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The Genetics of Hybrid Dwarfing in Wheat

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With 3 figures and 3 tables

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Abstract

Monosomic and intervarietal chromosome substitution lines were used to confirm the locations of four hybrid dwarfing genes, *D*1, *D*2, *D*3 and *D*4. Hybrid dwarfs with six different combinations of hybrid dwarfing genes were produced. The phenotypes of these lines demonstrated that *D*3 was necessary to give type I dwarfs. Multiple allelism was shown at the *D*2 locus and postulated at the *D*1 locus. Modifier genes affecting the vigour of the hybrid dwarfs were shown to occur and to be constant within homoeologous groups.

Hybrid dwarfing occurs after crossing wheat genotypes of normal height and results in the production of a short "grass clump" phenotype that often dies before flowering. Hybrid dwarfs may occur in the F_1 or as segregants in the F_2 and later generations. Three types of hybrid dwarf were recognised by Hermsen (1967) and Moore (1969). Hermsen classified his material under field conditions. Type I dwarfs had their dwarfing characteristics visible at the 1—2 leaf stage. A profusion of tillers with stiff dark green leaves formed a typical "grass clump". The plants had delayed growth and lived two to three months in the field before gradually dying without flowering. Type II dwarfs were indistinguishable from normal plants before tillering. In early tillering plants became dwarfed producing numerous tillers with short dark green leaves. Flowering generally occurred but dwarfing characters were retained until death. Type III dwarfs were normal as seedlings then became dwarfed for a short period at tillering before running up to flower some weeks later than the parents. Adult plants were nearly normal although often of reduced height.

MOORE (1966) agreed in principle with HERMSEN's classification of dwarf phenotypes but found it necessary to define both the day length and temperature regimes under which the three types could be distinguished. Type I dwarfs only became reproductive when grown under long 12 hour days at 26 °C. Type II dwarfs became reproductive under short 8 hour days at 26 °C or long 12 hour days at 21 °C. Type III dwarfs could be distinguished from the normals by growing them at low 16 °C temperatures under short 8 hour days when only normals would flower.

The first comprehensive genetical hypothesis on hybrid dwarfing was put forward by MCMILLAN (1937) who suggested that four genes were involved. A gene *G* gave hybrid dwarfness except in the presence of a gene *I* which suppressed the activity of *G* to give normal plants. Two other genes, *A-a* and *B-b* also occurred and acted in such a way as to suppress *I* when both the *A* and *B* alleles were present resulting in dwarf plants. The genes *B-b* and *I-i* were considered to be closely linked in repulsion.

As test crosses could not separate the proposed two linked genes, HERMSEN (1967) put forward a three gene theory using the same theoretical explanations as MCMILLAN. In HERMSEN's theory hybrid dwarfing is due to three gene pairs *D1d1*, *D2d2*, *D3d3* where:

— *D1* (*G* of MCMILLAN) is the most potent and is completely dominant.
— *D2* (*Bi*) is the next most potent and is partially dominant.
— *D3* (*A*) is the weakest and is also partially dominant. Dwarfness occurs when all three dominant genes are present in the homozygous or heterozygous condition or in the absence of *D3* where *D1* is present and *D2* is homozygous i.e. *D1-D2-D3-* and *D1-D2D2*.

HERMSEN used a series of four test crosses involving lines of known genotype to determine the genotype of any unknown variety. In this way it was possible to classify the variety as either Class I *D1D1d2d2D3D3*; Class II *d1d1D2D2D3D3*; Class III *D1D1d2d2d3d3*; Class IV *d1d1D2D2d3d3*; Class V *d1d1d2d2D3D3*; or Class VI *d1d1d2d2d3d3* and pure breeding dwarfs as either *D1D1D2D2D3D3* or *D1D1D2D2d3d3*.

The chromosomal location of the dwarfing genes has been determined by means of monosomic analysis and by the use of inter-varietal chromosome substitution lines. HURD and MCGINNIS (1958) using monosomics of 'Redman' (*d1d1D2D2d3d3*) located *D2* on chromosome 2B. HERMSEN (1963) using chromosome substitution lines of 'Timstein' (*D1D1d2d2D3D3*) into 'Chinese Spring' (*d1d1d2d2d3d3*) located *D1* on chromosome 2D and *D3* on chromosome 4B. Later SILBAUGH and METZGER (1970) using Selection 1403 (*D1D1 d2d2d3d3*) and chromosome substitution lines of 'Cheyenne' into 'Chinese Spring' confirmed *D2* on 2B but also discovered a new gene *D4* on chromosome 2D linked to *D1* with a recombination value of 12 per cent. *D4* was like *D2* being partially dominant and of similar potency. It produced hybrid dwarfs when present with *D1* and either *D2* or *D3* or both or when *D1* was present and *D4* was homozygous. Genotypes *D1-D2-D3-D4-*, *D1-D2-D4-*, *D1-D3-D4-* and *D1-D4D4* all produced hybrid dwarf phenotypes.

This paper reports the incidence, chromosomal location and behaviour of genes for hybrid dwarfism amongst a range of European wheats.

Materials and Methods

The genetical analysis of hybrid dwarfism was carried out using the monosomic series of 'Cappelle-Desprez' and a number of single chromosome substitution lines in this variety in which 'Vilmorin 27', 'Desprez 80' (Hybride du Joncquois), 'Mara', 'Poros' and 'Besostaya I' were used as donor parents. The monosomic series of 'Cappelle-Desprez' was produced by backcrossing for eight generations following the initial hybridisation to the monosomic series of 'Chinese Spring'. Test-crosses with the appropriate ditelocentric lines of 'Chinese Spring' (SEARS 1953, LAW and WORLAND 1973) showed the monosomics of 'Cappelle-Desprez' to be correct. Chromosome substitution lines were derived by backcrossing the donor varieties and subsequent monosomic hybrid selections to the 'Cappelle-Desprez' monosomics for four generations and then selfing to obtain disomics (LAW and WORLAND 1973). 'Vilmorin 27' and 'Desprez 80', which are the two parents of 'Cappelle-Desprez', were also used as donors in the development of chromosome substitution lines into 'Bersée', a variety which was also developed as a monosomic series at the Plant Breeding Institute, Cambridge using the backcross method. Some of these substitution lines were used in the experiments to be described.

Intercrosses between European wheat varieties rarely produce hybrid dwarfs so it can be assumed that the occurrence of the essential dwarfing gene *D*1 is unlikely in the above material. Its presence is most common in Australian varieties such as 'Timstein' (*D*1*D*1*d*2*d*2*D*3*D*3) which is used as a tester line here along with the substitution line of 'Timstein 2D' into 'Chinese Spring', CS (Timstein 2D) (*D*1*D*1*d*2*d*2*d*3*d*3) developed by Dr. E. R. SEARS (USA). The use of these two tester lines will detect the presence of dwarfing genes other than *D*1 in the above material.

The true breeding dwarf lines, *D*1*D*1*D*2*D*2 and *D*1*D*1*D*4*D*4, selected by Dr. R. METZGER (USA) from the cross of Selection 1403 with the 'Cheyenne' substitution lines of 'Chinese Spring' for chromosomes 2B and 2D were also grown for comparative purposes. In addition the Chinese Spring (Cheyenne 2D) substitution line obtained from Dr. R. MORRIS (USA) was used in crosses to obtain further true breeding dwarf selections.

Hybridisations were made under glasshouse conditions to provide clean viable grain. All material was germinated in petri-dishes at 24 °C and transplanted into 3½" plastic pots containing John Innes No.2 compost. Seedlings of the F_1 generation of the first experiment were grown in a lighted glasshouse at 18 °C minimum temperature with long 18 hour days for the first few weeks. Subsequently the temperature was increased to a minimum of 21 °C for the remainder of the experiment. Under these conditions all except type I dwarfs would be expected to flower (MOORE 1966). A second experiment re-classifying selected F_1 lines along with all F_2 lines from normal F_1 plants that might be expected to segregate dwarfs in later generations was grown in an unlighted glasshouse from an April sowing. Here long days and warm temperatures would again permit all except type I dwarfs to flower. In both experiments, germination was very good so any semi-lethality of the hybrid dwarf genotype could be ignored in segregating populations.

All progeny of hybridisations involving monosomics had their chromosome count determined on excised root tip squashes pretreated in 1-bromonaphthalene, hydrolysed and stained in Feulgen.

Results

Gene locations

On crossing 'Timstein' (*D*1*D*1*d*2*d*2*D*3*D*3) to each of the monosomics of 'Cappelle-Desprez', all the disomic progeny and monosomics for all

chromosomes except 2D were hybrid dwarfs. Monosomic progeny of 2D were of normal height indicating that 'Cappelle-Desprez' carries a dwarfing gene or genes on this chromosome. Two genes *D*1 and *D*4 have been located on chromosome 2D. According to SILBAUGH and METZGER (1970) the presence of both these genes in 'Cappelle-Desprez' would produce a true breeding hybrid dwarf so presumably 'Cappelle-Desprez' carries either *D*1 or *D*4. Since the genotype of 'Timstein' is *D*1*D*1*d*2*d*2*D*3*D*3 then the presence of *D*1 alone in 'Cappelle-Desprez' would not produce hybrid dwarfs in this test so that *D*4 must be present and the genotype of 'Cappelle-Desprez' must be *d*1*d*1*d*2*d*2

Tab. 1 Incidence of hybrid dwarf plants amongst crosses of 'Timstein' and Chinese Spring (Timstein 2D) with 'Cappelle-Desprez', 'Desprez 80', 'Bersée', Vilmorin 27', 'Besostaya I', 'Mara' and 'Poros' and a range of substitution lines for chromosomes 2B, 2D and 4B in 'Cappelle-Desprez' and 'Bersée'

Variety or substitution line	Proposed genotype	Hybrid with Timstein (*D*1*D*1*D*3*D*3)		Hybrid with Chinese Spring (Timstein 2D) (*D*1*D*1)	
		phenotype	genotype	phenotype	genotype
Cappelle-Desprez (CD)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
Desprez 80 (Des)	*D*2*D*2	Dwarf	*D*1-*D*2-*D*3-	Normal	*D*1-*D*2-
CD (Des 2B)	*D*2*D*2*D*4*D*4	Dwarf	*D*1-*D*2-*D*3-*D*4-	Dwarf	*D*1-*D*2-*D*4-
CD (Des 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Des 4B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
B (Des 2B)	*D*2*D*2	Dwarf	*D*1-*D*2-*D*3-	Normal	*D*1-*D*2-
B (Des 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
B (Des 4B)	—	Normal	*D*1-*D*3-	Normal	*D*1-
Vilmorin 27 (Vil)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Vil 2B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
CD (Vil 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Vil 4B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
B (Vil 2B)	—	Normal	*D*1-*D*3-	Normal	*D*1-
B (Vil 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
B (Vil 4B)	—	Normal	*D*1-*D*3-	Normal	*D*1-
Besostaya I (Bes)	*D*2*D*2	Dwarf	*D*1-*D*2-*D*3-	Normal	*D*1-*D*2-
CD (Bes 2B)	*D*2*D*2*D*4*D*4	Dwarf	*D*1-*D*2-*D*3-*D*4-	Dwarf	*D*1-*D*2-*D*4-
CD (Bes 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Bes 4B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
Mara	*D*2*D*2	Dwarf	*D*1-*D*2-*D*3-	Normal	*D*1-*D*2-
CD (Mara 2B)	*D*2*D*2*D*4*D*4	Dwarf	*D*1-*D*2-*D*3-*D*4-	Dwarf	*D*1-*D*2-*D*4-
CD (Mara 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Mara 4B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
Poros	*D*2*D*2	Dwarf	*D*1-*D*2-*D*3-	Normal	*D*1-*D*2-
CD (Poros 2B)	*D*2*D*2*D*4*D*4	Dwarf	*D*1-*D*2-*D*3-*D*4-	Dwarf	*D*1-*D*2-*D*4-
CD (Poros 2D)	—	Normal	*D*1-*D*3-	Normal	*D*1-
CD (Poros 4B)	*D*4*D*4	Dwarf	*D*1-*D*3-*D*4-	Normal	*D*1-*D*4-
Bersée (B)	—	Normal	*D*1-*D*3-	Normal	*D*1-

d3d3D4D4. Dwarfing genotypes in this test would be *D1d1d2d2D3d3D4d4* whilst the monosomic hybrid of 2D would be *D1d1d2d2D3d3d4* and have the normal phenotype.

The range of substitutions into 'Cappelle-Desprez' and 'Bersée' was tested for hybrid dwarfing genes by crossing the donor and recipient varieties and each of the three substitution lines involving chromosome 2B, 2D or 4B with both 'Timstein' and CS (Timstein 2D). The results (*Table 1*) show that of the donor varieties, 'Besostaya I', 'Desprez 80', 'Mara' and 'Poros' produce dwarfs when crossed with 'Timstein' and normals when crossed with CS (Timstein 2D). This would indicate the presence of either *D2* or *D4* in each of these varieties. If both *D2* and *D4* had been present then crosses with CS (Timstein 2D), the *D1* carrier, would have produced dwarf phenotypes. Neither 'Bersée' nor 'Vilmorin 27' carry *D2* or *D4* since hybrids with 'Timstein' were normal.

The results of the crosses with the 'Bersée' and 'Cappelle-Desprez' substitution lines (*Table 1*) clearly implicate chromosome 2B, since substitutions of this chromosome from 'Besostaya I', 'Desprez 80', 'Mara' and 'Poros' all give dwarfs on hybridisation with either 'Timstein' or CS (Timstein 2D). The gene *D2* carried by chromosome 2B therefore presumably occurs in all these varieties.

Dwarf phenotypes where *D2* or *D4* is required to be homozygous would not be expected to appear until the F_2 generation, so progeny of a number of crosses where the F_1 was predicted to be either *D1d1D2d2* or *D1d1D4d4* and of normal height were grown on for a further generation. Classification of this progeny gave dwarf plants as expected.

Tab. 2 F_2 segregation from hybrids having *D1* combined with either *D2* or *D4*

Cross	F_2 segregation		χ^2 13 : 3 {1}
	normal	dwarf	
a) Segregation of *D1d1D2d2* hybrids			
Mara × CS (Timstein 2D)	165	32	0.81
Poros × CS (Timstein 2D)	154	32	0.29
b) Segregation of *D1d1D4d4* hybrids			
Cappelle-Desprez (CD) × CS (Timstein 2D)	90	6	9.85***
CD (Desprez 80 4B) × CS (Timstein 2D)	374	32	31.48***
CD (Besostaya I 4B) × CS (Timstein 2D)	209	17	18.70***
CD (Mara 4B) × CS (Timstein 2D)	322	33	20.83***
CD (Poros 4B) × CS (Timstein 2D)	182	15	16.04***
	1177	103	

*** $P < 0.001$.

In the *D1d1D4d4* hybrids the frequency of normals : dwarfs is $\frac{1}{4}(4-2p+p^2) : \frac{1}{4}(2p-p^2)$ where p = the recombination frequency between *D1* and *D4*. For 1177 normal plants to 103 dwarfs, $p = 0.18 \pm 0.019$.

In two of the crosses involving either 'Poros' or 'Mara' with CS (Timstein 2D) to give *D1d1D2d2* hybrids, the F_2 segregated normal to dwarf plants with the expected 13 : 3 ratio (*Table 2*). However, the relative frequencies of normal to dwarf plants among the F_2 progeny of *D1d1D4d4* hybrids departed consistently from the 13 : 3 expected for independent segregation and thus confirmed the linkage between *D1* and *D4* reported by SILBAUGH and METZGER (loc. cit.). Pooling the results of the five hybrid populations segregating for *D1 and D4* (Heterogenity $\chi^2\{_4\} = 1.38$, $P < 0.9—0.8$) gave a recombination frequency of 0.18 ± 0.019 between the two genes. This is close to the estimate of 0.12 % given by SILBAUGH and METZGER (loc. cit.).

Types of dwarfism

This experiment brings together genes *D1* and *D3* from 'Timstein', *D2* from four different varieties and *D4* from 'Cappelle-Desprez' in a range of precisely known genetical combinations. Hybrid dwarfs can be selected with each of the six known dwarfing genotypes *D1-D2D2*, *D1-D4D4*, *D1-D2-D3-*, *D1-D2-D4-*, *D1-D3-D4-* and *D1-D2-D3-D4-*. A comparison could therefore be made between the different phenotypes produced.

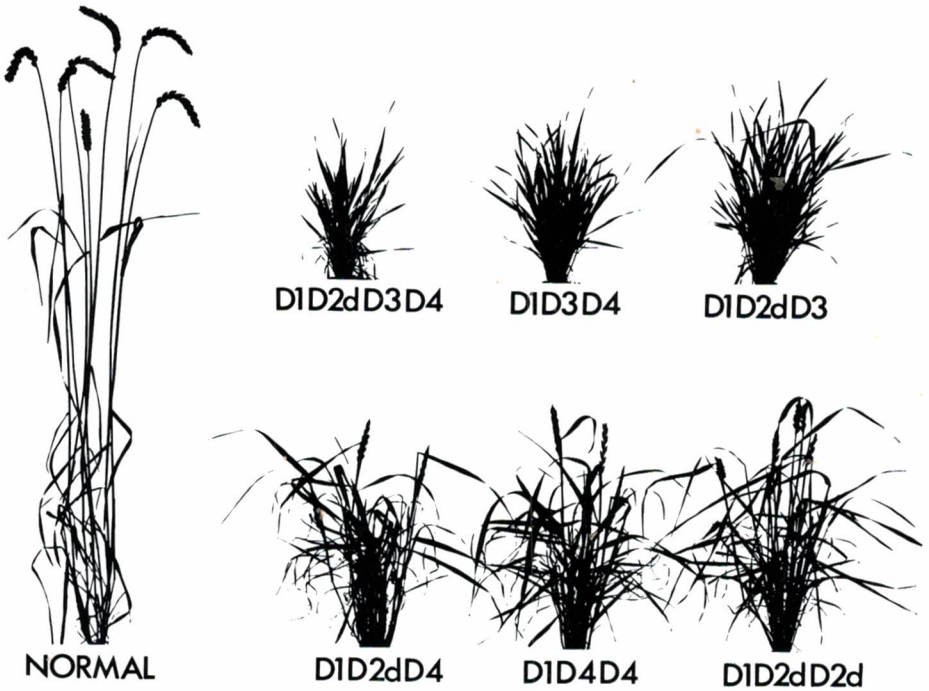

Fig. 1 Phenotypes of Type I and Type II dwarfs compared with normal plants. The two types of dwarf depend upon the presence or absence of *D3*. Within each type, variation occurs and can be related to different alleles at the *D2* locus or the presence or absence of *D2* or *D4*. The symbols *D1*, *D2*, *D3* and *D4* in the figure refer to either the homozygous dominant or heterozygous state at each locus. *D2d* refers to the allele from 'Desprez 80'

In the first lighted glasshouse experiment all the genotypes would have been classified by MOORE as type I as none flowered when grown under 18 hour days at 21°C minimum for a period in excess of three months. However, in the second series of experiments grown in an unlit glasshouse in summer, plants were easily classified into type I and type II (*Fig. 1*). Genotypes carrying *D*3 were all of type I whilst the three genotypes not carrying *D*3 were all of type II. Within these two phenotypic classes variation in vigour was present between genotypes and also where different alleles were present within a genotypic class.

*D*1*d*1*D*2*d*2*D*3*d*3*D*4*d*4 dwarfs carrying all four dwarfing genes in a heterozygous state were the weakest phenotypically, both as juveniles and adult plants. All dwarfs carrying *D*1, *D*3 and *D*4 were of similar vigour and were the next weakest to the four gene dwarf and weaker than lines carrying *D*1, *D*2 and *D*3. All three genotypes carrying *D*3 failed to flower in both experiments, confirming previous work indicating that *D*3 was necessary to produce type I dwarfs.

Progeny carrying *D*1, *D*2 and *D*4 were more vigorous as juvenile and adult plants than any of the lines carrying *D*3. In the second series of experiments these dwarfs flowered but maintained their dwarfing characteristics as type II dwarfs. Similar phenotypes were obtained in the F_2 dwarfs carrying *D*1 with either *D*2 or *D*4 homozygous. Both these genotypes were of similar juvenile and adult vigour to those carrying *D*1, *D*2 and *D*4 although of the three, those with *D*2 homozygous were probably the most vigorous plants.

Comparing the potency of the three non-essential dwarfing genes in promoting dwarfism, *D*3 would appear to be the most potent followed by *D*4 being slightly more potent than *D*2. The ranking of the genotypes would be *D*1-*D*2-*D*3-*D*4- > *D*1-*D*3-*D*4- > *D*1-*D*2-*D*3- > *D*1-*D*2-*D*4- > *D*1-*D*4*D*4 > *D*1-*D*2*D*2. It is interesting that whilst gene *D*3 would rank as the most potent non-essential gene in promoting dwarfism it is the only one of the three that cannot produce dwarfs when homozygous and in the presence of *D*1. The conclusion that the *D*4 gene is stronger than *D*2 is supported by the phenotypes of METZGER's true breeding dwarfs carrying *D*2 or *D*4 from 'Cheyenne' which were also grown in these experiments. Here *D*1-*D*2*D*2 dwarfs were much more vigorous than *D*1-*D*4*D*4 lines although both were clearly type II.

Multiple allelism

In the *D*1-*D*2-*D*3-*D*4- four gene dwarf, *D*2*m*, from 'Mara' produced a more vigorous plant than when *D*2 alleles came from 'Besostaya I', 'Desprez 80' or 'Poros'. A similar result was obtained when the *D*1-*D*2-*D*3- dwarfs were compared (*Fig. 2*). Again when *D*2*m* was present the plant was more vigorous, whereas *D*2 alleles from the other three varieties produced very similar but less vigorous phenotypes. In the *D*1-*D*2-*D*4 dwarf plants all were more vigorous than genotypes carrying *D*3 so the allelic differences here were less pronounced. Allelic variation at the *D*2 locus was most apparent when

the F_2 *D1-D2D2* dwarf progeny were extracted; again plants with *D2m* homozygous were the most vigorous (*Fig. 2*).

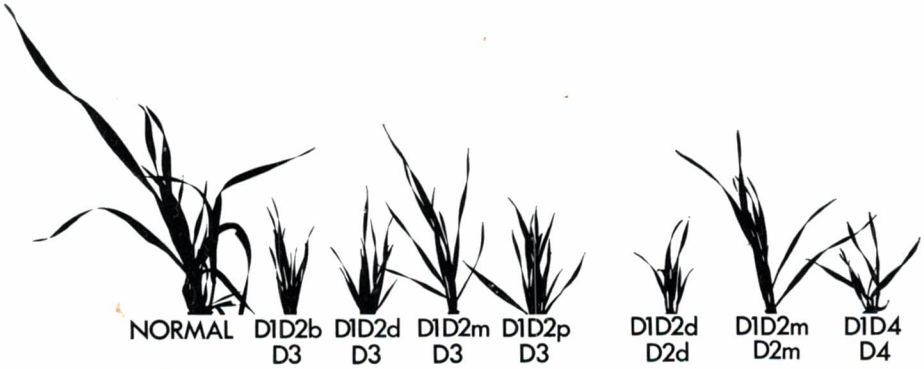

Fig. 2 Phenotypic differences produced by multiple allelism at the *D2* locus. *D2m* is less potent at producing dwarfism than *D2b*, *D2d* and *D2p*. *D2m*, *D2b*, *D2d* and *D2p* refer to different alleles from the varieties 'Mara', 'Besostaya I', 'Desprez 80' and 'Poros' respectively

All these tests were carried out using single chromosome substitution lines so that variation due to modifier genes in the background would be minimal. Furthermore all F_2 recombinant dwarf progeny carrying *D2m* maintained the increased vigour so that the presence of linked modifier genes is unlikely.

In these experiments the dominant genes for the other three loci came from similar sources so allelic variation would not be expected. Variation at the *D1* locus can be postulated by comparing the vigour of METZGER's true breeding *D1D1D2D2* and *D1D1D4D4* dwarf lines with that of similar dwarf lines extracted here. *D1* in METZGER's lines comes from Selection 1403, whilst in the present experiments it comes from 'Timstein'. Although still type II, the comparable dwarfs derived using 'Timstein' were much less vigorous. This was also confirmed when the substitution of 'Cheyenne 2D' into 'Chinese Spring', the source of the *D4* allele in METZGER's true breeding dwarf, was used in crosses with CS (Timstein 2D) to form a *D1-D4D4* dwarf line. The line with *D1t* from 'Timstein' was much less vigorous than the line with *D1s* from Selection 1403. Again, the complete correlation of variation in vigour with segregation at the *D1* locus suggests that modifiers are not responsible. Material is not at present available to test for variation at the *D3* and *D4* alleles.

Modifier genes

The hybrid dwarf progeny obtained when 'Timstein' was crossed onto the 'Cappelle-Desprez' monosomics were all of type I. Amongst the monosomic progeny, variation was found in vigour and was related to the missing chromosome. All plants had the characteristic thick dark green leaves but variation was seen in height and tillering. A rough classification was made into very poor clumps with few short tillers, poor clumps of intermediate habit and secondary clumps. Secondary clumps had increased height and tiller number

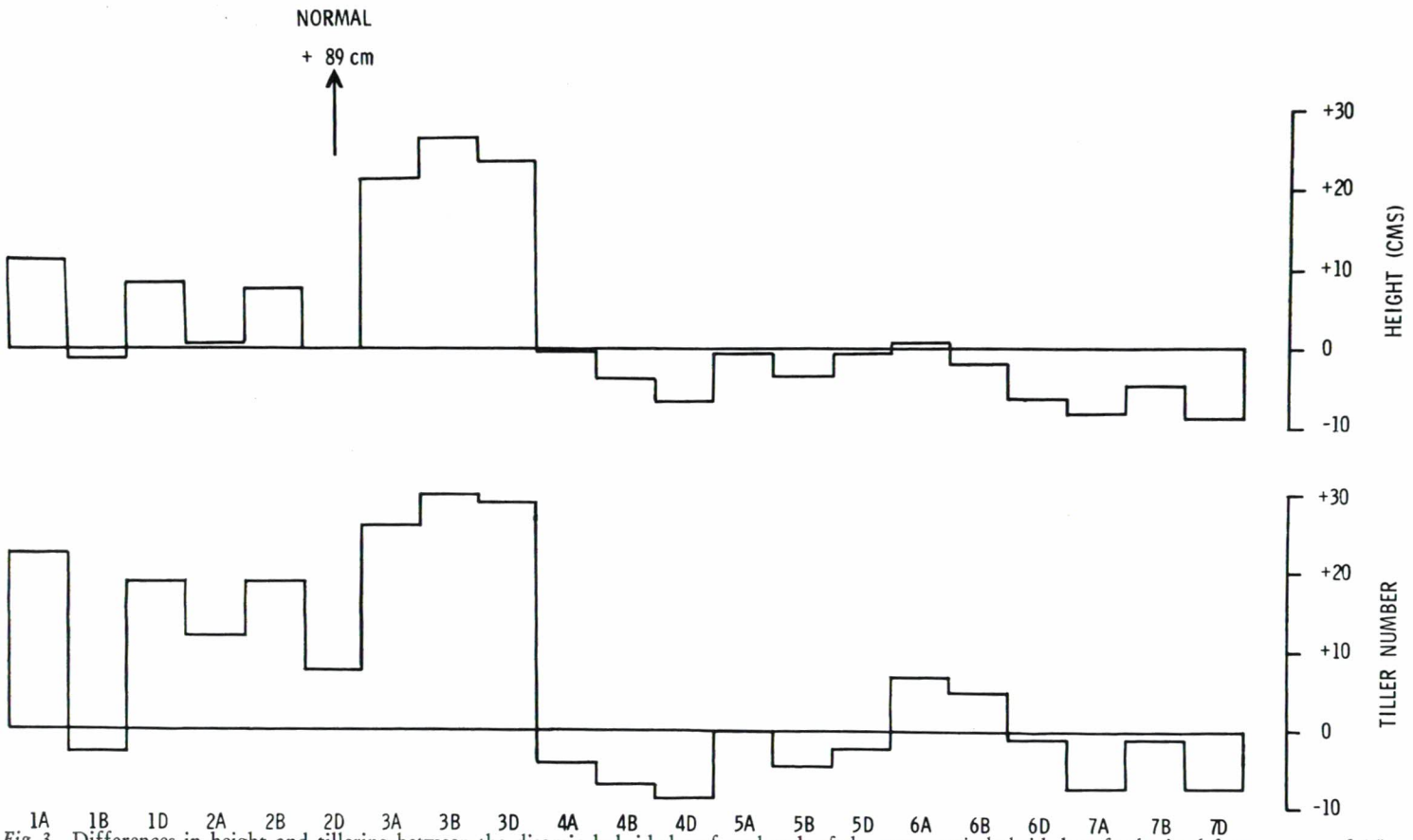

Fig. 3 Differences in height and tillering between the disomic hybrid dwarf and each of the monosomic hybrid dwarfs obtained from crosses of 'Timstein' onto each of the 21 monosomic lines of 'Cappelle-Desprez'. The hybrid monosomic for chromosome 2D lacks *D4* so that this hybrid is normal

and produced a second flush of growth giving tillers taller than those first produced but still not resulting in flowering. In the secondary clumps growth continued for up to twelve months before the plants finally died.

The degree of dwarfing was found to be constant within a homoeologous group although large variation was seen between groups (*Fig. 3*). All group VII plants produced extremely feeble dwarfs that usually died within a few weeks. About six tillers were produced with a height of about 10 cms. Group V plants were also feeble. The remaining groups were of intermediate growth with the exception of group III where all plants gave rise to secondary clumps producing about 40 tillers up to 40 cms high.

Discussion

The work described here confirms the already established chromosomal locations of the genes *D*1, *D*2, *D*3 and *D*4 (HURD and MCGINNIS 1958, HERMSEN 1963, SILBAUGH and METZGER 1970), and has established a second variety, 'Cappelle-Desprez', as carrying *D*4.

The work also emphasises the benefits of using precisely defined genetic stocks, such as monosomic series and whole chromosome substitution lines for carrying out genetical analyses as well as the need to use genetically pure stocks. Thus, the 'Vilmorin 27' used in these experiments carried no hybrid dwarfing genes but other lines of this variety have been classified previously as carrying *D*2 (HERMSEN 1967). Also, the 'Cappelle-Desprez' used in these studies carried *D*4, whilst stocks used at a much earlier date as donor parents in the development of single chromosome substitution series into 'Chinese Spring' carried no hybrid dwarfing genes.

The classification of parental varieties has previously been carried out by crossing unknown genotypes on to a series of 4 tester varieties (HERMSEN 1967). Such tests are based upon the 3 gene model excluding *D*4. As this gene has now been located in two unrelated varieties, 'Cappelle-Desprez' and 'Cheyenne', its presence cannot be ignored. Four homozygous genotypes carrying *D*4 which are not true breeding dwarfs are possible. If these genotypes, *d*1*d*1*d*2*d*2*d*3*d*3*D*4*D*4, *d*1*d*1*D*2*D*2*d*3*d*3*D*4*D*4, *d*1*d*1*D*2*D*2*D*3*D*3*D*4*D*4 and *d*1*d*1*d*2*d*2*D*3*D*3*D*4*D*4 are hybridised with HERMSEN's tester lines (*Table 3*) it is clear that misclassifications occur. Three of the genotypes would be classified as Class II lines carrying genes *D*2 and *D*3 whilst the fourth cannot be distinguished from the *D*2 carriers in Class IV. With HERMSEN's grouping Class II lines can only be said to carry at least two of the genes *D*2, *D*3 and *D*4 in any combination and Class IV lines to carry either *D*2 or *D*4. The former could most readily be distinguished by cytogenetical tests in which monosomics for chromosomes 2B, 2D and 4B are test-crossed with a *D*1 carrier, whereas the two Class IV genotypes could be distinguished by also crossing with a *D*1 carrier and establishing the presence or absence of linkage with *D*1.

HERMSEN (1967) lists hybrid dwarfing genotypes of 315 varieties. Of these, only 32 are classified as carrying no dominant genes. The widespread

Tab. 3 Hermsen's test for determining the genotype of an unknown variety

Tester varieties				Gametal genotype of unknown variety	Genotypic class
Pure breeding Dwarf (*D1D2d3*)	Kenya Farmer (*D1d2D3*)	Mendel (*d1D2D3*)	Big Club (*D1d2d3*)		
Phenotype of hybrid between tester and unknown variety					
Dwarf	Dwarf	Normal	Normal	*d1D2d3*	II
Dwarf	Dwarf	Normal	Dwarf	*d1D2D3*	IV
Classification of possible *D4* genotypes					
Dwarf	Dwarf	Normal	Normal	*d1d2d3D4*	IV
Dwarf	Dwarf	Normal	Dwarf	*d1D2d3D4*	II
Dwarf	Dwarf	Normal	Dwarf	*d1D2D3D4*	II
Dwarf	Dwarf	Normal	Dwarf	*d1d2D3D4*	II

N. B. Only gametal genotypes are shown for the tester and unknown genotypes.

occurrence of these hybrid dwarfing genes may indicate that they confer some selective advantage. Many of the lines used in the present study in which different chromosomes carrying dominant hybrid dwarfing genes have been substituted into 'Cappelle-Desprez' and other varieties have also been studied under field and glasshouse conditions. Scores for various agronomic characters indicate that there is no obvious correlation between any of these characters and the presence of dominant hybrid dwarfing genes. Certainly, on their own the genes do not appear to reduce height.

However, a possible character that could be associated is that of day-length sensitivity. It is known that the 2B, 2D and 4B chromosomes that carry *D1*, *D2*, *D3* and *D4* also carry genes for day-length sensitivity (HALLORAN and BOYDELL 1967, LAW et al. 1978). WELSH et al. (1973), in crosses of the insensitive variety 'Sonora 64' onto the 21 monosomics of the sensitive variety 'Cheyenne', showed that chromosomes 2D and 2B carried the major genes, *Ppd* 1 and *Ppd* 2 respectively for day-length insensitivity. 'Cheyenne' therefore carries the *Ppd* 1 allele for sensitivity and *D4* on chromosome 2D and the *Ppd* 2 allele for sensitivity and *D2* on chromosome 2B. It thus may be possible to establish a correlation between varieties having dominant dwarfing genes and day-length sensitivity genes. Varietal information about these two characters is not readily available at the moment, and, in any case, the definitive proof of a causel relationship between hybrid dwarfing and day-length response will depend upon the establishment of a genetic correlation rather than one based on varieties. Such a genetical investigation is currently being carried out at this Institute.

In conclusion, it should be mentioned that no Type III dwarfs were found in the investigations reported here, although other genotypes producing this phenotype have recently been observed in related material. Preliminary ana-

lyses of these lines suggest that a completely different genetical system not involving *D*1 is involved in the control of this type of hybrid dwarfism.

Zusammenfassung

Die Genetik des Zwergwuchses bei Weizenbastarden

Monosome Chromosomensubstitutionslinien wie auch Substitutionslinien innerhalb der Sorten wurden benutzt, um vier Gene — *D*1, *D*2, *D*3 und *D*4 —, die die Verzwergung in Hybriden steuern, zu lokalisieren. Zwerge mit sechs verschiedenen Kombinationen von Zwergwuchsgenen wurden hergestellt. Die Phänotypen dieser Linien zeigten, daß *D*3 unentbehrlich war, um Zwerge des Typs I zu erhalten. Multiple Allelie wurde am Locus *D*2 bestimmt und am Locus *D*1 postuliert. Es ist bewiesen, daß Modifikatorgene, die auf das Wachstum der Hybridzwerge einwirken, vorkommen und innerhalb der homöologen Gruppen konstant bleiben.

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