Different genetic components control coat-imposed and embryo-imposed dormancy in wheat

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Abstract

Wheat grain dormancy is a multigenic trait controlled both by *R* genes conferring red testa pigmentation and by other genes, at least one of which has a major effect in the embryo. Enhanced grain dormancy and red testa colour are inherited as pleiotropic effects of dominant *R* alleles at triplicate loci in hexaploid wheat. However, polymorphism for *R* genes cannot account for the wide variation in dormancy observed among different red-grained varieties. A variety of different dominant *R* alleles all have equivalent effects on dormancy when introgressed into white-grained wheats, although the latter vary in dormancy both in the absence and in the presence of dominant *R* alleles. As a result, certain red-grained genotypes can exhibit intermediate dormancy, similar to that of some white-grained genotypes with different genetic backgrounds. A new major gene (*Phs*) was identified as controlling the difference between two red-grained cultivars with widely different dormancies. The *Phs* gene appeared to exert its effect in the embryo of the grain, in contrast to *R* gene expression in maternal testa tissue. Discrete genetic functions thus underlie physiologically distinct mechanisms of coat-imposed dormancy and embryo-imposed dormancy in wheat.

Keywords: Plant breeding, Pre-harvest sprouting, Red grain colour, *Triticum aestivum* L.

Introduction

Biffen (1905) was the first to describe Mendelian inheritance of grain colour in hexaploid bread wheat, with red grain dominant over white. The existence of three independent genetic loci for redness and their association with enhanced grain dormancy was postulated by Nilsson–Ehle (1914) and confirmed in numerous subsequent reports. White-grained (white) wheats are homozygous for the recessive alleles *R-A1a, R-B1a* and *R-D1a*; red-grained (red) wheats carry one or more of the dominant alleles *R-A1b, R-B1b, R-D1b*. Cytogenetic analyses identified chromosomes 3A, 3B and 3D as each carrying a single *R* locus (Sears, 1944; Allan and Vogel, 1965; Metzger and Silbaugh, 1970). *R* loci were located to the long arms of 3A and 3D by telocentric mapping (Sears, 1954; Rao, 1973; McIntosh *et al.*, 1984), and DNA markers flanking all three *R* loci have been identified by restriction fragment length polymorphism (Flintham and Humphray, 1993; Nelson *et al.*, 1995; Flintham and Gale, 1996). Taken together these findings indicate that the *R* loci represent a series of functionally equivalent genes, situated at homoeologous loci on chromosomes 3A, 3B and 3D of hexaploid wheat (Gale *et al.*, 1995).

Pre-harvest sprouting damage leads to occasional massive losses in all wheat producing areas for which data are available (Derera, 1990). Red grain colour is a traditional marker for resistance to sprouting in wheat breeding programmes, and selection for the red-grained phenotype is especially intense in north-west European temperate, maritime climates. In the United Kingdom pre-harvest sprouting occurs sporadically despite the fact that all currently grown commercial varieties are red, with the implication that the red-grained phenotype alone does not always guarantee effective resistance (Flintham and Gale, 1988; Kettlewell *et al.*, 1999).

White-grained crops are more susceptible to sprouting on average than red wheats, although both groups vary in this respect. Additional genetic effects, independent of seedcoat pigmentation, have been implicated in the control of dormancy in white wheats. Some of these genes are located on the same chromosomes as the *R* genes (Mares, 1996) while others map to different chromosomes (Anderson *et al.*, 1993). Variation between different red wheats may also be affected by such genes, leading to the frequent

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observation that certain white genotypes express stronger dormancy than the weakest reds (McCrate *et al.*, 1981; DePauw and McCaig, 1983; Flintham, 1993; Lawson *et al.*, 1997; Wu and Carver, 1999).

Gene dosage effects (deepening intensity of pigmentation with increasing dosage of dominant *R* alleles) might be an additional factor in variation between different red wheats (Wang *et al.*, 1999 and references cited therein). However, *R* gene dosage effects cannot account for the wide variation in dormancy between varieties carrying all three dominant *R* alleles (Noll *et al.*, 1982; Flintham, 1993). These and other observations have led to some uncertainty as to the relationship between red grain colour and dormancy, in particular as to whether dormancy is a direct, pleiotropic effect of dominant *R* alleles, or whether these genes are acting as linked markers for other dormancy genes on the group 3 chromosomes.

The research reported here was undertaken to elucidate the relationship between genotypic variation for dormancy and polymorphism for *R* alleles among white and red near-isogenic lines and to investigate genetic variation for dormancy between different red-grained varieties. The results indicate that dominant *R* alleles from diverse varieties all have functionally equivalent effects on dormancy, which are expressed via the seedcoat as a pleiotropic effect of red pigmentation. Further evidence suggests that different genetic backgrounds confer differential responses to the introgression of defined dominant *R* alleles. Differences in genetic background also result in variation between the dormancy of two red wheats, both carrying three dominant *R* alleles, and this variation can be accounted for by a previously uncharacterized single major gene expressed in the embryo.

Materials and methods

Genetic Stocks

Five red-grained near-isogenic lines (NILs), each carrying a dominant *R* allele from a different donor variety in the genetic background of the white-grained, spring-habit wheat Novosibirskaya 67 (NS67), were a gift from the Russian Academy of Science. One NIL carries *R-A1b*, two carry *R-B1b*, and two carry *R-D1b* (Koval, 1997). Additional NILs were produced from the locally adapted, white winter wheat varieties Abele, Holdfast and Wilma and from the breeder's line JBW (a white segregant from the former Plant Breeding Institute, Cambridge, UK). Each white wheat was used as recurrent female parent for 22 independent sets of six serial backcrosses from their F_1 hybrids with the donor varieties Red Bobs (*R-A1b* / *R-B1a* / *R-D1a*), Chinese Spring (*R-A1a* / *R-B1a* / *R-D1b*), Cappelle Desprez (*R-A1b* / *R-B1b* / *R-D1a*) and RL4137 (*R-A1b* / *R-B1b* / *R-D1b*). These donor varieties have intermediate dormancy except for RL4137 which is extremely dormant (DePauw and McCaig, 1983). Each backcross was followed by selection of red-grained progeny to retain dominant *R* alleles in a heterozygous condition. Pairs of homozygous white- and red-grained sibling NILs segregating for single dominant alleles were selected following self-pollination of BC_6F_1 plants. For each recurrent parent the original aim was to produce 22 independent pairs of NILs (two pairs from the Red Bobs cross, two pairs from the cross with Chinese Spring, and six or twelve pairs, respectively, from the crosses with Cappelle Desprez and RL4137). Occasional chance losses of the red-grained phenotype occurred in individual pedigrees, and 21 pairs of NILs were finally obtained from Abele, 21 pairs from Wilma, 20 from JBW and 19 from Holdfast. Each white-grained parent was thus used to develop two or more independent pairs of NILs differing for single dominant *R* alleles introgressed from each of seven different allelic sources. Genetic variation for dormancy was also investigated in 34 homozygous recombinant lines derived from F_1 hybrids of Boxer × Soleil (both *R-A1b* / *R-B1b* / *R-D1b*) by the doubled-haploid method of Laurie and Reymondie (1991).

Glasshouse Experiments

Reciprocal crosses between white-grained plants of NS67 and each of its five red-grained NILs were made in a glasshouse in the summer of 1995 by emasculating and hand-pollinating synchronous batches of two spikes per cross. Emasculations followed by self-pollinations were made synchronously on other spikes of the same plants (two for each NIL, ten for NS67). Between 20 and 28 grains from each spike were tested for germinability in a separate Petri dish. One week following physiological maturity (as judged by complete loss of chlorophyll from stems and spikes), grains were gently hand threshed and germinated on wet filter paper at 25°C (4 ml deionised water and two 9 cm Whatman no.1 filter circles per dish). Germinated grains were counted and discarded at daily intervals for ten days. Viability of ungerminated grains was then proved by chilling at 4°C followed by germination at 25°C. A similar experiment was carried out in the same glasshouse and season with self-pollinations and reciprocal crosses between the varieties Boxer and Soleil, with four spikes per pollination and after-ripening extended to three weeks to maximize discrimination between genotypes. Standard errors for the germination

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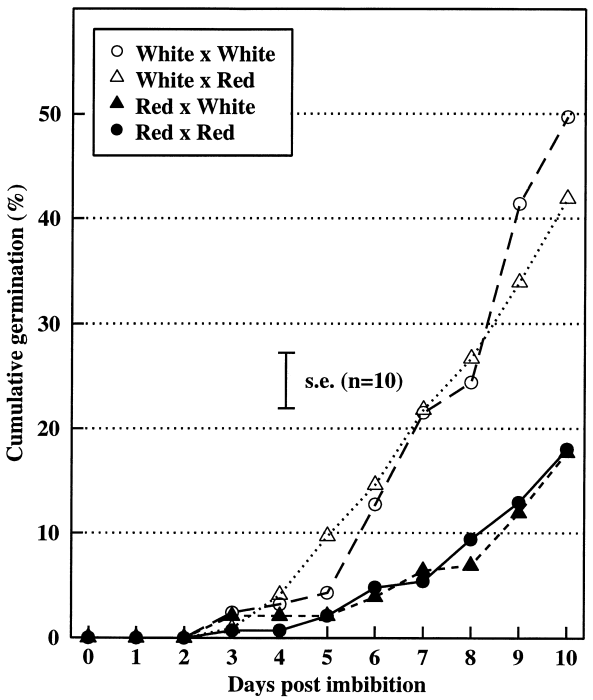


Figure 1. Dormancy associated with red maternal grain colour, independent of embryo genotype in reciprocal near–isogenic crosses. Cumulative germination curves are shown for self–pollinated NS67 (White × White), its red–grained NILs (Red × Red) and for F_1 grains from reciprocal crosses. Data points for NS67 are means over ten different spikes, while other points are means over two spikes from each of five different crosses or self–pollinations (see text)

curves derived from these experiments were calculated from variances between cumulative percentage germination in different dishes of each genotype on each day, excluding dishes with zero germination and pooled over genotypes and days.

Field Trials

All field trials were conducted at the Morley Research Centre, Norfolk, UK. Each entry was hand sown as a one metre row of 23 plants and harvested promptly at ripeness (grain moisture content less than twenty percent of fresh weight, spot-tested by inability to mark with a thumbnail and subsequently confirmed by oven drying of subsamples). Each sheaf was then stored in a dry, unheated glasshouse pending sampling of intact spikes for sprouting tests. The NILs from Abele, Holdfast, JBW and Wilma were grown from an October sowing in the 1997/98 season, harvested on 18 August and subjected to a sprouting test started on 7 September. The doubled-haploid recombinant lines from Boxer × Soleil, interspersed with 5 replicates of the parental varieties, were grown in 1995/96, harvested on 19 August, and subjected to sprouting tests started on 2 September, on 16 September, and again on 30 September. A second trial of the doubled-haploids and parents was grown in 1996/97, harvested on 12 August, and tested for sprouting on 4 September and again on 17 September. For logistic convenience, dormancy in these trials was assessed by tests of sprouting in intact spikes rather than by germination of threshed grains.

Sprouting Tests

The progressive loss of dormancy during after-ripening of sheaves was monitored in Petri dish germination tests of genotypes representing the expected extremes of low or high dormancy in each trial. Sprouting tests of complete trials were carried out in a 'sprouting cabinet' at 21 ± 2°C (Mares, 1989) at times when the Petri dish tests predicted maximum differences between genotypes. In each test twelve intact spikes from each sheaf were held erect in mesh racks and subjected to seven days' continuous misting with water. The spikes were then dried, threshed and scored for percentage sprouted grains with visible rupture of the pericarp over the emergent shoot or radicle.

Results

Red testa pigmentation and enhanced grain dormancy as pleiotropic effects of dominant maternal R *alleles*

Red NILs consistently germinated more slowly than white NS67 in preliminary experiments, with no significant differences between the different red NILs (Flintham and Gale, 1996). The data were homogeneous over the five red NILs in the present experiment, and the results for red NILs were pooled for statistical analysis. Germination of F_1 grains from NIL × NS67 crosses was slow and similar to that of grains from self-pollination of the same maternal NILs, whereas germination of grains from reciprocal crosses was more rapid and similar to white NS67 (Fig. 1). Thus, grains with embryos heterozygous for single *R* alleles displayed maximum dormancy when surrounded by a red maternal seedcoat (testa) and minimum dormancy when surrounded by a white seedcoat. This difference in dormancy is attributed to a tissue or developmental signal derived from the maternal plant, since the hybrid embryonic and cytoplasmic genotypes are both identical across reciprocal near-isogenic crosses. The effect of grain colour on dormancy was quantitative rather than absolute. Even NS67 expressed some dormancy in the germination tests depicted in Fig. 1 (following full

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Table 1. Analysis of variance for arcsin percentage sprouting in red– and white–grained near–isogenic lines of different wheat varieties. Data were from the experiment summarized in Fig. 2. Pooled variance between red lines within each varietal background (d) was tested against variance between white lines in the same varieties (e). Other effects (a, b, c) were tested according to a fixed effects model, against pooled variance (f) between lines within variety × colour combinations (NS non–significant, *** P<0.1%).

ITEM	DF	SS	MS	F	P
Between Variety × Colour combinations:					
a) Varieties	3	12994.4	4331.5	164.6	***
b) Colour	1	27383.2	27383.2	1040.8	***
c) V × C interactions	3	3915.3	1305.1	49.6	***
Between lines within Variety × Colour combinations:					
d) Between reds	77	1921.9	25.0	<1.0	NS
e) Between whites	77	2129.1	27.7		
f) Pooled lines (Error)	154	4051.0	26.3		

after-ripening all genotypes gained the capacity for 100% germination within two days of imbibition, data not shown).

Variation for dormancy determined by interactions between different R *alleles and genetic backgrounds*

Scores for percentage induced sprouting in the white- and red-grained NILs from Abele, Holdfast, JBW and Wilma were transformed to arcsin for analysis of variance to remove statistical artefacts caused by inequalities of variance at intermediate and extreme percentages. Variance between arcsin scores for different white NILs within each of the four varieties (combining residual differences between backcrosses, environmental effects and measurement errors) was homogenous across varieties and was pooled to estimate experimental error. Differences between red NILs were not significant within any one genetic background and were therefore pooled with the error variance (Table 1). The effects of different genetic backgrounds, red versus white grain colour, and colour × background interaction were all highly significant. Thus although different dominant *R* alleles all had similar effects on dormancy, these varied according to the genetic background into which they were introduced.

Holdfast and JBW both exhibited extremely low dormancy in their white NILs. However, red NILs of Holdfast were markedly more dormant than red NILs of JBW (Fig. 2). Dormancy of white NILs of Abele and Wilma was similar to red NILs of JBW, and their red NILs behaved similarly to those of Holdfast. One set of difference(s) between these four genetic backgrounds thus affected dormancy in the absence of red pigmentation (Fig. 2, white Holdfast and JBW versus white Abele and Wilma), while an additional effect must be invoked to account for the interaction between variety and grain colour (Fig. 2, red Holdfast versus red JBW).

Pre-harvest sprouting occurred fortuitously in the field trial of JBW NILs, to a mean of 10.5 ± 3.2 % sprouted grains in white lines (ranging from 3% to 17%) and a mean of 2.0 ± 0.6 % in the red lines (ranging from 0% to 4%). This provided a rare

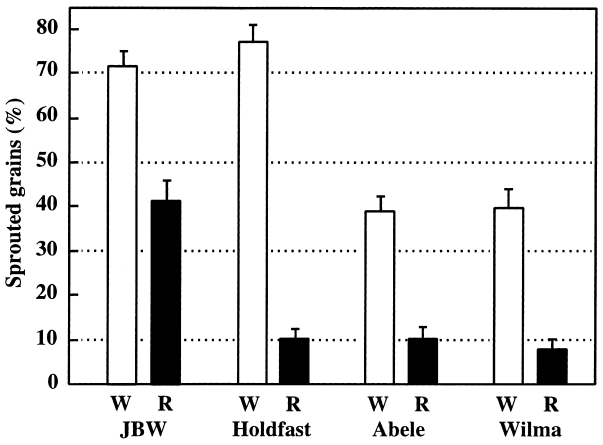


Figure 2. Variation in dormancy between white– and red–grained near–isogenic lines of four different wheats. For each of four varieties, histograms depict the percentages of sprouted grains in intact, partially after–ripened spikes after seven days' misting with water (see text). The two histograms for JBW show the means for 20 pairs of white–grained (**W**, open fill) and red–grained sibling NILs (**R**, black fill). Holdfast, Abele and Wilma were represented by 19, 21 and 21 pairs of NILs, respectively. Error bars depict upper 95% confidence limits per mean.

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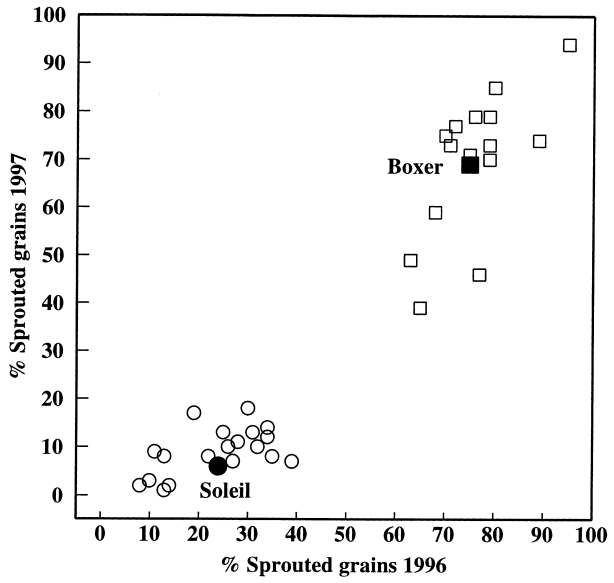


Figure 3. Segregation for the *Phs* dormancy gene among doubled–haploid recombinant lines from the cross Boxer × Soleil. Sprouting was induced as for Fig. 2. Data for 1996 are means over three successive tests, and data for 1997 are means over two tests for the parental varieties (solid symbols), 19 dormant DH lines (open circles) and 15 nondormant lines (open squares).

opportunity to compare the dormancy of defined genetic stocks, as measured artificially in after-ripened samples, with their resistance to sprouting in the field at earlier stages of grain maturity. No significant pre-harvest sprouting was detected in the other field trials.

Phs, *a new major gene for wheat grain dormancy determined by embryo genotype*

The varieties Boxer and Soleil both have the *R-A1b* / *R-B1b* / *R-D1b* genotype. However, Boxer has moderately weak dormancy while Soleil is extremely dormant (Flintham, 1993). Among the doubled-haploid recombinants from Boxer × Soleil, 19 lines were as dormant as Soleil and the remaining 15 lines had low dormancy, similar to Boxer (Flintham *et al.*, 1999). This segregation ratio can only be accounted for by a single-gene model ($\chi^2_{(1:1)}$=0.47, P≈0.5; $\chi^2_{(3:1)}$=6.63, P≈0.01). This monogenic segregation among triple-dominant red recombinants is evidence for a new dormancy gene, for which we propose the symbol *Phs* (*P*re-*h*arvest *s*prouting).

The effect of *Phs* was stable over the two years of field trials and accounted for the majority of genotypic variance in the population (Fig. 3). There was some evidence of residual genetic variation within both the highly-dormant and the low-dormancy groups of lines, with between-year correlations for percentage induced sprouting of r=0.544 (P<5%) for the former and r=0.676 (P<1%) for the latter. This residual genotypic variation was not statistically significant when tested against genotype × year interaction (analysis of variance not shown) and did not result in overlapping distributions for dormancy of the two groups of lines in either year.

The dormancy of F_1 grains from crosses between Boxer and Soleil was unaffected by maternal genotype and was intermediate between the dormant and non-dormant phenotypes of grains from self-pollinations (Fig. 4). Thus, the semi-dominant effect of *Phs* appears to be expressed via the zygotic genotype, independent of the seedcoat, in contrast with the dominant maternal effects of the *R* genes (Fig. 1). Although quantitative comparisons of dormancy effects across different experiments are problematic, the magnitude of the effect of *Phs* on dormancy appears to be comparable to that of the *R* genes (cf. Figs 1 vs. 4; 2 vs. 3).

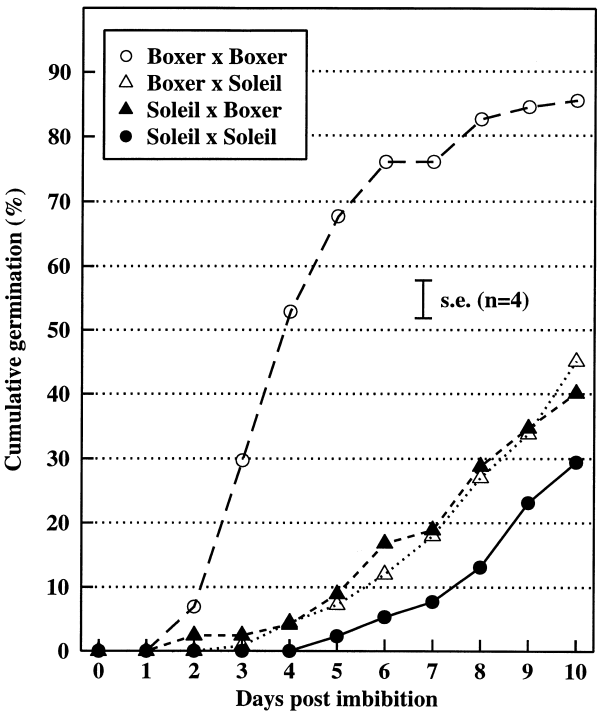


Figure 4. Dormancy associated with the *Phs* gene is independent of maternal genotype in reciprocal crosses. Cumulative germination curves are shown for self–pollinated Boxer and Soleil and for F_1 grains from reciprocal crosses. Data points are means over four different spikes.

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Discussion

Phenotypic differences between red-grained NILs and their white-grained parents are ascribed to the *R* genes, since other genetic differences will have been diluted out by backcrossing. The possibility that the dormancy effect is caused by other genes, tightly linked with the *R* loci, cannot formally be discounted (Stam and Zeven, 1981). However, the consistency of the results obtained with dominant alleles from different donor varieties strongly suggests a pleiotropic association of enhanced grain dormancy with red grain colour (Koval, 1997). Furthermore, a direct effect of the maternal seedcoat pigment on dormancy would account for the phenotypic differences between reciprocal F_1 grains shown in Fig. 1 and the common observation that dormancy can be relieved by abrading or piercing the seedcoat (Czarnecki, 1988). It seems most likely that the enhanced dormancy of red wheats is a direct effect of dominant *R* allele expression in the testa. Definitive proof of pleiotropy, by genetic transformation of white wheat and recovery of the red/dormant phenotype, will have to await the identification and cloning of wheat *R* alleles.

Differences between the dormancy of F_1 grains from reciprocal crosses between red and white wheats, similar to those shown in Fig. 1, were reported by Freed *et al*. (1976), Noll *et al*. (1982), Mares (1993), and Miura *et al*. (1997). However, the crosses in these previous reports were made between non-isogenic varieties for which information concerning other genetic differences in dormancy was not available, precluding conclusions as to the role of *R* genes. Results from NILs in the present study confirm that specific *R* alleles can indeed account for such observations and confirm the hypothesis that different dominant *R* alleles have quantitatively similar effects (McEwan, 1980).

Different white-grained wheats can vary with respect to the dormancy of red-grained NILs derived from them (JBW and Holdfast in Fig. 2). Such differences between red genotypes with identical *R* alleles must be due to other genes in the genetic background. Whether these other genes also affect dormancy in the white-grained condition was not clear from the present evidence, as the extremely high levels of sprouting induced in white-grained NILs of JBW and Holdfast may have obscured any latent differences between these genotypes under the conditions of the test. The observation in 1998 of genuine pre-harvest sprouting among the white JBW NILs but not in Holdfast supports this hypothesis. Moreover, the observed reduction in natural pre-harvest sprouting among red NILs of JBW validates the use of after-ripened dormancy scores as an index of pre-harvest resistance, at least for the grain colour effect.

Crosses between red wheats sometimes reveal dormancy differences between reciprocal F_1 grains (e.g. Noll *et al*., 1982) and sometimes do not (e.g. Miura *et al*., 1997). Little information is available concerning the genetic differences between the parental varieties in these previous studies, beyond the existence of genotypic effects other than seedcoat colour (DePauw and McCaig, 1983). In contrast, most of the difference in dormancy between Boxer and Soleil is caused by a single major gene (*Phs*, Fig. 3), and an approximate analysis of this gene's effects can therefore be made in crosses between these two non-isogenic varieties. It is unlikely that *Phs* operates via effects in the triploid endosperm, since hybrid grains born on Soleil plants will have two doses of the Soleil *Phs* allele in the endosperm, while hybrid grains on Boxer plants will have only one. With partial dominance this would lead to the expectation of gene dosage differences between reciprocals (Gale, 1976). No such reciprocal effects were detected (Fig. 4), and the hypothesis that *Phs* exerts its effects in the embryo is therefore preferred.

The *Phs* gene accounts for major variation in dormancy between different wheats with three dominant *R* alleles. It is tempting to speculate that this zygotic mechanism for dormancy might also operate in the absence of the red seedcoat pigment, and the *Phs* allele from Soleil is being introgressed into white wheats to test this possibility. Further trials of recombinant lines from Boxer × Soleil are also being made, in a bid to obtain data for natural pre-harvest sprouting in the field. Another question to be resolved is whether *Phs* polymorphism alone can account for the variation in dormancy among a wider sample of red-grained varieties. This will probably prove not to be the case in view of the evidence for other group 3 chromosome effects (Mares, 1996; Flintham *et al*., 1999) and multiple dormancy loci in quantitative trait genetic maps (Anderson *et al*., 1993; Roy *et al*., 1999). Even so, the identification of DNA markers for *Phs* can be expected to have a substantial impact on the efficiency of selection for improved grain dormancy in wheat, and genetic mapping of the gene is in progress.

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References

Allan, R.E. and Vogel, O.A. (1965) Monosomic analysis of red seed color in wheat. *Crop Science* **5**, 474–475.

Anderson, J.A., Sorrells, M.E. and Tanksley, S.D. (1993) RFLP analysis of genomic regions associated with resistance to pre-harvest sprouting. *Crop Science* **33**, 453–459.

Biffen, R.H. (1905) Mendel's laws of inheritance and wheat breeding. *Journal of Agricultural Science* **1**, 4–48.

Czarnecki, E. (1988) A method for germinating immature spring wheat. *Canadian Journal of Plant Science* **68**, 797–799.

DePauw, R.M. and McCaig, T.N. (1983) Recombining dormancy and white seed colour in a spring wheat cross. *Canadian Journal of Plant Science* **63**, 581–589.

Derera, N.F. (1990) A perspective of sprouting research. pp. 3–11 *in* Ringlund, K.; Mosleth, E.; Mares, D.J. (Eds) *Fifth international symposium on pre-harvest sprouting in cereals.* Boulder, USA, Westview Press.

Flintham, J.E. (1993) Grain colour and sprout-resistance in wheat. pp. 30–36 *in* Walker-Simmons, M.K.; Ried, J.L. (Eds) *Pre-harvest sprouting in cereals 1992*. St. Paul, USA, American Association of Cereal Chemists.

Flintham, J.E., Adlam, R.E. and Gale, M.D. (1999) Seedcoat and embryo dormancy in wheat. pp. 67–76 *in* Weipert, D. (Ed) *Eighth international symposium on pre-harvest sprouting in cereals*. Detmold, Germany, Association of Cereal Research.

Flintham, J.E. and Gale, M.D. (1988) Genetics of pre-harvest sprouting and associated traits in wheat: review. *Plant Varieties and Seeds* **1**, 87–97.

Flintham, J.E. and Gale, M.D. (1996) Dormancy gene maps in homoeologous cereal genomes. pp. 143–149 *in* Noda, K.; Mares, D.J. (Eds) *Pre-harvest sprouting in cereals 1995*. Osaka, Center for Academic Societies Japan.

Flintham, J.E. and Humphray, S.J. (1993) Red coat genes and wheat dormancy. *Aspects of Applied Biology* **36**, 135–141.

Freed, R.D., Everson, E.H., Ringlund, K. and Gullord, M. (1976) Seedcoat colour in wheat and the relationship to seed dormancy at maturity. *Cereal Research Communications* **4**, 147–149.

Gale, M.D. (1976) High α-amylase – breeding and genetic aspects of the problem. *Cereal Research Communications* **4**, 231–243.

Gale, M.D., Atkinson, M.D., Chinoy, C.N., Harcourt, R.L., Jia, J., Li, Q.Y. and Devos, K.M. (1995) Genetic maps of hexaploid wheat. pp. 29–40 *in* Li, Z.S.; Xin, X.Y. (Eds) *Proceedings of the eighth international wheat genetics symposium.* Beijing, China Agricultural Scientech Press.

Kettlewell, P.S., Sothern, R.B. and Koukkari, W.L. (1999) U.K. wheat quality and economic value are dependent on the North Atlantic oscillation. *Journal of Cereal Science* **29**, 205–209.

Koval, S.F. (1997) The catalogue of near-isogenic lines of Novosibirskaya 67 common wheat and principles of their use in experiments. *Russian Journal of Genetics* **33**, 995–1000.

Laurie, D.A. and Reymondie, S. (1991) High frequencies of fertilization and haploid seedling production in crosses between commercial hexaploid wheat varieties and maize. *Plant Breeding* **106**, 182–189.

Lawson, W.R., Godwin, I.D., Cooper, M. and Brennan, P.S. (1997) Genetic analysis of pre-harvest sprouting tolerance in three wheat crosses. *Australian Journal of Agricultural Research* **48**, 215–221.

Mares, D.J. (1989) Pre-harvest sprouting damage and sprouting tolerance: assay methods and instrumentation. pp. 120–170 *in* Derera, N.F. (Ed) *Pre-harvest field sprouting in cereals.* Boca Raton, USA, CRC Press Inc.

Mares, D.J. (1993) Genetic studies of sprouting tolerance in red and white wheats. pp. 21–29 *in* Walker-Simmons, M.K.; Ried, J.L. (Eds) *Pre-harvest sprouting in cereals 1992*. St. Paul USA, American Association of Cereal Chemists.

Mares, D.J. (1996) Dormancy in white wheat: mechanism and location of genes. pp. 179–184 *in* Noda, K.; Mares, D.J. (Eds) *Pre-harvest sprouting in cereals 1995*. Osaka, Center for Academic Societies Japan.

McCrate, A.J., Nielsen, M.T., Paulsen, G.M. and Heyne, E.G. (1981) Pre-harvest sprouting and α-amylase activity in hard red and hard white winter wheat cultivars. *Cereal Chemistry* **58**, 424–428.

McEwan, J.M. (1980) The sprouting reaction of stocks with single genes for red grain colour derived from Hilgendorf 61 wheat. *Cereal Research Communications* **8**, 261–264.

McIntosh, R.A., Dyck, P.L., The, T.T., Cusick, J.E. and Milne, D.L. (1984) Cytogenetical studies in wheat. XIII. *Sr35* – a third gene from *Triticum monococcum* for resistance to *Puccinia graminis*. *Zeitschrift für Pflanzenzüchtung* **92**, 1–14.

Metzger, R.J. and Silbaugh, B.A. (1970) Location of genes for seed coat color in hexaploid wheat, *Triticum aestivum* L. *Crop Science* **10**, 495–496.

Miura, H., Fukuda, Y. and Sawada, S. (1997) Expression of dormancy in diallel F_1 and F_2 seed of wheat ripened under controlled environment. *Journal of Genetics and Breeding* **51**, 195–200.

Nelson, J.C., Van Deynze, A.E., Autrique, E., Sorrells, M.E., Lu, Y.H., Negre, S., Bernard, M. and Leroy, P. (1995) Molecular mapping of wheat. Homoeologous group 3. *Genome* **38**, 525–533.

Nilsson-Ehle, H. (1914) Zur Kenntnis der mit der Keimungsphysiologie des Weizens in Zusammenhang stehenden inneren Faktoren. *Zeitschrift für Pflanzenzüchtung* **2**, 153–187.

Noll, J.S., Dyck, P.L. and Czarnecki, E. (1982) Expression of RL4137 type of dormancy in F_1 seeds of reciprocal crosses in common wheat. *Canadian Journal of Plant Science* **62**, 345–349.

Rao, M.V.P. (1973) Mapping the gene *R1* for red seed colour on chromosome 3D of wheat. *Wheat Information Service* **36**, 9.

Roy, J.K., Prasad, M., Varshney, R.K., Balyan, H.S., Blake, T.K., Dhaliwal, H.S., Singh, H., Edwards, K.J. and Gupta, P.K. (1999) Identification of a microsatellite on chromosomes 6B and a STS on 7D of bread wheat showing an association with preharvest sprouting tolerance. *Theoretical and Applied Genetics* **99,** 336–340.

Sears, E.R. (1944) Cytogenetic studies with polyploid species of wheat. II. Additional chromosomal aberrations in *Triticum vulgare*. *Genetics* **29**, 232–246.

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Sears, E.R. (1954) The aneuploids of common wheat. *Missouri Agricultural Experiment Station Research Bulletin* **572**, 59pp.

Stam, P. and Zeven, A.C. (1981) The theoretical proportion of the donor genome in near-isogenic lines of self-fertilizers bred by backcrossing. *Euphytica* **30**, 227–238.

Wang, D., Dowell, F.E. and Lacey, R.E. (1999) Predicting the number of dominant R alleles in single wheat kernels using visible and near-infrared reflectance spectra. *Cereal Chemistry* **76**, 6–8.

Wu, J. and Carver, B.F. (1999) Sprout damage and pre-harvest sprout resistance in hard white winter wheat. *Crop Science* **39**, 441–447.

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