969; Bhowal, 1970), 1B and 5D (Singhal, Singh and Kalia, 1973) and

2A and 4B (Baier, Zeller and Fischbeck, 1974) have been proposed by other workers using monosomic analysis.

Along with other dwarfs, Norin 10 has been shown to have a remarkable lack of response to the plant hormone gibberellic acid (GA) (Allan, Vogel and Craddock, 1959; Radley, 1970; Gale and Marshall, 1973). This GA-insensitive reaction is associated with high levels of GA in plant tissues (Radley, 1970; Gale and Marshall, 1973) and has been attributed to the plants' inability to utilise both endogenous and applied GA. Unlike final plant height with which GA-insensitivity is closely associated (Gale and Marshall, 1973) the sensitive/insensitive reaction may be scored as a qualitative character in large numbers of seedlings with relative ease. Using this approach Norin 10-Brevor 14, the dwarf ancestor of the British semi-dwarf wheats, has been shown to carry GA-insensitivity alleles at two loci, *Gai*₁ and *Gai*₂. One of these, *Gai*₂, has been transferred to the new semi-dwarf varieties Maris Hobbit and Maris Fundin.

*Gai*₂ is dominant in a seedling response test. Sensitive *gai*₂*gai*₂ seedlings can be identified from insensitive seedlings by the length of the second leaf internode after 10 days growth at 18°C in a nutrient solution supplemented with 10 p.p.m. GA₃. For the genotypes *Gai*₂*gai*₂ and *Gai*₂*Gai*₂ internode lengths ranged between 56 and 88 mm whereas for *gai*₂*gai*₂ the lengths were between 107 and 124 mm.

Figure 1 shows the segregation of *Gai*₂ and final plant height in a sample of 129 F₂'s from the cross of Maris Hobbit with the GA-sensitive variety Chinese Spring. The classification of the F₂ was carried out on the F₃ progeny and it is clear that the three classes obtained fit closely a 1:2:1 segregation confirming the presence of the single gene, *Gai*₂. These three classes are also different in their mean height values indicating that *Gai*₂ is strongly associated with this character. Indeed, the mean heights of the two homozygotes *Gai*₂*Gai*₂ and *gai*₂*gai*₂, differ by 18 cm which represents 70 per cent of the difference between the two parental varieties. *Gai*₂ is therefore either closely linked to the Norin 10 derived dwarfing gene or is responsible for the dwarfing effect itself. Although it is not possible to distinguish between these alternatives on the basis of the present data, the association between height and *Gai*₂ must indicate that the identification of the chromosome carrying *Gai*₂ must also locate the chromosome carrying the dwarfing factor, *Rht*₂.

This chromosome was identified by F₁ monosomic analysis (Sears, 1953). Nineteen of the 21 possible monosomics of Maris Hobbit were derived by recurrent backcrossing to the Chinese Spring monosomic series using standard cytogenetic procedures (Law and Worland, 1972). Each monosomic was produced as a duplicate and underwent at least four, and in most cases five backcrosses. For each of the 19 lines, including duplicates, the chromosome in the hemizygous condition was established by check-crossing with the appropriate ditelocentric lines of Chinese Spring (Law and Worland, 1972).

Each monosomic line was crossed to the tall GA-sensitive variety Poros and the F₁ seedling progeny screened for response to GA after removal of root-tips for cytological examination using Feulgen staining techniques. The hybrid plants obtained from each of these crosses will either be monosomic, with the hemizygous chromosome from Poros, or disomic with all the chromosomes heterozygous. Since *Gai*₂ is dominant and is found to be

hemizygous effective then all the progeny should have the insensitive phenotype except in the single critical case where the Poros chromosome carrying *gai*₂ is hemizygous. In this cross monosomics will be responsive and disomics insensitive.

GA-responsive progeny may, however, be obtained in another way. Because Chinese Spring, from which the Maris Hobbit monosomics were

* F₂ genotypes ascertained by testing 20 F₃ progeny from each F₂ in seedling GA response test.

FIG. 1.—Segregations of final plant height and *Gai*₂ in an F₂ population from Maris Hobbit × Chinese Spring.

derived, is GA-sensitive, then, for the situation of four backcrosses, each of the non-critical Maris Hobbit monosomics will have $\frac{1}{16}$ chance of being heterozygous at the *Gai*₂ locus. In this event F₁ hybrids could still show segregation. This residual heterozygosity can, however, be distinguished from the critical case in two ways. First the segregation will not be related to the segregation of 41 and 42 chromosome progeny, and second, it is unlikely that both duplicate lines of a monosomic will be heterozygous ($p = \{\frac{1}{16}\}^2$ or $\frac{1}{256}$). Differences between duplicates will therefore denote residual heterozygosity.

In 16 of the monosomic crosses, including duplicates, all hybrids were GA-insensitive. In two crosses GA-responsive individuals were found in one duplicate but not in the other and these segregations were not related to chromosome number. In one cross, Maris Hobbit monosomic 4D $\times$ Poros, both duplicate lines gave sensitive and insensitive seedlings as expected for the critical chromosome (table 1). In the second duplicate all the responders

TABLE 1

Results of F_1 monosomic analysis to detect location of Gai_2 in Maris Hobbit

Maris Hobbit monosomic 4D $\times$ Poros	Chromosome number	GA response	
		Insensitive	Sensitive
First duplicate	41	1	6
	42	3	—
Second duplicate	41	—	12
	42	2	—

$\chi^2_{(1)}$ for independence = 14.23, $P < 0.001$.

were monosomic and all the insensitive were disomic. In the first duplicate a similar assortment occurred except for one plant which gave a chromosome count of 41 and was insensitive. This anomalous plant could have arisen by univalent shift (Person, 1956), in which case the plant would be heterozygous at the Gai_2 locus but hemizygous for another chromosome than 4D.

This location of Gai_2 on chromosome 4D is consistent with previous results that have shown involvement of the group 4 chromosomes with GA insensitivity and dwarfism. Thus chromosome 4A has been shown to carry Gai_3 in the variety Minister Dwarf (Gale, Law, Marshall and Worland, 1975). It may be that a series of homeoalleles are present in this group which is made up of alleles of similar function but different potency. The precise mapping experiments to confirm this are in hand at present.

The recognition of chromosome 4D as the carrier chromosome for Gai_2 and thus Rht_2 will now allow its directed insertion into different genetic backgrounds by chromosome substitution techniques (Law and Worland, 1972). Investigations using lines developed in this way will allow the advantages and disadvantages of this genetic source of semi-dwarfism to be assessed in terms of other agronomic characters that are almost certainly affected by Rht_2 either directly or indirectly. At present such comparisons may only be made between varieties and are thus confounded by other genetic differences.

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