The use of reciprocal monosomic analysis to detect variation between certain chromosomes of the wheat varieties Bersée and Sava

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To study the importance of particular chromosomes in the control of a number of agronomic characters in the high yielding semi-dwarf Yugoslav winter wheat Sava, reciprocal monosomics were developed between homologous Bersée and Sava monosomics. Chromosomes 2A, 2D, 5A, 5D and 7D are investigated.
Chromosome 2D is shown to be the most important of the chromosomes studied in controlling allelic differences between Bersée and Sava.

Aneuploids have been widely used in the genetic studies of several characters in wheat. Much information can be obtained by comparing homologous chromosomes from the many available monosomic series (Law et al 1983, Worland 1987). This method can indicate which chromosomes show allelic variation for a particular character and are suitable candidates for more intensive analysis.

Another promising approach for obtaining preliminary information is the reciprocal monosomic method. This was first suggested by McKewan and Kaltsikes (1970) and has been used to study the chromosomal control of a number of characters (Law et al 1981, Law 1982, Law et al 1983). It permits the study of allelic differences between homozygous homologous chromosomes from different varieties in genetically equivalent backgrounds.

The aim of this paper is to determine the importance of particular chromosomes on the control of a number of agronomic characters between the semi-dwarf variety Sava and the tall variety Bersée utilising monosomics developed in both these varieties and crossing them reciprocally.

METHODS AND MATERIALS

The Yugoslavian variety Sava is a high-yielding, early maturing, semi-dwarf winter wheat. Bersée, of French origin, is also a high yielding winter wheat but is tall and late flowering. Monosomic series are available in Bersée (developed by Law & Worland) and Sava (developed by Petrović). As earlier comparison of the phenotypes of each of these monosomic series suggested that chromosomes from groups 2, 5 and 7 might be important in the control of allelic differences between these two varieties, reciprocal monosomics were developed for some of the chromosomes from these three groups.

In making reciprocal monosomic comparisons for a particular chromosome, the two homologous monosomics from the different varieties are crossed reciprocally and monosomic F_1 progeny selected. These monosomic hybrids carry a hemizygous chromosome from the male parent. In one of the reciprocals this chromosome will derive from one of the varieties and in the other from the second variety. In both reciprocals the back-grounds will be identical and heterozygous. On

Table 1. Means of F_3 lines, homozygous for chromosomes 2A, 2D, 5A, 5D or 7D of either Bersée or Sava, derived by reciprocally crossing monosomics of these two varieties (grown Novi Sad 1983/4).

Investigated chromosome	Height (cm)	Tillers (plant)	Plant yield (g)	50 grains (g)
2A B	82.3 ± 1.82	9.4 ± 0.37	12.37 ± 1.10	1.53 ± 0.01
S	94.5 ± 1.22*	9.2 ± 0.23	13.66 ± 0.29	1.49 ± 0.05
2D B	95.2 ± 2.09	8.6 ± 0.52	11.46 ± 0.96	1.53 ± 0.05
S	77.0 ± 2.27*	7.6 ± 0.43	13.23 ± 1.61	1.76 ± 0.04*
5A B	86.9 ± 1.70	10.5 ± 0.39	11.63 ± 0.74	1.41 ± 0.02
S	91.4 ± 1.21*	10.3 ± 0.35	12.05 ± 0.64	1.59 ± 0.01*
5D B	86.2 ± 1.63	9.6 ± 0.28	13.53 ± 0.74	1.66 ± 0.00
S	89.9 ± 1.70	10.3 ± 0.51	13.46 ± 0.49	1.55 ± 0.01*
7D B	85.4 ± 1.28	9.6 ± 0.43	12.68 ± 0.72	1.59 ± 0.02
S	82.9 ± 2.35	8.6 ± 0.51	12.89 ± 1.26	1.59 ± 0.03
	Ear Length (cm)	**Spikelet No.**	**Grains/ear**	**Ear yield (g)**
2A B	9.3 ± 0.49	20.1 ± 0.46	48.8 ± 2.66	1.50 ± 0.13
S	11.3 ± 0.33*	21.0 ± 0.26	47.3 ± 1.44	1.41 ± 0.04
2D B	11.7 ± 0.44	23.2 ± 0.52	49.0 ± 2.52	1.53 ± 0.04
S	9.7 ± 0.26*	21.1 ± 0.42*	53.7 ± 2.81	1.90 ± 0.12*
5A B	10.4 ± 0.30	20.0 ± 0.33	46.8 ± 1.35	1.33 ± 0.09
S	9.7 ± 0.16	20.1 ± 0.36	47.2 ± 1.39	1.51 ± 0.06
5D B	9.2 ± 0.18	20.2 ± 0.31	49.7 ± 1.07	1.65 ± 0.05
S	9.8 ± 0.30	20.0 ± 0.37	49.3 ± 1.37	1.53 ± 0.04
7D B	9.6 ± 0.30	21.0 ± 0.60	47.8 ± 1.07	1.57 ± 0.04
S	10.2 ± 0.24	21.7 ± 0.59	48.6 ± 1.97	1.54 ± 0.10

*Differences significant <0.05
B = Bersée; S = Sava

selfing a number of disomic F_2 lines can be extracted which will be homozygous for the investigated chromosome. If a number of lines from the two reciprocal populations are compared, then the backgrounds of the two populations will on average be the same so that any differences will relate to allelic variation carried by the chromosomes under study.

In this study, from 8 to 15 F_3 lines for chromosomes 2A, 2D, 5A, 5D and 7D, for each reciprocal were grown for comparison under the contrasting environments of Cambridge, UK and Novi Sad, Yugoslavia. Plants were sown in dibbed rows, eleven plants per row, three replicates being planted in each environment. In Cambridge chromosome 5A and 5D lines were sown in early October and chromosome 2A, 2D and 7D lines in the following January. In Novi Sad all material was sown in mid October.

RESULTS

Comparisons between the overall means of the F_3 lines from paired reciprocal monosomic families measure allelic differences between homologous chromosomes. In this experiment large differences were associated with chromosome 2D, indicating that its gene array plays an important role in varietal adaptation. No differences were found for chromosome 7D indicating this chromosome has little effect on varietal adaptation. Intermediate results were associated with chromosomes 2A, 5A and 5D (Tables 1-3).

Chromosome 2A comparisons (Tables 1, 2) showed that in both environments genes on the

Table 2. Means of F_3 lines homozygous for chromosomes 2A, 2D, 5A, 5D or 7D of either Bersée or Sava, derived by reciprocally crossing monosomics. Experiment grown in Cambridge 1983/4. Chromosomes 5A and 5D sown October 1983, 2A, 2D and 7D sown January 1984.

Investigated chromsome	Height (cm)	Tillers (plant)	Plant yield (g)	Ear emergence (days)
2A B	93.5 ± 1.57	5.7 ± 0.48	11.78 ± 1.69	6.28 ± 0.55
S	99.0 ± 1.17*	6.3 ± 0.35	13.07 ± 0.76	8.23 ± 0.48*
2D B	103.5 ± 2.58	5.7 ± 0.44	12.88 ± 1.21	7.05 ± 0.48
S	85.5 ± 1.22*	4.1 ± 0.20*	8.88 ± 0.85*	3.47 ± 0.48*
5A B	116.9 ± 2.35	9.7 ± 0.36	19.44 ± 1.24Δ	8.91 ± 0.33
S	122.9 ± 2.23	9.6 ± 0.38	29.01 ± 1.35*	7.89 ± 0.27*
5D B	118.1 ± 2.64	8.9 ± 0.41	28.27 ± 1.06	7.49 ± 0.60
S	118.4 ± 1.91	9.1 ± 0.46	28.69 ± 0.97	7.96 ± 0.52
7D B	90.4 ± 2.79	5.9 ± 0.52	11.21 ± 1.29	7.28 ± 0.28
S	88.8 ± 2.50	6.1 ± 0.49	11.80 ± 1.29	7.00 ± 0.71

*Differences significant <0.05; Δ Necrotic following ear emergence
B = Bersée; S = Sava
Ear emergence in days from 1st June

Sava 2A homologue increased height relative to Bersée 2A. In England, where ear emergence was recorded, the reciprocal population carrying Sava 2A flowered significantly later than the population with the Bersée homologue. This suggests that Sava 2A carries an allele for increased sensitivity to daylength at the *Ppd3* locus which, through extending the growing period, may increase plant height and could also be responsible for the associated increase in spike length. No effects of chromosome 2A were seen on other yield components.

In the reciprocal crosses involving 5A, Sava 5A also promotes a height increase of about 5cm compared to the Bersée homologue. This difference is probably due to allelic variation amongst height suppressing genes known to occur on chromosome 5A (Law & Worland 1973). Normally a chromosome 5A height reduction is associated with reductions in yield, and here the shorter Bersée 5A line reduces plant yields in England and grain size in Yugoslavia. Yield reductions in England were increased by necrotic patches developing at ear emergence time on the foliage of reciprocals carrying Bersée 5A. Similar symptoms were not seen in Yugoslavia. This might be a resistance reaction to the presence of yellow rust (*Puccinia striiformis*). Only one difference was found for chromosome 5D, where the Bersée 5D line showed increased grain size.

Significant allelic variation for ear emergence, height, spike length, spikelet number, ear and plant yield and grain size were associated with chromosome 2D (Tables 1-3). Ear emergence time is accelerated by Sava 2D in both environments. Although in this experiment the effect was greatest in Yugoslavia (9 days), it is known that this character is very sensitive to climatic conditions prevailing at flowering time and will vary over seasons (Worland, Petrovic & Law 1988). Orthogonal comparisons show a major genotype effect probably due to *Ppd1*, a gene for daylength insensitivity (Worland & Law 1986), and an environmental interaction (Table 3).

A highly significant height reduction of about 18cm is associated with Sava 2D in both environments. This reduction is thought to be due to the combined effects of *Rht8*, an Akakomugi height reducing gene, and *Ppd1* which reduced height by shortening the growing period (Worland & Law 1986). Orthogonal comparisons show height reduction to be independent of environmental influence. A reduction in spikelet number, also associated

Table 3. Comparisons between means of F_3 lines homozygous for chromosome 2D of Bersée v Sava grown in England and Yugoslavia. Estimates of genotype, environmental and genotype × environment interactions are shown.

	England			Yugoslavia			Genetic estimates		
	Bersée 2D (X_1)	Sava 2D (X_2)	Difference	Bersée 2D (X_3)	Sava 2D (X_4)	Difference	Genotype	Environment	G × E
Ear Emergence (days)	7.05	3.47	+3.58***	9.00	1.00	+8.00***	+2.90***	+0.13	−1.10**
Spikelet no.	24.69	23.55	+1.14***	23.25	21.14	+2.11***	+0.81***	+0.96***	−0.24
50 grain wt. (g)	1.99	2.23	−0.24*	1.53	1.76	−0.23**	−0.12*	−0.23**	+0.02
Grains/ear	52.46	47.24	+5.22	49.41	53.71	−4.30*	+0.23	−0.86	+2.38*
Plant yield (g)	12.88	8.88	+4.00*	9.93	11.28	−1.35	+0.66	−0.14	+1.34*
Tiller no.	5.73	4.11	+1.59**	8.56	7.64	+0.92	+0.66*	−1.59***	+0.18
Height	103.50	85.54	−17.96***	95.20	77.00	−18.20***	+9.04***	+4.21**	−0.06

Prob * 0.05–0.01 **0.01–0.001 ***<0.001

Genetic estimates
- Genotype (Bersée v Sava) $\frac{1}{4}(X_1 - X_2 + X_3 - X_4)$
- Environment (England v Yugoslavia) $\frac{1}{4}(X_1 + X_2 - X_3 - X_4)$
- Genotype v Environment $\frac{1}{4}(X_1 - X_2 - X_3 + X_4)$

with Sava 2D, is probably an effect of *Ppd1* shortening the period of time available for initiation of floral primordia. The significant reduction in tiller number, of Sava 2D lines could also be a pleiotropic effect of the same gene.

Whilst Sava 2D increases grain size in both environments without environmental interaction, the effects of the 2D gene array on both grain number per ear and final plant yield are environmentally sensitive. In England both the number of grains developing in the ear and the final plant yield are increased by the Bersée 2D gene array. This could be correlated with *Ppd1* increasing spikelet number and ear length thus providing more primordia and space for grain development. In Yugoslavia, however, it is the Sava 2D gene array that is associated with increases in the number of grains per ear and in ear and plant yield. As *Ppd1* is here reducing spikelet number, the increased number of grains per ear must be due to increased spikelet fertility. Studies of reciprocal monosomics, measuring whole chromosome effects, do not allow the increased fertility to be associated with particular members of the Sava 2D gene array. Both grain number per ear and plant yield show significant genotype environmental interactions confirming the importance of the 2D gene arrays to varietal adaptation.

CONCLUSIONS

The reciprocal monosomics developed between chromosomes of Bersée and Sava demonstrate that the gene array on chromosome 2D is of particular importance in determining the adaptability of the two varieties to contrasting environments.

Interestingly, although Sava is considerably shorter than Bersée, two of its five chromosomes examined promote height in comparison to the tall variety by a combined minimum of 11cm. Only Sava 2D reduced height suggesting that other important height reducing genes may still await discovery in this genotype.

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