*Euphytica* **115:** 215–220, 2000.



# The effects of homoeologous group 3 chromosomes on grain colour dependent seed dormancy and brittle rachis in tetraploid wheat

N. Watanabe & N. Ikebata
*Watanabe Laboratory, Faculty of Agriculture, Gifu University, 1-1 Yanagido, Gifu 501–1193 Japan*

Received 18 June 1999; accepted 13 February 2000

*Key words:* brittle rachis, chromosome substitution, grain colour, seed dormancy, *Triticum durum*, *Triticum dicoccoides*

**Summary**

'Langdon' (LDN), a durum wheat (*Triticum turgidum* L. var. *durum*) cultivar, and a set of chromosome substitution lines of Langdon, where A or B genome chromosome were replaced with a homologous chromosome of wild emmer wheat, *T. turgidum* ssp. *dicoccoides* (DIC), were used to assess the effect of the specific chromosome on seed dormancy in tetraploid wheat. The LDN(DIC 3A) and LDN (DIC 3B) lines showed significantly lower seed germination than Langdon. It appears that LDN(DIC 3A) and LDN(DIC 3B) have red grain whose allele were designated as *R-A1b* and *R-B1b*, respectively and the rachises of LDN(DIC 3A) and LDN(DIC 3B) were fragile. The alleles for brittle rachis were designated as $Br_2$ for LDN(DIC 3A) and $Br_3$ for LDN(DIC 3B). From the $F_2$ of the crosses, Langdon/LDN(DIC 3A) and Langdon/LDN(DIC 3B), $Br_2$ was located approximately 44.2 cM from the *R-A1b* locus and $Br_3$ approximately 47.0 cM from the *R-B1b* locus, respectively. Recombinant inbred chromosomal lines for 3A and 3B were used to assess (1) the linkage relationship between grain colour and fragile rachis, and (2) the effect of grain colour on germination. Estimated distance between *R-B1b* – $Br_2$ was 39.6 cM. For the 3A population, germination percentage of both colour groups was 12.4% for the red grain group and 68.6% for the amber group, respectively. For the 3B population, germination percentage of the red group was 7.3% and that of the amber group was 82.1%. For both populations, differences were statistical significant by *t*-tests. We considered that seed dormancy of *T. turgidum* ssp. *dicoccoides* was dependent on grain colour. It raised the possibility that brittle rachis is due to a paralogous gene set on homoeologous group 3 chromosomes.

## Introduction

Seed dormancy is one of the important characteristics of durum wheat. Preharvest sprouting caused by low seed dormancy may reduce end-use quality. Clarke et al. (1994) reported considerable genetic variation in sprouting resistance in durum wheat. Wild progenitors of crop species depend on seed dormancy and spike shattering to adjust their survival to the ecological niche. Seed dormancy of the wild subspecies might be utilized to develop resistance to preharvest sprouting in domesticated durum wheat. Wild emmer wheat (*T. turgidum* ssp. *dicoccoides*) is the only progenitor that is fully interfertile with cultivated *T. turgidum* (Zohary, 1983). Disarticulation of ssp. *dicoccoides* occurs in the field at maturity and the kernels of ssp. *dicoccoides* have considerable dormancy.

Joppa & Cantrell (1990) developed a complete set of Langdon – ssp. *dicoccoides* substitution lines. The objective of our study was to identify chromosomal location of the genes for seed dormancy and brittle rachis and their possible linkage relationships in ssp. *dicoccoides*.

## Materials and methods

### *Plant materials*

In this study, a durum wheat cultivar Langdon (LDN) and a set of chromosome substitution lines of Lang-

don, where A or B genome chromosomes were replaced with homologous chromosome of wild emmer wheat, ssp. *dicoccoides* (DIC), were used to assess the effect of the specific chromosomes on seed dormancy. Langdon–DIC substitution lines were provided by Dr L.R. Joppa, USDA-ARS, Fargo, ND, USA. For example, in this study, a pair of LDN 1A chromosomes was replaced with a pair of chromosome 1A of DIC for LDN(DIC 1A) line. The designation for chromosome 4A and 4B are in accordance with the approval at the Seventh International Wheat Genetics Symposium (Gale & Snape, 1988). LDN(DIG 2B) was not available for the experiments. In the 1995/1996 season, LDN, ssp. *dicoccoides* and 20 lines of Langdon–DIC substitutions were grown in the experimental fields of Gifu University. In the 1996/1997 season, the LDN 3D(3A) D-genome chromosome substitution line (Joppa & Williams, 1988) was added for the experimental material.

*Genetic analysis*

In the 1996/1997 season, $F_2$ plants of two cross combinations, Langdon/LDN(DIC 3A) and Langdon/LDN(DIC 3B) were grown in the experimental fields of Gifu University. Also, in the 1996/1997 season, 82 lines of recombinant inbred chromosomal lines (RICL's) for DIC 3A and 91 lines of RICL's for DIC 3B were grown in the experimental fields of Gifu University. The recombinant inbred chromosomal lines (RICLs) for DIC 3A and DIC 3B were produced by Dr L.R. Joppa. For example, LDN (DIC 3A) was crossed with LDN and several $F_1$ plants were grown. Pollen from $F_1$ plants was used to pollinate emasculated heads of LDN 3D(3A). The crossed seeds were grown in individual pots in a greenhouse and were selfed and sampled to determine chromosome pairing ($13'' + 2'$) at metaphase one (MI) of meiosis. One of the univalents was chromosome 3D and the other was a recombined chromosome consisting of portions of the DIC 3A chromosome and portions of the LDN 3A chromosome. Each recombined 3A chromosome pair should differ from all other recombined 3A chromosomes unless crossovers were identical. Several selfed seeds from each $F_1$ plant were grown in individual pots in a greenhouse. Each $F_2$ plant that had $14''$ at MI of meiosis was crossed with double ditelosomic 3A line of LDN and the testcrosses were grown in the greenhouse to differentiate $F_2$ plants with a pair of 3D chromosomes from those with a homozygous pair of recombined 3A chromosomes (Joppa, personal communication).

*Assessment of seed characteristics*

*Rachis fragility.* The trait of brittle rachis can be defined as a spike having a rachis that can be easily broken. The rachis of ssp. *dicoccoides* breaks at the node above the insertion point of the spikelet, thus creating a wedge-shaped spikelet unit attached to the rachis internode beneath. Two observers independently assessed rachis fragility and classified into two classes, tough and brittle.

*Seed germination.* Six weeks after anthesis, spikes of each line were harvested, and dried for 2 weeks in greenhouse to avoid rain. After assessment of rachis fragility, the spikes were threshed for germination tests, which were started 2 weeks after harvest. Seeds were embedded in filter paper moistened with distilled water in 9 cm diameter Petri dishes at 20 °C. The number of seeds germinated was recorded daily. The number of seed per replication was 50 with three replications. Germination tests were repeated with an interval of two weeks until 2 months after harvest.

*Grain colour.* After the seeds were soaked in 5% (w/v) NaOH solution for 1 hour, the grain colour of each line was classified as red or amber.

*Statistical analysis*

Variance analysis was used to determine whether differences exist between lines. Differences between lines were compared using LSD methods. For statistical analysis, germination percentages were transformed into the Arcsine scale. In the text, arcsine-transformed data are indicated in parenthesis following the germination percentage, when required.

## Results

*Homoeologous group 3 chromosomes for seed dormancy and brittle rachis*

Table 1 describes the results of the experiments in 1995/1996 (Table 1). Seed germination of *T. turgidum* ssp. *dicoccoides* was 3% at 7 days after the start, whereas Langdon germinated 99% after 7 days. Germination percentage of LDN(DIC 3A), LDN(DIC 3B) and LDN(DIC 4B) lines differed significantly from

*Table 1.* Seed germination (%) at 7 and 14 days starting at two weeks after harvest in 1996

| Genotype | 7 days | | 14 days | |
|---|---|---|---|---|
| | Germination (%) | Arcsine-transformed data | Germination (%) | Arcsine-transformed data |
| *T. dicoccoides* | 3 | 1.72* | 7 | 4.02 ± 0.6 |
| Langdon | 99 | 81.9 | | |
| LDN(DIC 1A) | 97 | 76.5 ± 2.72 | | |
| LDN(DIC 2A) | 98 | 81.9 | | |
| LDN(DIC 3A) | 15 | 8.64 ± 2.01* | 25 | 14.5 ± 1.6 |
| LDN(DIC 4A) | 99 | 81.9 | | |
| LDN(DIC 5A) | 99 | 81.9 | | |
| LDN(DIC 6A) | 98 | 79.2 ± 2.72 | | |
| LDN(DIC 7A) | 99 | 81.9 | | |
| LDN(DIC 1B) | 99 | 79.2 ± 2.7 | | |
| LDN(DIC 3B) | 78 | 51.7 ± 4.4* | 94 | 71.5 ± 5.4 |
| LDN(DIC 4B) | 90 | 64.4 ± 4.4* | 96 | 74.7 ± 3.9 |
| LDN(DIC 5B) | 99 | 81.9 | | |
| LDN(DIC 6B) | 99 | 79.2 ± 2.7 | | |
| LDN(DIC 7B) | 97 | 76.5 ± 2.7 | | |
| Lsd ($p = 0.05$, df = 28) | | 6.01 | | |

* Significantly different from Langdon at $p = 0.05$.

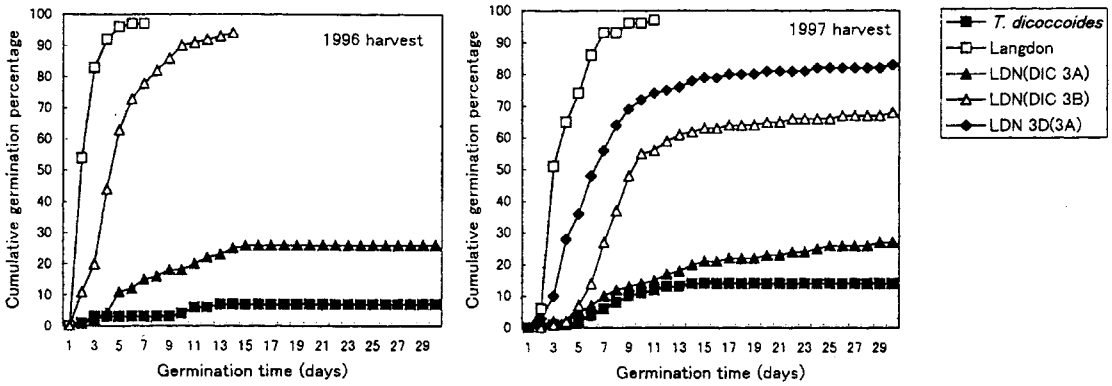


*Figure 1.* Time course of seed germination of Langdon, *T. turgidum* ssp. *dicoccoides* and chromosome substitution lines of homoeologous group 3. Germination tests were started 2 weeks after harvest in 1996 (left) and 1997 (right).

Langdon (Table 1). The percentage of germination in IDN(DIC 4B) was 90%, although LDN(DIC 4B) had significantly lower germination percentage than Langdon. The percentage of germination of ssp. *dicoccoides* and LDN(DIC 3A) were significantly lower than Langdon at the 14 days. We considered that the chromosomes of 3A and 3B were mainly concerned with seed germination and LDN(DIC 3A) had a stronger effect on seed dormancy than LDN(DIC 3B) (Figure 1). Even at two months after harvest, the germination percentage of ssp. *dicoccoides* was 20% and a special application of low temperature or GA was required to break dormancy (data not shown). Line LDN(DIC 3A) completely lost seed dormancy 6 weeks after harvest.

We found that the grain of LDN(DIC 3A) and LDN(DIC 3B) were red. Grain colour of Chinese Spring is red and it is controlled by the allele on the *R-D1b* focus. As shown in Figure 1, LDN 3D(3A) line had significantly lower germination than Langdon in the experiment in 1996/1997.

*Table 2.* Joint segregation for brittle rachis and grain colour in the $F_2$ of two crosses, associated $\chi^2$ values and map distances

a) Langdon/LDN(DIC 3A)

| Grain colour | Rachis | | $\chi^2$ analysis | |
|---|---|---|---|---|
| | Brittle | Tough | Ratio | Value[1] |
| Red | 114 | 26 | Dihybrid (9:3:3:1) | 9.07* |
| | | | Brittle rachis (3:1) | 0.09 |
| Amber | 28 | 19 | Grain colour (3:1) | 0.001 |
| | | | Linkage $\chi^2$ | 8.99* |

Linkage (*R-A1* – $Br_2$): 44.2 ± 8.4 cM.

b) Langdon/LDN(DIC 3B)

| Grain colour | Rachis | | $\chi^2$ analysis | |
|---|---|---|---|---|
| | Brittle | Tough | Ratio | Value[1] |
| Red | 106 | 29 | Dihybrid (9:3:3:1) | 12.03* |
| | | | Brittle rachis (3:1) | 0.57 |
| Amber | 32 | 23 | Grain colour (3:1) | 1.58 |
| | | | Linkage $\chi^2$ | 9.88* |

Linkage (*R-B1* – $Br_3$): 47.0 ± 8.5 cM.

[1] Values for significance at $p = 0.05$; 3.84 (df = 1), 7.81 (df = 3), respectively.
* Significant at $p = 0.05$.

*Table 3.* Linkage relationship between brittle rachis and grain colour in the the random inbred chromosomal lines (RICL's) for 3A and 3B chromosomes and associated $\chi^2$ values

a) Chromosome 3A

| Grain colour | Rachis | | $\chi^2$ analysis | |
|---|---|---|---|---|
| | Brittle | Tough | Ratio | Value[1] |
| Red | 26 | 26 | Dihybrid (9:3:3:1) | 6.00 |
| | | | Brittle rachis (3:1) | 0.05 |
| Amber | 14 | 16 | Grain colour (3:1) | 5.90* |
| | | | Linkage $\chi^2$ | 0.05 |

b) Chromosome 3B

| Grain colour | Rachis | | $\chi^2$ analysis | |
|---|---|---|---|---|
| | Brittle | Tough | Ratio | Value[1] |
| Red | 25 | 14 | Dihybrid (9:3:3:1) | 13.31* |
| | | | Brittle rachis (3:1) | 0.89 |
| Amber | 16 | 36 | Grain colour (3:1) | 1.86 |
| | | | Linkage $\chi^2$ | 10.56* |

Linkage (*R-B1* – $Br_3$): 39.6 ± 11.8 cM.

[1] Values for significance at $p = 0.05$; 3.84 (df = 1), 7.81 (df = 3), respectively.
* Significant at $p = 0.05$.

From the two years' experiments, it was concluded that the genes on the chromosomes of homoeologous group 3 induced seed dormancy of *T. turgidum* ssp. *dicoccoides* and seed dormancy may be related to grain colour. Chromosome 3A had the strongest effect on seed dormancy among the chromosomes of homoeologous group 3.

*Association of brittle rachis with grain colour*

The rachis of ssp. *dicoccoides* breaks at the node above the insertion point of the spikelet, thus creating a wedge-shaped spikelet unit attached to the rachis internode beneath. Disarticulation of LDN(DIC 3A) and LDN(DIC 3B) lines were similar to that of ssp. *dicoccoides*. The rachis of the other lines was tough. As single dominant gene ($Br_1$) controlling brittle rachis on the short arm of the 3D chromosome was reported in Tibetan weedrace of common wheat (Chen et al., 1998), we designated the allele for rachis fragility as $Br_2$ for LDN(DIC 3A) and $Br_3$ for LDN(DIC 3B). We did not find any spelt ($q$) factors, that may affect rachis fragility, in LDN(DIC 5A). Genetic analysis indicated that there was a linkage relationship between rachis fragility and grain colour, with distances 44.2 cM for $Br_2$ – *R-A1b* and 47.0 cM for $Br_3$ – *R-B1b*, respectively (Table 2).

*Grain colour dependent seed dormancy*

Recombinant inbred lines are the most suitable to assess the genetic basis for a physiological trait, because respective lines are homozygous. They offer an alternative way to assess linkage relationships of grain colour and brittle rachis. For RICL's 3A, rachis fragility segregated into 1:1 ratio, but grain clour did not segregate into 1:1. Eighty-two lines of RICL's for DIC 3A were re-assessed for grain colour in the 1997/1998 season and the result did not differ with Table 3.

We obtained excessive number of lines for red grain colour. For RICL's 3B, rachis fragilty and grain colour segregated into 1:1 ratio, respectively. Estimated distance between *R-B1* – $Br_3$ was 39.6 cM (Table 3). The result supports the hypothesis that brittle rachis and grain colour are genetically linked with recombination distance of 40–45 cM.

It is known that red seed coat was advantageous for seed dormancy (Gordon, 1979; Noll et al., 1982; Dyck et al., 1986). As shown in Figure 2, the germination percentage of the two groups was compared for 3A and 3B RICIL's populations for grain colour. For the

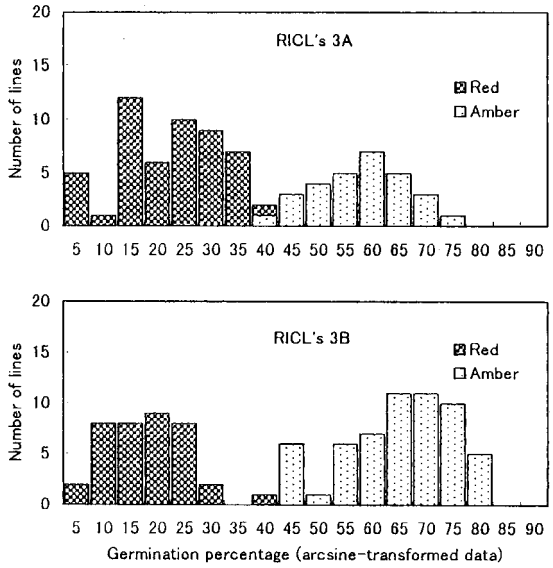


*Figure 2.* Comparison of germination percentage of two grain colour groups in RICL's populations for 3A and 3B chromosomes. Mean germination percentage of 3A population: 12.4% (20.6 ± 1.3) for the red group and 68.6% (55.9 ± 1.5) for the amber group. Mean germination percentage of 3B population: 7.3% (15.7 ± 1.1) for the red group, and 82.1% (65.0 ± 1.1) for the amber group. For both populations, differences between grain colour groups were statistical significant by *t*-tests.

3A population, the red group shows 12.4% (20.64 ± 1.3) and the amber group shows 68.6% (55.9 ± 1.5). For the 3B population, germination percentage of the red group was 7.3% (15.7 ± 1.1) and that of the amber group was 82.1% (65.0 ± 1.1). For both populations, differences were statistical significant by *t*-tests. We concluded that the level of seed dormancy was dependent on grain colour.

DePauw & McCaig (1983, 1987) and McCaig & DePauw (1992) recovered sprouting resistance from red kernelled wheats transferred into white-kernelled segregates. Four lines in RICL's for 3A and one line RICL's for 3B with amber grain fit into 40–50% class of germination percentage. We will assess them further whether their levels of dormancy are applicable for cultivars of durum wheat.

## Discussion

In this study, it was determined that the genes for grain colour and brittle rachis are located on chromosome 3A and 3B. Red grain colour is associated with dormancy. Dyck et al. (1986) found that seed dormancy was dependent on red grain colour in two populations of random inbred lines of spring bread wheat. The role of the red grain genes in resistance to sprouting was demonstrated in dormancy tests of near-isogenic red-grained lines of a white spring wheat, and the wheat (A, B and D) and barley (H) genomes share extensive homoeology (Flintham & Gale, 1996). The genes for red grain have been located on the long arms of chromosomes of homoeologous group 3 (McIntosh et al., 1998). Urbano et al. (1988) demonstrated that chromosome 3VS of *Dasypyrum villosum* induced red grain in the Creso/3VS addition line. The chromosome 3N of *Aegilops uniaristata* induced red grain in substitution lines in which 3N replaces wheat chromosome 3A, 3B or 3D (Miller et al., 1995).

There were several reports in which brittle rachis was controlled by the genes on homoeologous group 3 chromosomes. Riley et al. (1966) determined the chromosome $3S^b$ of *Aegilops bicornis* carries a brittle rachis gene. Urbano et al. (1988) located the brittle rachis genes on the chromosomes of homoeologous group 3, namely, 3VS in *Dasypyrum villosum*, $3S^b$ in *Ae. bicornis*, $3S^l$ in *Ae. sharonensis*, $3S^l$ in *Ae. longissima*. Miller et al. (1995) demonstrated that chromosome 3N of *Ae. uniaristata* induce brittle rachis in the CS/3N addition lines as well as in substitution lines of in which 3N replaces wheat chromosome 3A, 3B or 3D. King et al. (1997) found that the gene responsible for brittle rachis in × *Tritipyrum* is located on the chromosome $3E^b$ of *Thinopyrum bessarabicum.* Tibetan weedrace of common wheat has brittle rachis controlled by the gene ($Br_1$) on the short arm of the 3D (Chen, 1998).

Genetic analysis indicated that there is linkage relationship between rachis fragility and grain colour, with distances 44.2 cM for $Br_2$ – *R-A1b* and 47.0 cM for $Br_3$ – *R-B1b*, respectively (Table 2). Let us consider the skewed segregation for grain colour in RICL's 3A (Table 3). To develop recombinant inbred lines, the plants from each of LDN3D(3A)//Langdon /LDN(DIC 3A) were selfed, and sampled to determine chromosome pairing ($13'' + 2'$) at MI of meiosis. It was expected that one of the univalents was chromosome 3D and the other was a recombined chromosome 3A. Several plants from selfed seeds were grown and checked chromosome pairing ($14''$) at MI of meiosis, and then the plant with $14''$ were crossed with double ditelosomic 3A line ($26+ 2t_{3AL}+2t_{3AS}$)of Langdon. The testcross progenies were grown to differentiate the plants with a pair of 3D chromosomes from those with a pair of recombined 3A chromosomes. At MI of meiosis, it is expected that chromosome pairing of the

progenies are $13'' + 1' + 2t'$ for progenies with a pair of 3D chromosomes, and $13'' + t1t'''$ for those with a homozygous pair of recombined 3A chromosomes. We speculate that several lines with a pair of 3D chromosome were classified as the lines with a homozygous pair of recombined 3A chromosomes in these procedures, provided homoeologous pairing between 3A and 3D chromosomes were relatively higher. The grain colour of the plants with a pair of 3D chromosome will be red. Another possibility was that the allele for red grain was transmitted preferentially when a cross was made of LDN 3D(3A) with the $F_1$ of Langdon/LDN(DIC 3A). However, we did not find the skewed segregation of the cross, Langdon/LDN(DIC 3A) as shown in Table 2.

As mentioned, in the discussion concerning *T. turgidum* ssp. *diccoccoides, Ae. uniaristata* and *Dasypyrum villosum*, it is interesting that the genes to adjust seed colour and shattering are located on the same chromosome with linkage relationships in the wild related species. In *T. turgidum* ssp. *dicoccum*, a primitive cultivated group, two genes controlled grain colour and brittle rachis respectively and a linkage relationship is hypothesized (Watanabe, unpublished data). Schiemann & Staudt (1958) proposed that two complementary genes control tough rachis in ssp. *dicoccum*. Numerous genetic studies have identified hexaploid varieties carrying one, two, or all three red grain alleles (McIntosh et al., 1998), but not durum wheat. It is of interest how cultivated wheat lost the brittle rachis and how cultivated wheat differentiated for red grain colour.

## Acknowledgements

N.W. acknowledges Dr L.R. Joppa, USDA-ARS, Fargo, USA for providing him the seed of Langdon-ssp. *dicoccoides* substitution lines and recombinant inbred chromosomal lines for 3A and 3B chromosomes, and Dr J.G. Waines, University of California, Riverside, CA, USA for his helpful comments on the manuscript.

## References

Chen, Q.-F., C. Yen & J.-L. Yang, 1998. Chromosome location of the gene for brittle rachis in the Tibetan weedrace of common wheat. Genet Res Crop Evol 45: 407–410.

Clarke, J.M., R.M. DePauw, J.G. McLeod & T.N. McCaig, 1994. Variation for preharvest sprouting resistance in durum wheat. Crop Sci 34: 1632–1635.

DePauw, R.M. & T.N. McCaig, 1983. Recombining dormancy and white seed color in a spring wheat cross. Can J Plant Sci 63: 581–589.

DePauw, R.M. & T.N. McCaig, 1987. Recovery of sprouting resistance from red kernelled wheats in white-kernelled segregates. In: D.J. Mares (Ed.), Fourth Intenatl. Symp. on Pre-harvest Sprouting in Cereals, Westview Press, Boulder, Colorado, USA, pp. 54–63.

Dyck, P.L., J.S. Noll & E. Czanecki, 1986. Heritability of RL4137 type of dormancy in two populations of random inbred lines of spring wheat. Can J Plant Sci 66: 855–861.

Flintham, J.E. & M.D. Gale, 1996. Dormancy gene in homoeologous cereal genomes. In: K. Noda & D.J. Mares (Eds.), Preharvest Sprouting in Cereals 1995, pp. 143–149. Center for Acad Soc Japan, Osaka, Japan.

Gale, M.D. & J.W. Snape, 1988. Business meeting. In: T.E. Miller & R.M.D. Koebner (Eds.). Proc. 7th Internatl. Wheat Genetics Symp., p. 1219. IPSR Cambridge Lab., Cambridge, UK.

Joppa, L.R. & N.D. Williams, 1988. Langdon durum disomic substitution lines and aneuploid analysis in tetraploid wheat. Genome 30: 222–228.

Joppa, L.R. & R.G. Cantrell, 1990. Chromosomal location of genes for grain protein content of wild tetraploid wheat. Crop Sci 30: 1059–1064.

King, I.P., C.N. Law, K.A. Cant, S.E. Orford, S.M. Reader & T.E. Miller, 1997. *Tritipyrum* a potential new salt-tolerant cereal. Plant Breed 116: 127–132.

McIntosh, R.A. G.E. Hart, K.M. Devos, M.D. Gale & W.J. Rogers, 1998. Catalogue of gene symbols for wheat. Proceedings of the 9th Internatl. Wheat Genet Symp Vol 5, pp. 1–235. University of Extension Press, Univ. of Saskatchewan, Saskatoon, Canada.

McCaig, T.N. & R.M. DePauw, 1992. Breeding for preharvest sprouting tolerance in white-seed-coat spring wheat. Crop Sci 32: 19–23.

Miller, T.E., S.M. Reader, A. Mahmood, K.A. Purdie & I.P. King, 1995. Chromosome 3N of *Aegilops uniaristata* – a source of tolerance to high levels of aluminum for wheat. In: Z.S. Li & Z.Y. Xin (Eds.), Proc. 8th Internatl Wheat Genet Symp 1993, pp. 1037–1042. China Agricultural Scientech Press, Beijing, China.

Riley, R.G., G. Kimber & C.N. Law, 1996. Correspondence between wheat and alien chromosomes. Ann Rep Plant Breed Inst 1964–65, 108–109.

Schiemann, E. & G. Staudt, 1958. *T.* × *dimococcum*, an amphiploid with genomes AAAABB. Züchter 28: 166–184.

Urbano, M., P. Resta, S. Benedettelli & A. Blanco, 1988. A *Dasypyrum villosum* (L.) Candargy chromosome related to hornoeologous group 3 of wheat. In: T.E. Miller & R.M.D. Koebner (Eds.), Proc. 7th Internatl Wheat Genet Symp, pp. 169–173. IPSR Cambridge Lab., Cambridge, UK.

Zohary, D., 1983. Wild genetic resources of crops in Israel. Israel J Botany 32: 97–127.