Heredity (1983), **51** (2), 455–459

THE LOCATION OF A GENE FOR INCOMPATIBILITY BETWEEN *HORDEUM VULGARE* L. AND *H. BULBOSUM* L.

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Received 10.iii.83

SUMMARY

A single dominant gene conditioning partial incompatibility in *Hordeum vulgare* L. *cv.* Vada×*H. bulbosum* L. crosses is shown to be linked with the gene controlling susceptibility to DDT and is thus located on barley chromosome 7. A recombination fraction of 0·112±0·032 was obtained. Certain similarities are described between this incompatibility and others known to exist in the Triticeae.

1. INTRODUCTION

Doubled haploid production of barley has been successfully achieved by pollinating *Hordeum vulgare* L. with *H. bulbosum* L. (Kasha and Kao, 1970). Following fertilisation the *H. bulbosum* chromosomes are usually eliminated resulting in a haploid *H. vulgare* embryo which is rescued to an artificial nutrient medium. Subsequently haploid plants are treated with an aqueous solution of colchicine to double the chromosome number and restore fertility.

One problem sometimes associated with the technique was observed early in the development of the programme at the Welsh Plant Breeding Station. This was a partial incompatibility between *H. vulgare cv.* Vada and *H. bulbosum* leading to reduced seed setting because of pollen tube inhibition in the stylodium and upper ovary wall transmitting tract (Pickering, 1981). The reaction is known to be controlled by a single dominant gene in Vada (Pickering and Hayes, 1976). Since then several other cultivars, some unrelated to Vada, have been reported as possessing a similar incompatibility with *H. bulbosum* (Pickering, 1980*a*) but there is no evidence to suggest that a different gene is involved (Pickering and Morgan, 1981).

This incompatibility has not been completely overcome but significant increases in seed setting have been obtained after screening a range of *H. bulbosum* genotypes (Pickering, 1980*a*), the best of which are now used in the doubled haploid programme.

The present investigation was carried out to determine the location of the incompatibility gene using progeny from an appropriately marked *H. vulgare* testcross pollinated with *H. bulbosum*.

2. MATERIALS AND METHODS

Plants were grown and crosses made in the glasshouse from 28 October to 17 December 1982. Conditions were as described previously (Pickering,

1980*b*) except that temperatures were maintained at 15°C ± 3°C (day) and 11°C ± 3°C (night). Plants (102) were raised from a *H. vulgare* backcross of (Vada × Sultan) F_1 × Sultan (Vada being incompatible and Sultan compatible with *H. bulbosum*). The contrasting characters associated with these parent cultivars and therefore segregating among the progeny are presented in table 1.

TABLE 1

Genetic markers of cvs Vada and Sultan and their incompatibility reaction with H. bulbosum

Character	Genetic markers Vada	Sultan	Gene location (chromosome no.)	References
Purple (Pau) vs nonpurple (pau) auricle	Pau	pau	2	Nilan (1964)
Esterase alleles at *Est 1* locus	Ca	Pr	3	Nielsen and Frydenberg (1971); Linde-Laursen *et al.* (1982)
Hordein alleles at *Hor 2* locus	Rf	Pr	5	Linde-Laursen *et al.* (1982); Shewry *et al.* (1980)
DDT susceptible (Ddt) vs resistant (ddt)	Ddt	ddt	7	Hayes and Rana (1966); Linde-Laursen *et al.* (1982)
Incompatible (Inc)† vs compatible (inc) with *H. bulbosum*	Inc	inc	—	Pickering and Hayes (1976)

† Provisional gene designation

Endosperm hordein patterns of the 102 progeny were determined on distal halves of individual seeds (kindly carried out by Dr P. R. Shewry, Rothamsted Experimental Station; method as Shewry *et al.*, 1983), and the remaining embryo-bearing portion of each seed was sown. Second leaves were tested for DDT reaction (Jensen, 1979) and esterase isozyme assays were undertaken on 3–4 cm portions of fourth leaves using the technique of Hvid and Nielsen (1977). Plant pigmentation was assessed throughout the growing period.

In order to determine the incompatibility reaction, two spikes from each of the 102 *H. vulgare* plants were emasculated and pollinated with *H. bulbosum* selections S1 (Pickering and Hayes, 1976) and Cb 2984 (derived from C.P.I. 18968) by the procedures of Pickering (1980*b*). The incompatibility reaction of the 102 genotypes was then determined after recording seed sets 14–17 days after pollination.

χ^2 analyses were performed to detect the presence of linkage, and recombination fractions and standard errors calculated using the methods described by Shewry *et al.*, (1980).

3. RESULTS

Apart from four crosses which gave ambiguous results and were excluded from the calculations, mean percentage seed setting on compatible lines was 82·0 falling below 60·0 only on three days towards the end of

the crossing period, when values of 30·2, 46·2 and 48·8 per cent were obtained. Mean percentage seed setting on incompatible lines was 2·1 and did not exceed 11·6 per cent on any day. Compatible and incompatible cross combinations were therefore readily identified. There were no significant deviations from 1:1 ratios when segregation ratios of the five genes were analysed independently, and the only linkage to be detected was that between the genes for incompatibility and DDT susceptibility on chromosome 7 (tables 2 and 3). A recombination fraction of $0{\cdot}112 \pm 0{\cdot}032$ was obtained.

TABLE 2

χ^2 tests for linkage between the gene for incompatibility and four genetic markers after pollinating progeny from the H. vulgare *cross (Vada × Sultan) F_1 × Sultan with* H. bulbosum *pollen*

Phenotype	Observed frequency	Phenotype (*Est 1*)	Observed frequency	Phenotype† (*Hor 2*)	Observed frequency	Phenotype	Observed frequency
Pau/Inc	22	CaPr/Inc	26	Rf/Inc	25	Ddt/Inc	39
pau/Inc	23	PrPr/Inc	19	Pr/Inc	20	ddt/Inc	6
Pau/inc	24	CaPr/inc	30	Rf/inc	28	Ddt/inc	5
pau/inc	29	PrPr/inc	23	Pr/inc	25	ddt/inc	48
χ^2(3df)	1·18		2·65		1·34		60·61
P	0·8–0·7		0·5–0·3		0·8–0·7		<0·001

† Genotypes as follows: Rf = Rf Rf Pr; Pr = Pr Pr Pr (triploid endosperm tissue)

TABLE 3

Partitioning of χ^2 analysis relating to DDT and incompatibility responses

Sources of variation	df	χ^2	P
Segregation Ddt-ddt	1	1·02	0·5–0·3
Segregation Inc-inc	1	0·65	0·5–0·3
Linkage	1	58·94	<0·001
(Total)	(3)	(60·61)	

4. DISCUSSION

It is already known that two dominant genes (Kr_1 and Kr_2) located on wheat chromosomes 5B and 5A inhibit crossability between wheat (*cv.* Hope) and rye (Riley and Chapman, 1967). Factors on these chromosomes have also been implicated in the crossabilities of wheat × *H. bulbosum* (Snape *et al.*, 1979) and barley (*cv.* Betzes) × wheat (Fedak and Jui, 1982) although other chromosomes slightly influenced the response in all these cases (Falk and Kasha, 1981; Fedak and Jui, 1982; Snape *et al.*, 1979). Wheat cultivars possessing high crossabilities with rye and *H. bulbosum* have also been reported as being more compatible with other related species such as *Aegilops*, *Agropyron* and *Elymus* (Thomas *et al.*, 1981). In this paper, the gene conditioning the incompatibility response between *H. vulgare cv.* Vada when pollinated with *H. bulbosum* (S1 and Cb 2984) has been shown to be located on barley chromosome 7.

Although, high seed sets have been obtained after pollinating Vada with rye (76·7 per cent—Thomas and Pickering, 1979; 90·1 per cent—

Pickering unpublished), the incompatibility systems of Vada × *H. bulbosum*, wheat × rye, wheat × *H. bulbosum* and barley × wheat bear some resemblance to each other. For example, some homoeology exists between barley chromosome 7 and wheat chromosome 5 (Islam and Shepherd, 1981), on both of which are located dominant incompatibility genes. Furthermore, pollen tube inflation and bursting which is found in the present material (Pickering, 1981), has also been shown to occur in incompatible hybridisations between wheat × rye (Jalani and Moss, 1980; Lange and Wojciechowska, 1976; Tozu, 1966; Zeven and van Heemert, 1970) and barley × wheat (Fedak and Jui, 1982). Similarly pollen tubes are inhibited before entry into embryo sacs of non-crossable wheats pollinated with *H. bulbosum* (Snape *et al.*, 1980). However, it must be borne in mind that similar disturbances in pollen tube growth have also been observed between other grass species (see for example Heslop-Harrison, 1982).

Acknowledgements. I wish to thank Mr P. W. Morgan for technical assistance, Dr P. R. Shewry for the hordein analysis, and Dr T. W. A. Jones and Miss A. Thomas for the esterase assay.

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