1. Gross Morphology: Spike characteristics

Major hexaploid wheat types are categorized into groups with respect to three major gene pairs; viz. *Q, C* and *S1* {1038}.

1. Common wheat *Q c S1* v: vulgare group.
2. Club wheat *Q C S1* v: compactum group.
3. Shot wheat *Q c s1* v: sphaerococcum group.
4. Spelt wheat *q c S1 and q C S1* v: spelta group (including vavilovi).

The majority of hexaploid wheat stocks are already, or can be readily, classified into these groups.

Diploid wheat is assumed to be *q.* Durum and carthlicum groups have the genotype *Q* {1049}.

1.1. Squarehead/spelt

1.2. Club/Compact spike

Tetraploid wheat: A compact spike gene C^{17648} in mutant line MA 17648 wad located in chromosome 5AL {10541}. *Xbarc319-5A* - 9.7 cM - C^{17648} - 24.8 cM - *Xgwm179-5A* {10541}. C^{17648} was distal to the *Q* locus {10541}.

1.3. Sphaerococcum

The naturally-occurring sphaerococcum gene in chromosome 3D and various mutant alleles conferring a similar phenotype form a homoeologous series. The sphaerococcoid alleles are either recessive or incompletely dominant. All three mapped loci are closely linked to the respective centromeres {0030}. The "a" alleles are allocated to Chinese Spring or "normal" wheats.

1.4. Branched spike

Synonyms: branched spike, four-rowed spike, multi-rowed spike, supernumerary spikelet, tetrastichon spikelet.

Branched spike and multi-rowed spike are phenotypes involving the presence of supernumerary spikelets, or the presence of additional spikelets at rachis nodes. A similar condition in rye is known as 'monstrosum ear' (reviewed in {10637}). Genetic studies of branched spike in tetraploid and hexaploid wheats indicate that the phenotype is recessive, involves one or more genes, and is strongly influenced by environmental effects. Comparative genetic studies suggest an orthologous gene series in homoeologous group 2 {10637}.

1.5. Elongated glume

Elongated glume is the phenotype associated with the polonicum group of tetraploid wheats. Expression in hexaploid wheat is much reduced compared with tetraploids. Matsumura {911} reported linkage of gene *P* and a gene for red coleoptiles implicating chromosomes 7A or 7B. A different gene was subsequently located in chromosome 7B {9990}.

1.6. Ear length

1.7. Multi-gynoecium

Synonym: three pistils (TP).

This trait describes a dominant phenotype consisting of 3 kernels within each wheat floret; that is, the flower consists of 3 separate ovaries, 3 anthers and 2 lodicules.

2. Accumulation of Abscisic Acid

A QTL was mapped on 5AL between *Xpsr575-5A* {proximal} and *Xpsr426-5A* {distal} {1180}.

3. Alkylresocinols Content in Grain

4. Aluminium Tolerance

Allelic variation at the promoter of *Almt-D1* is associated with differences in Al tolerance.

Molecular and pedigree analysis suggest that Al resistance in modern wheat germplasm is derived from several independent sources {10532}.
QTL: Atlas 66/Century: A QTL in the region *Xdgm125-4DL - Xwmc331-4DL* accounted for nearly 50% of the phenotypic variation in root growth rate in hydroponic solution {10265}. An Al-activated malate transporter (*LMT1*) was earlier mapped to the same location {10266}. Atlas 66 (insensitive)/Chisholm (sensitive) RILs: One QTL, located in chromosome 4DL, corresponded to ALMT1 and accounted for 50% of the phenotypic variation {10483}. A second QTL was located on 3BL(R^2 = 0.11); nearest marker *Xbarc164-3B* {10483}. Both QTLs were verified in Atlas/Century {10483}.
FSW (A1 tolerant) / ND35 (A1 sensitive): 3 QTLs for tolerance, *Qalt.pser-4DL* co-segregating with *Xups4*, a marker for the promoter of the *ALMT1* gene, *Qalt.pser-3BL* (*Xbarc164-3B - Xbarc344-3B*) and *Qalt.pser-2A* (*Xgwm515-2A - Xgwm296-2A*) {10605}. In D genome introgression lines of Chinese Spring a major QTL was located in the interval *Xgwm125-4D - Xgwm976-4D*, R^2=0.31 {10598}, probably coinciding with *Alt2*. A second QTL from CS, *Qalt$_{cs}$ipk-3B*, R^2=0.49, occurred in interval *Xgwm1029-3BL - Xgwm1005-3BL* in a CS / CS (Synthetic 3B) population {10598}.

5. Anthocyanin Pigmentation

The genetic determinants of anthocyanin pigmentation of various tissues are largely located in homoeologous regions in group 7, viz. 7BS (*Rc-B1, Pc-B1, Plb-B1, Pls-B1*) and 7DS (*Rc-D1, Pc-d1, Plb-D1*), and appear to be linked clusters rather than multiple alleles on each chromosome {10700}. Their relationship with genes for purple auricle and purple pericarp are still not clear.

5.1. Purple anthers.

A single, dominant factor was reported {1326}.

5.2. Purple/Red auricles. Purple leaf base/sheath

For review see {1641}.
Melz and Thiele {983} described a "purple leaf base" phenotype where anthocyanin pigmentation extended to the leaf base as well as auricles. Purple leaf base was expressed only when pigmentation occurred in the coleoptiles.

5.3. Red/purple coleoptiles.

There is an orthologous gene series on the short arms of homoeologous group 7. The 'a' alleles confer red coleoptiles.

The *Rc* gene appears to encode a transcription activator of late biosynthesis genes involved in the light-regulation of anthocyanin systhesis (studies carried out on CS(Hope 7A) substitution line) {10317}.

5.4. Purple/red culm/straw/stem

Purple or red colour is dominant.

5.5. Purple grain/pericarp

Genes for purple pericarp were transferred from tetraploid wheats to the hexaploid level {112,214,941,1138}. At the hexaploid level duplicate genes {112,941} and complementary genes {112,939,1138,438} were reported. At the tetraploid level, duplicate-gene {941} and single-gene {1327} inheritances were observed. Purple colour is dominant and may be affected by environment and genetic background. Complementary genes were located in chromosomes 3A and 7B {1138}. Possible pleiotropic relationships of genes affecting pigmentation of various tissues have not been studied in detail. *Pc2* and *Rc-B1a* may be the same gene {769}. Also, complementary genes involved in determination of purple pericarp could be related to culm colour {112}.

For review, see {1643}.
Complementary dominant genes.

5.6. Purple glume

5.7. Purple leaf blade

6. Awnedness

6.1. Dominant inhibitors

6.1.1. Hooded

6.1.2. Tipped 1

In a common genetic background, carriers of *B1a* have the shortest tip-awned phenotype; carriers of *B1b* and *B1c* have awns 2 to 3 times longer depending on environment. In F1 hybrids, differences between the substitution line combinations are significant. The postulation of *B1* in both CS and Courtot {0309} based on the phenotype of a CS deletion stock is not supported by genetic observations

6.1.3. Tipped 2

6.1.4. Awnless

Genotypes *Hd B2* (e.g., Chinese Spring) and *B1 B2* (e.g., Federation) are awnless. Presumably *Hd B1* is awnless. Watkins & Ellerton {1551} noted the probability of a third allele "*b1a*" leading to a half-awned condition, and in discussion they consider the possibility of a similar third allele at the *B2* locus. In view of more recent cytogenetic analyses, it seems that the half-awned condition could result from epistatic interactions between the alleles *B1* and/or *B2* and various promotor genes.
Although hooded, half-awned, tip-awned and awnless variants occur among tetraploid wheats, these are relatively infrequent. It has not been established with certainty that the above inhibitors are involved.
The inhibitor alleles have a pleiotropic effect on glume-beak shape {1348}. Acuminate beak is associated with full beardedness and occurs only in *b1 b2* types. *B2* reduces beak length producing an acute beak shape. *B1* reduces beak length producing an obtuse beak shape. In this effect *B1* is epistatic to *B2*.

6.2. Promotors

The effects of (recessive) awn-promoting genes were documented in a number of studies, mainly through monosomic and disomic F1 comparisons, and in tetraploids, whereas Heyne & Livers {549} provided genetic evidence of their effects. A series of "a" genes was documented, but the evidence for the existence of at least some of these was not well supported. Hence symbols for this gene series are not recognized.

6.3. Smooth awns

Smooth-awned tetraploid wheats were reported {016,045,690,1259} and genetic analyses {016,045,690} suggested a single recessive factor, with modifiers in most instances, relative to rough awns. The phenotype has not been reported in hexaploid wheats. No gene symbol is applied.

7. Basal Sterility in Speltoids

The presence of gene *Q* ensures the fertility of the first and subsequent florets in wheat spikelets {378}. In speltoids lacking *Q*, fertility of the second and subsequent florets is ensured by the dominant allele *Bs* (designated *A* in {378}) located on chromosome 5D {377}. In the presence of *Bs* the fertility of the first floret is under polygenic control.
In *bs bs* speltoids floret development is under polygenic control, and stocks with varying levels of basal fertility were isolated.
All group *vulgare* genotypes so far studied carry *Bs*.
The following stocks were described {378}:

	Genotype		Approx. sterile-base score
Group *vulgare*	**----**	***QQ Bs Bs***	**0.00**
Speltoids	**StFF**	***qq Bs Bs***	**0.00**
	StF	***qq Bs Bs***	**0.08**
	St1A	***qq Bs Bs***	**0.39**
	St1	***qq Bs Bs***	**0.96**
	St2	***qq bs bs***	**1.41**

8. Blue Aleurone

The *Ba* allele in *T. monococcum* spp. *aegilopoides* acc. G3116 determines a half-blue seed phenotype and is different from the allele present in *Elytrigia pontica* that determines a solid blue phenotype {282}. They are treated as different genes.
For review see {1643}.

9. Brittle Rachis

Brittle rachis in *T. durum* was defined as a spike that disarticulated when the tip was bent by 45 degrees relative to the peduncle {10242}.

10. Boron Tolerance

Genes controlling tolerance to high concentrations of soil boron act additively.

In contrast to tolerance, boron efficiency was studied in {10135}. Monogenic segregation occured in Bonza (B inefficient)/SW41 (moderately B inefficient) and SW41/Fang60 (B efficient). Two genes, designated *Bod1* and *Bod2* segregated in Bonza/Fang60.

11. Cadmium Uptake

11.1. Low cadmium uptake

12. Chlorophyll Abnormalities

12.1. Virescent

12.2. Chlorina

12.3. Striato-virescens

A mutant of this type was described {376} but has been lost.

13. Cleistogamous Flowering in Durums

Cleistogamy, a rare flowering habit in durum wheats, is controlled by a single recessive gene relative to chasmogamy {191}.
Cleistogamous genotypes ***clcl.*** **tv**: HI8332 {191}; WH880 {191}.
Chasmogamous genotypes ***ClCl .*** **tv**: IWP5308 {191}; PWB34 {191}; WH872 {191}.

14. Copper Efficiency

Copper efficiency is a genetic attribute that enhances plant growth in copper deficient soil.

15. Corroded

16. Crossability with Rye and *Hordeum* and *Aegilops* spp.

16.1. Common wheat

High crossability of some wheats, particularly those of Chinese origin, viz. Chinese 446 {790}, Chinese Spring {1216}, and TH 3929 {939}, with cereal rye, weed rye (*S. segetale L.*) {1646}, and other species, e.g., *Aegilops squarrosa* {691}, *Hordeum bulbosum* {1387,1397,1469} and *H. vulgare* {349,693], is determined by additive recessive genes. The *kr* genes influence crossability with *H. vulgare*. Allele *kr1* is more potent in suppressing crossability than *Kr2* which is stronger in effect than *Kr3* {1387}. According to Zheng et al. {1649}, the effect of *Kr4* falls between *Kr1* and *Kr2*.

16.2. Tetraploid wheat

The Chinese tetraploid, Ailanmai, possesses recessive crossability genes on chromosomes 1A, 6A and 7A with the 6A gene being the least effective {0017}.

17. Dormancy (Seed)

Seed dormancy in wheat has several components, including factors associated with vivipary and red grain colour. Dormancy is an important component of resistance/tolerance to pre-harvest sprouting (PHS).

17.1. Vivipary

Orthologues of maize viviparous 1 (*Vp-1*) are located in chromosomes 3AL, 3BL and 3DL {9961} approximately 30 cM distal to the *R* loci. Variability at one or more of these loci may be related to germination index and hence to PHS {10468}.
Three sequence variants of ***Vp-B1*** identified in {10468} were used to develop STS marker VpiB3 whose amplified products showed a significant, but not complete, association with germination index used as one measure of PHS.

Alleles of *Vp-B1* were recognised using STS marker Vp1B3 {10615, 10621}.

There was a suggestion of a relationship between alleles and PHS response {10615}. *Vp-B1* allelic identifications for Chinese landraces, historical and current wheat cultivars are listed in {10621}.

17.2. Pre-harvest sprouting

QTL: Several QTL for falling number and alpha-amylase activity, two indicators for pre-harvest sprouting resistance, were identified in {0169}. The most significant were associated with *Xglk699-2A* and *Xsfr4(NBS)-2A*, *Xglk80-3A* and *Xpsr1054-3A*, *Xpsr1194-5A* and *Xpsr918-5A*, *Xpsr644-5A* and *Xpsr945-5A*, *Xpsr8(Cxp3)-6A* and *Xpsr563-6A*, and *Xpsr350-7B* and *Xbzh232(Tha)-7B* {0169}.
In cross AC Domain/Haruyutaka, one major QTL in chromosome 4AL and two lesser possibly homomeologous QTLs for dormancy in 4BL and 4DL {0226} were found.
Tolerance to preharvest sprouting (PHS) in the cross SPR8198/HD2329 was associated with *Xwmc104-6B* and *Xmst101-7D* {0032}. In AC Domain (red seeded, PHS resistant) / RL4137 (white seeded, PHS moderately resistant) most measures of PHS occurred as clusters at the *R* loci. However, *QSi.crc-5D* for sprouting index, R^2=0.44, was independent of seed colour {10626}.
QTL for preharverst sprouting were identified on chromosomes 3A (associated with *Xfbb293-3A* at P=0.01), 3B (associated with *Xgwm403-3B* and *Xbcd131-3B* at P=0.001), 3D (associated with *Xgwm3-3D* at P=0.001) and 5A (associated with *Xbcd1871-5A* at P=0.001) in the population Renan/Recital {0347}. The resistant alleles on the group 3 chromosomes and on 5A were contributed by Renan and Recital, respectively. All QTL for preharvest sprouting co-located with QTL for grain colour {0347}. Zenkoujikomugi/CS: *Qphs.ocs-3A.1* on chromosome 3AS was associated with *Xbcd1380-3A* and *Xfbb370-3A* accounting for 38% of the phenotypic variation {10195}. Zenkoujikomugi/Spica: White seeded wheats with the dormancy-related QTL, *QPhs-3AS* from Zenkoujikomugi were more resistant to PHS than counterparts with the contrasting allele from Spica {10377}. White seeded wheats with contrasting alleles of *QPhs-4AL* were not different {10377}.

QPhs.ocs.3A-1 was localized to a 4.6 cM interval flanked by *Xbarc310-3A* and *Xbcd907-3A* {10245}. A weaker QTL, *Qphs.ocs-3A.2* in 3AL, was not associated with *TaVp1* {10195}, the wheat orthologue of the maize transcription factor Viviparous-1.
Qphs.ocs-4A.1 may be the same as a QTL in AC Domain/Haruyutaka due to tight linkage

with *Xcdo785-4A* {10245}.
QPhs.ocs.4B.1, a CS allele contributing to dormancy, was located in the region of *Xgwm495-4B* {10245}.
In cross SPR 8198 (dormant)/HD2329, *QPhs.occsu-3A* was located in the *Xgwm155-3A* - *Xwmc153-3A* region with R^2=75% across 6 environments {10261}.
QTL analyses in several crosses {10275} indicated a common region in chromosome 4A associated with dormancy, dormant genotypes included AUS1408, SW95-50213 and Halberd. The location was consistent with Japanese and U.K. work even though different flanking markers were involved.
CN10955 (PHS resistant white seeded) / Annuello (PHS susceptible, white seeded) F8 RIL population: *QPhs.dpivic-4A.2* in the *Xgwm637-4AS - Xgwm937/Xgwm894-4AL* region and *QPhs.dpivic-4A.1* in the *Xwmc48-4AS - Xgwm397-4AS* region {10599}.

Rio Blanco (white seeded, PHS resistant) / NW97S186 (white seeded, PHS susceptible) RIL population: *QPhs.pseru-3AS*, R^2=0.41, *Xgwm369-3A - Xbarc12-3A*, and one minor QTL {10634}. This major QTL was confirmed in a Blanco / NW98S079 RIL population, R^2 up to 0.58 {10634}.

RL4452 (red seeded, low PHS tolerance)/AC Domain (red seeded, high PHS tolerance): DH lines: Genes associated with falling number, germination index and sprouting index contributing to PHS were locatged on chromosomes 3A, 4A (locus-2) and 4B in AC Domain and 3D, 4A (locus-1) and 7D in RL4452 {10671}.

SPR8198 (red seeded, PHS tolerance)/HD2329 (white seeded, PHS susceptible): RIL population: 7 QTL located on chromosomes 2AL, 2DL, 3AL and 3BL, the most important on 2AL and 3AL {10670}.

Sun325B (dormant white seeded)/QT7475 (semi-dormant white seeded), both parents with the chromosome 4A QTL: DH population: A QTL was located in the *Xgwm77-3B - Xwmc527-3B* interval (R^2=0.19) in the approximate region of the *R-B1* locus {10669}.

Diploid wheat
QTL:*T. monococcum* KT3-5 (non-dormant)/*T. boeoticum* KT1-1 (dormant): RIL population: QTL on chromosome $5A^mL$, *Xcdo1236c-5A - Xabc302-5A*), R^2=0.2-0.27. Weaker QTLs were found on $3A^m$(*TmAB18 - Xwmc102-3A* and *Xrz444-3A - TmABF*) and $4A^m$(*Xrz261-4A - Xrz141-4A*) {0892}. The $3A^m$QTL co-located with *TmABF* and *TmAB18* {10417}, derived from orthologous ABA signaling genes in *Arabidopsis*. The 5A QTL may be orthologous to the barley dormancy gene *SD1* {10417}.

18. Ear Emergence

19. Earliness Per Se

Genes for earliness *per se* {0023} affect aspects of developmental rate that are independent of responses to vernalization and photoperiod.

QEet.fcu.5AL identified in *Xfcp359-5A - Xfcp231-5A* interval (R^2=0.38), at or near the *Q* locus in Grandin/BR34 {10256}. Grandin was the earlier parent.

20. Flowering Time

The isolation of wheat genes orthologous to the Arabidopsis *Co* and rice *Hd1* genes was reported in {10054}. The genomic clones TaHd1-1, TaHd1-2 and TaHd1-3 originate from the long arms of chromosomes 6A, 6B and 6D, respectively. The orthology of the *TadHd1* genes

with *Co/Hd1* was demonstrated by complementation of a rice line deficient in *Hd1* function with the TaHd1-1 genomic clone. It should be noted that the wheat *TaHd1* and rice *Hd1* genes are located in non-syntenic locations {10054}. To date, no variation for flowering time has been identified on the wheat group 6 chromosomes.

Winter wheat cross, Arina (149 days)/Forno (150 days): Six QTL were detected over six environments. The 3 most important, all from Arina, were in chromosomes 6DL (R^2=16%), 3DL (R^2=14%) and 7BL (R^2=13%); 3 others in 2AL, 5BL and 6DL were from Forno {10172}.

Winter wheat cross Ernie (early)/MO94-317 (late), days to anthesis (dta):
Qdta.umc-2D, linked to *Xbarc95-2D*, R^2 = 0.74 {10456}.
Spring wheat cross: Nanda 2419 / Wangshuibai: Seven QTLs for flowering time identified with earlier alleles for five coming from Nanda 2419: *QFlt.nau-1B* (closest marker *Xbarc80-1B*, R^2=11 %), *QFlt.nau-1D* (*Xbarc62-1D, Xgwm232-1D*, R^2=6.13 %), *QFlt.nau-2B* (*Xwmc35-2B*, R^2=10 %), *XFlt.nau-2D* (*Xwmc601-2D*, R^2=10 %), *XFlt.nau-4A.1* (*Xcfd2-4A*, *Xmag1353-4A*, R^2=10 %), *XFlt.nau-4A.2* (*Xmag3386-4A*, *Xwmc161-4A*, R^2=18-19 %), *XFlt.nau7B (Xmag2110-7B, Xmag1231-7B, Xgwm537-7B, Xwmc218-7B*, R^2=18 %) {10566}.

Heading date QTL: CI 13227/Suwon 92 RIL population: AFLP marker - 2.6 cM - *QHd.pser-2DS* - 121.1 cM - *Xgwm261-2D* {10269}. This QTL could be *Ppd-D1* {10269}.
Karl 92*2/TA 4152-4 F2:F4 population: Two QTLs, *QHd.ksu-2D*, associated with *Xgwm261-2D* (R^2=0.17), and *QHd.ksu-3D*, associated with *Xgwm161-2D* 9 (R^2) {10273}.

21. Flour Colour

Loci controlling flour colour were identified and mapped in a recombinant inbred population derived from Schomburgk/Yarralinka {9936}. Regions in 3A and 7A accounted for 13% and 60% of the genetic variation, respectively, and *Xbcd828-3A*, *Xcdo347-7A* and *Xwg232-7A.1* were significantly associated with flour colour. The association was highly significant in all three replicates only for the 7A QTL. Symbols were not assigned to the flour colour loci. See also 29.2. Flour, semolina and pasta colour.

22. Free-threshing Habit

23. Frost Resistance

QTL:Norstar(tolerant)/Winter Manitou(non-tolerant): DH population: Norstar possessed major and minor QTL for tolerance on chromosomes 5A and 1D. The 5A QTL was 46 cM proximal to the *vrn-A1* locus (R^2=0.4); its peak co-incided with *Xwmc206-5A* and *Xcfd2-5A*, and expression of C-repeat Binding Factor genes with strong homology to *Cfb14* and *Cfb15* located at the *Fr-2* locus in *T. monococcum* {10414}.

24. Gametocidal Genes

24.1. Gametocidal activity

24.2. Suppression of gametocidal genes

25. Gibberellic Acid Response (insensitivity)

26. Glaucousness (Waxiness/Glossiness)

Glaucousness refers to the whitish,wax-like deposits that occur on the stem and leaf-sheath surfaces of many graminaceous species. The expression of glaucousness depends on the arrangement of wax deposits rather than the amount of wax {603}. Non-glaucous variants also occur and genetic studies indicate that non-glaucousness can be either recessive or

dominant. Recessive forms of non-glaucousness are apparently mutants of the genes that produce the wax-like deposits.
Dominant non-glaucous phenotypes (as assessed visually) appear to be due to mutations that affect the molecular structure, and reflectance, of the wax-like substances {10001}. The genes involved in wax production and the "inhibitors" are duplicated in chromosomes 2B and 2D. There appear to be independant genes for wax production and "inhibitors" {912,1493,10001}. In earlier issues of the gene catalogue the two kinds of genes were treated as multiple alleles {1432}. All forms of wild and cultivated einkorn are non-glaucous {10001}.
Orthologous loci occur in barley chromosome 2HS (*gs1, gs6, gs8*) {467}, rye chromosome 7RL (*wa1*) {725} and maize (*gl2*) {211}.
A gene for spike glaucousness, *Ws*, was mapped distally on chromosome 1BS in the cross *T. durum* cv. Langdon / *T. dicoccoides* acc. Hermon H52 {0171}.

26.1. Genes for glaucousness

26.2. Epistatic inhibitors of glaucousness

Each inhibitor inhibits all genes for glaucousness.

A dominant gene (*Vir*) for non-glaucousness was located in chromosome 2BL of cv. Shamrock, a derivative of *T. dicoccoides* {10543}. This gene mapped 2 cM distal to *Xgwm614-2B* {10543} whereas the *W1/Iw1* locus was placed distal to *Xgwm614-2B* in {10189}. Lines with *Vir* had delayed senescence ('staygreen') and an average yield advantage over their glaudous sibs {10543}.

26.3. Spike glaucousness

Spike glaucousness is recessive {10666}.

27. Glume Colour and Awn Colour

Black glumes are now included in the following homoeologous series with red/brown/bronze glumes.

27.1. Red (brown/bronze/black) glumes

The majority of studies report a single dominant gene for red glume colour. A few papers report two factors {1009,1477,1520}. Red glume colour in Swedish land cultivars is apparently associated with hairy glumes {1277} suggesting, because *Hg* is located in chromosome 1A, that a red glume factor different from *Rg1* is involved in the Swedish stocks. Nothing was known of the possible association of such a gene with *Bg*, another glume colour gene on chromosome 1A. See {1640} for review. A chromosome 1A gene, *Rg3,* was eventually identified by linkage with *Gli-A1* {1405} and shown to cosegregate with *Hg* {624}.

27.2. Pseudo-black chaff

This is a blackening condition transferred from Yaroslav emmer to Hope wheat by McFadden at the same time as stem-rust resistance was transferred. The association of this condition with mature-plant stem-rust reaction (*Sr2*) has been noted in a number of papers. According to {742}, the condition is recessive. Pan {1102} considered linkage with stem-rust reaction could be broken, but this seems unlikely.

27.3. Black-striped glumes

This phenotype was reported in group *dicoccon*. **v:** E4225 {1417}.

27.4. Inhibitor of glume pigment

An inhibitor of glume pigment was reported on chromosome 3A {106}.

27.5. Chocolate chaff

27.6. Awn colour

The literature on awn colour is not clear. In general, awn colour is associated with glume colour {045}. Occasionally, however, awn colour and glume colour may be different. According to Panin & Netsvetaev {1103}, black awns were determined by three complementary genes designated *Bla1, Bla2, Bla3. Bla1* was located in chromosome 1A and linked with *Gld 1A* (= *Gli-A1*) and *Hg*.

28. Grain Hardness/Endosperm Texture

Grain hardness or endosperm texture significantly influences flour milling, flour properties and end-use. The difference in particle size index between a hard wheat (Falcon) and a soft wheat (Heron) was reported by Symes {1452} to be due to a single major gene. Symes {1452} also found evidence for "different major genes or alleles" which explained differences amongst the hard wheats Falcon, Gabo and Spica. Using Cheyenne (CNN) substitution lines in CS and a Brabender laboratory mill, Mattern et al. {915} showed that the hard wheat milling and flour properties of Cheyenne were associated with 5D. Using Hope 5D substitution line in CS [CS(Hope 5D)] crossed to CS, and CS(Hope 5D) crossed to CS ditelosomic 5DL, Law et al. {777} showed that grain hardness was controlled by alleles at a single locus on 5DS. The dominant allele, *Ha*, controlling softness was present in Chinese Spring and the allele for hardness, *ha*, was present in the others. A similar study using CS (CNN5D)/CS recombinant inbred lines was reported by Morris et al. {03106}.
A pleiotropic result of hardness is the decreased level of a 15 kD starch granule protein, friabilin, on the surface of water-isolated starch {470}. In endosperm, soft and hard wheats have similar amounts of friabilin, consequently the distinction between the two textural types depends upon the manner in which the friabilin co-purifies with starch. Friabilin is also referred to by the name 'Grain Softness Protein' (GSP) {0384}, and was later shown to be comprised primarily of puroindoline a and puroindoline b {0295}. Grain hardness of reciprocal soft x hard F1 kernels was well correlated with friabilin occurrence on starch in triploid endosperm {0381}. See IV, Proteins: 5.8 Puroindoline. GSP-1 genes, which are closely related to puroindolines, are also listed in section 5.8.

Two QTLs were detected for grain hardness in RILs of the ITMI population (Synthetic / Opata 85) {10051}. The QTL on the short arm of chromosome 5D was associated with *Xmta10-5D*, and increased hardness was contributed by Opata {10051}. The locus located proximally on the long arm of 5D was associated with *Xbcd450-5D* and increased hardness was contributed by the Synthetic allele {10051}.
Two QTLs, *QHa.ksu-3B*, associated with *Xksum9-3B* (R^2=0.09, and *QHa.ksu-5D(Ha)*, associated with *Xcfd-5D* (R^2=0.3), were identified in Karl*2/TA 4152-4 {10273}.

Using proteomic analysis of 2D-protein gels applied to 101 lines of the Opata/W-7984 (ITMI) RI mapping population, and after a preliminary study of a sub-group of these lines {10086}, 446 amphiphilic protein spots were resolved, 170 specific to either of the two parents and 276 common to both {10087}. An important category of these proteins comprises the puroindolines. Seventy-two loci encoding amphiphilic proteins were conclusively assigned to 15 chromosomes. At least one Protein Quantity Locus (PQL) was associated with each of 96 spots out of the 170 spots segregating; these PQL were distributed throughout the genome. The majority of the amphiphilic proteins were shown to be associated with plant membranes and/or play a role in plant defence against external invasions. Not only the puroindolines were associated with kernel hardness - a number of other amphiphilic proteins were also found to influence this trait.
Neixiang 188 (hard)/Yanshan 1 (medium hard) RIL population: *QGh.caas-1B.1* with hardness allele from Yanshan 1, R^2=0.28, *Xwms153 - 1BL - Xbarc81 - 1BL*{10640}

29. Grain Quality Parameters

In the comprehensive study of 46 quality-related traits in a RL4452/AC Domain RIL population, 99 QTLs involving 41 traits were located in 18 chromosomes {10361}; 14 QTLs clustered in the *Glu-1B* region (50cM), 20 QTLs occurred in the *Xwmc617-4D* - *Xwmc48-4D* region (30cM), 10 QTLs mapped to the *Xgwm130-7D* - *Xwmc405-7D* region (14cM) and 66 QTLs were dispersed {10361}. In a large study of 11 seed quality traits in a AC Karma/87E03-S2B1 DH population, 26 QTLs were detected in 7 chromosomes {10434}; 6 were clustered in the *Glu-D1* region and 5 were clustered in the *Rht-D1* region.

QTL analyses of 10 milling and baking quality traits (grain hardness, flour yield, grain and flour protein, alkaline water retention capacity (AWRC), sedimentation properties, cookie properties, lactic acid retention, dough strength, extensibility and mixograph properties) in the ITMI population grown in Mexico, France and USA (California) are reported in {10436}. Neixing 188 / Yanshan 1 RIL population: 75 QTLs for 5 quality-related traits are reported in {10640}.

29.1. Sedimentation value

29.2. Flour, semolina and pasta colour

QTL: A QTL was detected on chromosome 7A {9936}. Cultivar Schomburgk contributed the yellow colour allele in a cross Schomburgk/Yarralinka {9936}. Markers *Xcdo347-7A* and *Xwg232-7A* accounted for 60% of the genetic variation {9936}. A Sequence Tagged Site PCR marker is available {0180}.
A major QTL was detected in the distal region of chromosome 7BL in the cross Omrabi 5/ *T. dicoccoides* 600545. The QTL explained 53% of the variation and was completely linked to microsatellite marker *Xgwm344-7B.* Omrabi 5 contributed the allele for high yellow pigment level. Two additional small QTLs were detected on 7AL {0365}. Other references to flour colour are given under Flour Colour, *Lr19*, and *Sr25*.

W9262-260D3 (low yellow colour)/Kofa (high colour): Four QTLs identified on chromosomes 2A (*Xgwm425-2A*), 4B (*Xgwm495-4B*), 6B (*Xgwm193-6B*) and *Psy-B1* (chromosome 7BL) {10230}. See also Enzymes Phytoene synthase.

Analysis of yellow flour pigment in a RIL population of PH82-2 (low)/Neixiang (high) revealed major QTL on chromosomes 7A co-segregating with marker *YP7A* (R^2 = 0.2 - 0.28) (see Phytoene synthase 1), and 1B (R^2 = 0.31 - 0.54) probably contributed by 1RS {10501}. Huapei 3 /Yumai 57: DH lines: 18 additive QTLs and 24 pairs of epistatic QTLs affected flour colour parameters; *qa-1B*, closely linked with *Xbarc372-1B* was associated with variation of a*, R^2=0.256 {10625}.

A further study confirmed major QTL on chromosome 1RS (R^2=0.319) and 7A (R^2=0.339), minor QTL occurred on 1A and 4A {10716}.

29.3. Amylose content

Amylose content has a significant effect on industrial quality; for example, reduced amylose wheats perform better in some types of noodles. The waxy protein genes have an important influence, but other genes are also involved.

29.4. Milling yield

QTL: A QTL was detected on chromosome 3A {0181}. Cultivar Schomburgk contributed an allele for the higher milling yield in cross Schomburgk/Yarralinka {0181}. RFLP markers *Xbcd115-3A* and *Xpsr754-3A* were associated with this QTL at LOD>3 {0181}.
A QTL associated with *Pinb* on chromosome arm 5DS was detected in RILs from the cross NY6432-18/Clark's Cream {0241}. Cultivar Clark's Cream contributed the higher flour yield allele {0241}. This QTL coincided with QTL for hardness, hydration traits (dough water

absorption, damaged starch and alkaline water retention capacity (AWRC)), and baked product traits (cookie diameter and cookie top grain) {0241}.

29.5. Alveograph dough strength W

QTL: QTLs for W were detected on chromosome arms 5DS (associated with *Xmta10-5D*), 1AS (associated with *Xfba92-1A*), and 3B (associated with *XksuE3-3B*) in cross Courtot/Chinese Spring {0141}. The first two QTLs coincided with those for hardness. Ten QTL for W (39% of the variation), nine QTL for P (48% of the variation) and seven QTL for P:L (38% of the variation) were mapped in Forno/Oberkulmer spelt {0280}.

29.6. Mixograph peak time

QTL: A QTL associated with *Glu-Dy1* on chromosome arm 1DL was detected in RILs from the cross NY6432-18/Clark's Cream {0241}. Clark's Cream contributed the higher mixograph peak time allele {0241}. This QTL coincided with a QTL for bread mixing time {0241}.

29.7. Starch characteristics

The Isoamylase-1 gene from *Ae. tauschii (Iso-1)* complements the deficient rice sugary-1 mutant line {10295}.

QTL: QTLs for starch viscosity and swelling were associated with the *Wx-B1* locus in Cranbrook (*Wx-B1a*)/Halberd (null *Wx-B1b*). An additional QTL for starch viscosity was found on 7BL between markers *Xgwm344-7B* and *Xwg420-7B* in the first cross. This QTL disappeared when amylase activity was inhibited indicating that it was determined by the late maturing a-amylase activity contributed by Cranbrook. A QTL for starch viscosity was associated with the *Wx-A1* locus in the cross CD87/Katepwa {0362}.

29.8. Loaf volume

QTL: Loaf volume score consistent across three environments was scored in a RIL population Renan/Recital and revealed major QTL on chromosomes 3A (flanking markers *Xfbb250-3A, Xgwm666-3A,* positive effect from Renan) and 7A (flanking markers *Xcfa2049-7A, Xbcd1930-7A,* positive effect from Recital) {10536}.

A total of 30 QTLs were located on 12 chromosomes, each of which explained between 5.85 and 44.69% of the phenotypic variation; the QTLs of largest effect were located on chromosomes 6B and 6D {10659}.

29.9. Dough rheological properties

QTL: In a Cranbrook/Halberd DH population, environmental factors were a major determinant of dough extensibility whereas additive effects of alleles at the hight and low molecular weight glutenin loci determined dough strength {10247}.

29.10. Grain fructan content

Fructans are non-digestible carbohydrates considered to have health benefits to consumers. QTL: Berkut (high fructan concentration) / Krickauff (low fructan concentration): QTL detected on chromosomes 2B, 3B, 5A, 6D, and 7A of which *QGfc.aww-6D.2* (R^2=0.17, nearest marker, *Xbarc54-6D*) and *QGfc.aww-7A.1* (R^2=0.27,*Xgwm681-7A*)had the largest effects {10631}.

29.11. Water absorption

Neixiang 188 / Yanshan 1 RIL population: *XAbs.caas-5D.1* with positive effects from Yanshan 1, R^2=0.3, *Xcfd18-5DS* - *Xcfd189-5DS* {10640}

29.12. Chinese dry noodle quality

Chuan 35050 / Shannong 483 RIL populations: 3 QTLs for noodle palate, elasticity and smoothness clustered near *Glu-D1* with beneficial effects associated with subunits 5+10 coming from Chuan 35050. A very significant taste QTL, *QStas.sdau-4A.1* and positive QTLs for stickiness and total score also on chromosome 4A came from Shannong 483 {10647}

30. Grass-Clump Dwarfness/Grass Dwarfness

Complementary dominant genes. Genotypes producing dwarfness: *D1-D2-D3-*, *D1-D2D2*, *D1-D4-D3-*, *D1-D2-D4* and *D1-D4D4*.

31. Grain Weight

QTL : Variation at locus *QGw1.ccsu-1A*, associated with *Xwmc333-1A*, accounted for 15% of the variation in a RIL population from RS111/CS {0143}.
Rye Selection 111 (high GW)/CS (low GW) RIL: two definitive QTLs *QGw.ccsu-2B.1* and *QGw.ccsu-7A.1* and one tentative QTL, *QGw.ccsu-1A.1*, were detected by CIM analysis {10363}. The chromosome 7A QTL co-located with a QTL for early heading {10363}.

32. Growth Rate and Early Vigour

QTL analyses in *Ae. tauschii*: chromosomes 1D, 4D, and 7D carried QTLs for relative growth rate, biomass allocation, specific leaf area, leaf area ratio, and unit leaf rate. Chromosome 2D had QTLs for rate and duration of leaf elongation, cell production rate, and cell length. Chromosome 5D harbored QTLs for total leaf mass and area, number, and growth rate of leaves and tillers {10293}.

33. Hairy/Pubescent Auricles

34. Hairy Glume

35. Hairy Leaf

A QTL analysis of the ITMI population identified loci determining hairiness of leaf margins and auricles in regions of chromosomes 4B and 4D orthologous ot *Hl1* {10516}.

36. Hairy Leaf Sheath

Levy & Feldman {795} concluded that complementary genes determined hairy leaf sheath in *T. dicoccoides*.

37. Hairy Neck/Pubescent Peduncle

38. Hairy Node/Pubescent Node

Inheritance of hairy (glabrous) node versus non-hairy node was attributed to a single, dominant gene difference {396,837,910,914} and the *Hn/hn* locus was shown to be linked with *B1* (awn inhibitor). Observations on 5A trisomics and telosomics of Chinese Spring confirmed this location. Love & Craig {837} studied a cross involving Velvet Node CI 5877, and Gaines & Carstens {396} studied an offtype single plant designated Velvet Node Wash. No. 1981.

39. Heat tolerance

QTL: QTLs contributing to grain-filling duration (GFD) under high temperatures were associated with *Xgwm11-1BS* (11% of variability) and *Xgwm293-5AS* (23% of variability) in Ventnor (tolerant) // Karl 92 (Non-tolerant) {0327}.

40. Height

Ht is the general symbol.

40.1. Reduced Height : GA-insensitive

Genotypes of Indian semi-dwarf wheats based on the Ellis et al. {0378}.

40.2. Reduced Height : GA-sensitive

Borner *et al*. {116} found no evidence of orthologous GA-sensitive genes in rye, but reviewed evidence for orthologous GA-insensitive genes. The close linkage of *Rht8* and *Xgwm261-2D* permitted the use of the microsatellite as a marker for the detection of allelic variants at the *Rht8* locus{9962}.

40.3. Reduced Height : QTL

In Courtot/CS:

41. Herbicide Response

41.1. Difenzoquat insensitivity

41.2. 2,4-D tolerance

Randhawa *et al*. {1190} reported a single dominant gene in each of WL711, CPAN1874 and CPAN1922 controlling tolerance. HD2009 and PBW94 were described as susceptible.

41.3. Chlortoluron Insensitivity

41.4. Imidazolinone resistance

Resistance alleles found in mutagenized populations were incompletely dominant and additive in effect {10099}. Resistance is due to single base pair changes in acetohydroxyacid synthase.

42. Hybrid Weakness

42.1. Hybrid necrosis

[Progressive lethal necrosis {155}; Firing {971}].

Complementary dominant genes. Descriptive alleles *w* (weak), *m* (medium) and *s* (strong) were allocated by Hermsen {532}. Phenotype is affected by modifying genes (and/or genetic background) and environment {566}. According to Dhaliwal *et al*. {257} progressive necrosis is suppressed at 28C.

42.2. Hybrid chlorosis type 1

42.3. Hybrid chlorosis

42.4. Apical lethality

Apical lethality is caused by complementary recessive genes and is characterized by stunting and tiller death at the 4-5 leaf stage. The lethal genotype was designated *apd1 apd1 apd2 apd2* {10492}.

43. Iron Deficiency

44. Lack of Ligules

The liguleless character is controlled by complementary recessive genes in hexaploid wheat {077,738,942} and by a single recessive in tetraploid wheat {047,050,939,10133}. One gene at the tetraploid level is allelic with one of those in the hexaploid {939,10133}. Evidence for orthology of *lg1* and *lg2* with *lg* of rice {170}, *lg1* of maize {004}, *li* of barley {1155} and *al* of rye was presented in {725}. **al:** Imperial rye chromosome 2R restored the liguled condition to a liguleless CS derivative {939}.

Genotypes of selected tetraploid wheat {10133}

Lg1Lg1 Lg3 Lg3: *T. turgidum* var. *durum* Ldn - dic DS 2A: *T. turgidum* var. *dicoccum* Khapli and Vernal; *T. turgidum* var. *dicoccoides* Israel A; MG4343

Lg1Lg1 lg3 lg3: *T. turgidum* var. *durum*: Altaiskaya Niva; Castelpoziano; Langdon; Ldn-GB DS 2B; Golden Ball; Modoc; PI349056

lg1lg1 Lg3Lg3: None identified.

45. Leaf Erectness

46. Leaf Tip Necrosis

47. Lodging

48. Male Sterility

48.1. Chromosomal

48.2. Sterility in hybrids with wheat

48.3. Photoperiod and/or temperature-sensitive male sterility (PTGMS)

49. Manganese Efficiency

QTL: Variation associated with *Xcdo583-4B* explained 42% of the variation for Mn efficiency in the durum cross Stojocri 2 (Mn efficient)/Hazar (MN inefficient) {0320}.

50. Maturity time

51. Megasporogenesis

51.1. Control of megasporogenesis

52. Meiotic Characters

52.1. Low-temperature pairing

52.2. Pairing homoeologous

52.3. Inhibitor of pairing homoeologous

53. Nitrate Reductase Activity

54. Nuclear-Cytoplasmic Compatability Enhancers

55. Nucleolus Organizer Regions

55.1. 18S - 5.8S - 26S rRNA genes

NORs have been observed as secondary constrictions associated with nucleoli on satellited chromosomes {e.g., 221}, and by *in situ* hybridization to chromosome spreads {039,294,1014} of 18S-5.8S-26S ribosomal-DNA probes {038,433}. Allelic variation in gene number has been demonstrated at all wheat *Nor* sites and at *Nor-R1* by filter {367} and *in situ* hybridization {1012}. Allelic variants of the *Nor* loci are detected by hybridization of rDNA probes to restriction endonuclease-treated DNA on Southern blots {037,288,917,1399}. Alleles *Nor-B2a* to *Nor-B2f* were identified using *Taq1* digests of genomic DNAs hybridized to derivatives of the plasmid pTa250 {433} containing spacer-DNA fragments pTa250.4 {367,917} and pTa250.15 {288}.
Other variants may have been isolated {1399} using *BamH1/EcoR1* double digests and pTa71 {433}. The variants may or may not be equivalent to those described below.

More detailed listings for allelic variation at *Nor-B1* and *Nor-B2* are given in {917,918}. Two sites designated temporarily as *Nor-Ax* and *Nor-Ay* were identified in *T. monococcum* ssp. *boeoticum*, but were absent in ssp. *urartu*.

56. Osmoregulation

Osmoregulation is a specific form of solute accumulation regulating turgor pressure and hydration during periods of stress with positive effects on growth. Wheat lines selected for higher osmoregulation in the greenhouse have greater growth and seed yields under water limited conditions in the field.

57. Phenol Colour Reaction of Kernels

Wheat genotypes vary in response when caryopses are treated with weak solutions of phenol, a dark colour response being indicative of a positive response. This response is believed to be related to the action of tyrosinase. There seems to a genetic relationship with polyphenol oxidase activity which causes a darkening of flour, pasta and noodle products (see also Polyphenol Oxidase (PPO) activity).

58. Pollen Killer

Kato & Maeda {10164} reported both partial pollen and seed sterility in crosses involving certain landraces and Chinese Spring. They attributed sterility to recessive alleles of three complementary genes. The genes were designated *Ki2, Ki3* and *Ki4* {10164}, but the relationship of *Ki3* to the earlier designated *Ki* was not established. Some genotypes:
Ki2 Ki3 Ki4: **v:** Aka Kawa Aka {10165}; Hope {10165}; Marquis {10165}; Red Russian {10165}
ki2 Ki3 Ki4: **v:** Akadaruma {10165}; Canthatch {10165}; Norin 61{10165}; Pakistani Landrace IL159 {10164}

Ki2 ki3 Ki4: **v:** Gabo {10165}; Thatcher {10165}; Timstein {10165}; Zlatiborka {10165}
Ki2 Ki3 ki4: **v:** Kagoshima {10165}; Komugi Jingoro {10165}; Sakobore {10165}
ki2 ki3 Ki4: **v:** Finnish Landrace WAG4339 {10165}; Hungarian Landrace WAG4458 {10165}; Novosadska Jara {10165}
ki2 Ki3 ki4: **v:** Chinese Spring {10165}; Eshima Shinriki {10165}; Ethiopian Landrace IL70 {10164}; Norin 26 {10165}
Ki2 ki3 ki4: **v:** Cadet {10165}; Iraqi Landrace IL171 {10165}; Rex {10165}

59. Polyphenol Oxidase (PPO) Activity

3,4 dihydroxyphenylalanine (L-DOPA) was used as a substrate in a non-destructive test of polyphenol oxidase activity in seeds. Chromosome 2D was shown to carry PPO gene(s) based on Langdon/Chinese Spring (2D) substitution lines and nullisomic-tetrasomic analysis {0342}. An orthologous series of genes affecting PPO activity in both common wheat and durum was proposed in {10149}. See also, Phenol Colour Reaction of Kernels

Chara (mod high)/WW2449(low): DH population: PPO activity Associated with *Xgwm294b-2A* (R^2=0.82), *Xwmc170-2A, Xgwm312-2A* and *Xwmc178-2A* (R^2>0.7) {10410}.

Chara (medium high PPO)/WW2449 (low PPO): one QTL was located on chromosome 2A. Two markers (one SNP, one CAPS) based on BQ161439 were polymorphic between the parents and showed linkage or allelism with PPO loci *Xtc1* and *XPPO-LDOPA*. *Xtc1* - 0.6 cM - *XPPO-LDOPA/XPPO18/BQ161439* {10484}.

A QTL on 2D, associated with *Xfba314-2D* was identified in an M6 / Opata 85 population using the L-DOPA assay. The high PPO activity was contributed by M6 {0344}. Markers significantly associated with PPO activity were also detected on chromosomes 2A, 2B, 3B, 3D and 6B in the population NY18 / Clark's Cream {0344}.

A multiplex of markers *PPO33* and *PPO16* was reliable for selecting genotypes with low PPO activity {10418}.

Tetraploid wheat

Messopia/*T. dicoccoides*: RILs: Associated with RFLP *Xutv1427-2A* {10411}.

Jennah Khetifa (high)/Cham 1 (low): Associated with *Xgwm312-2AL* {10411}.
STS marker PPO18 based on a polyphenol oxidase (*PPO*) gene (GenBank AY596268) was closely linked to SSR markers *Xgwm312* and *Xgwm294* on chromosome arm 2AL. PPO18 explained 28-43% of the variation in PPO activity in the cross Zhongyou 9507/CA9632 {10290}.

60. Red Grain Colour

Red colour is probably due to the polyphenol compounds phlobaphene or proanthocyanidin, synthesized through the flavanoid pathway. Himi & Noda {10107} provided evidence that the D genes were wheat forms of Myb-type transcription factors (*Ntb10-3A, Myb10-3B,Myb10-3D*).
Red colour is dominant to white. At each locus, the white allele is assigned *a* and the red allele, *b*. White-grained *T. aestivum* and amber-grained *T. durum* wheats carry recessive *a* alleles at each locus. White-grained CS*7/Kenya Farmer and CS*6/Timstein are considered near-isogenic to CS with *R-D1b*.

61. Reaction to Black-Point of Grain

Black-point, a common grain defect, is a dark discoloration of the embryo region of the kernels. Whereas black-point is often attributed to infection by a number of fungi, the presence of such fungi may be a consequence of saprophytic colonization of affected tissues rather than the cause (see {10148} for references). The condition may be triggered by high humidity {0845}.
QTL: Sunco/Tasman DH populaion: QTL located in chromosomes 2B (15% of phenotypic variation), 3D, 4A (from Sunco) and 1D, 5A and 7AS (from Tasman {10148}. The 2B gene was associated with the presence of *Sr36* {10148}.

Markers *Xgwm319-2B* and *Xgwm048-4AS* were confirmed in a Batavia/Pelsart (resistant) DH population {10494}.

Cascades/AUS1408 DH population: QTL from Cascades located in chromosomes 2D (5 cM from *Xgwm484-2D*, 18% of phenotypic variation), 2A (13%), and 7AS (12%) {10148}.

62. Response to Photoperiod

One-gene {1169} and two-gene {638,1137,1170} differences were reported in inheritance studies. In Chinese Spring/Hope substitution lines for chromosomes 1A, 4B and 6B greater sensitivity to short photoperiod was found, whereas substitutions of 3B and 7D were less sensitive {487}.
'a' alleles are dominant.
There is an orthologous gene series on the short arms of homoeologous group 2. The "a" alleles confer the insensitive response {0063}, the contrasting allele may be referred to as "b".

QTL: Trident (early)/Molineux (late): In addition to an effect associated with chromosome 2B, three QTLs were designated as follows: ***QPpd.agt-1AL*** *(Xwmc304 - Xgwm497),* ***QPpd.agt-7AS*** *(Xbarc154 - Xbarc108)* and ***QPpd.agt-7BS*** *(Xgwm46 - Xgwm333)* {10382}. The QTL in chromosome 1A is possibly orthologous to *Ppd-H2* in barley.

63. Response to Salinity

63.1. K+/Na+ discrimination

Variation in K+/Na+ discrimination ratios correlate with salt tolerance, high ratios being indicative of higher tolerance.

63.2. Salt tolerance

QTL: Opata 85/W7984. 77 QTLs effective at different growth stages were mapped to 16 chromosome {10384}.

63.3. Sodium exclusion

64. Response to Tissue Culture

65. Response to Vernalization

The requirement for vernalization is particularly important for winter cereals to avoid cold injury of the sensitive floral organs during the winter. In wheat, vernalization requirement is controlled by four major genes designated *Vrn-1, Vrn-2, Vrn-3,* and *Vrn-4*. The first three genes were identified using map based cloning aproaches {10014, 10299, 10421}. The *Vrn-1* gene encodes a MADS-box transcription factor closely related to the Arabidopsis *AP1/FRUITFULL* family, responsible for the transition of the shoot apical meristem from the vegetative to reproductive stage in wheat {10014}.

Deletions in the promoter (*Vrn-A1a, Vrn-A1b*) {10198} or the first intron of this gene (*Vrn-A1c, Vrn-B1a, Vrn-D1a*) {10202} are the most common sources of spring growth habit

among landraces and commercial cultivars of polyploid wheat worldwide {10617,10695,10709}.

The *Vrn-2* locus produces two linked and related proteins designated ZCCT1 and ZCCT2, characterized by the presence of a putative zinc finger and a CCT domain {10299}.

Deletions and mutations involving both the ZCCT1 and ZCCT2 genes are frequent in diploid wheat and are associated with recessive alleles for spring growth habit {10299}.

Among the cultivated tetraploid and hexaploid wheat species the *Vrn-B2* gene is generally functional whereas the *Vrn-A2* gene is not {10710}. At least one functional copy of *Vrn-2* combined with homozygous recessive alleles at all three *Vrn-1* loci is required to confer winter growth habit in hexaploid wheat.

The *Vrn-B3* locus (formerly known as *Vrn-5* or *Vrn-B4*) is homologous to the Arabidopsis *FT* gene {10421}. This dominant allele, found in the variety Hope, is associated with the insertion of a transposable element in the *Vrn-B3* promoter. Natural variation at the *Vrn-A3* and *Vrn-D3* loci has been also described in hexaploid wheat {10533}. *Vrn-3* promotes the transcription of *Vrn-1* and accelerates flowering {10421}.

The *Vrn-D4* allele for early flowering was originally identified in the Australian cultivar Gabo {671} and was backcrossed into Triple Dirk to develop the isogenic line TDF {1172}. This locus was mapped on the centromeric region of chromosome 5D between markers *Xcfd78* and *Xbarc205* {10711}. Natural variation for flowering time at the centrometric region of homoeologous group5 chromosomes has been found, so far, only in the D genome. Incorrect TDF seed stocks generated initial confusion about the existence of *Vrn-D4* but molecular markers are now available to separate the incorrect stocks {10711}. Using genetic analyses, Iwaki et al. {10003} found the *Vrn-D4* allele for spring growth habit occurred with a higher frequency in India and neighboring regions.

Allelic variations at the *Vrn-1* and *Vrn-B3* loci in Chinese wheat cultivars are summarized in {10617}.

Aneuploid and whole chromosome substitution experiments showed that all group 1 chromosomes of wheat carry genes affecting response to vernalization {773}.

Stem-elongation in winter wheat: In regions where wheat is used as a dual purpose crop for grazing and grain production a relatively long vegetative phase is required to maximize the vegetative tissue and to delay the stem elongation phase. Variation in this attribute occurs among winter wheats such as Jagger (early stem elongation) and 2174 (late elongation).

In a Jagger/2174 RIL population, QTL for stem elongation included *Qste.0cs-5A* (associated with the *Vrn-A1* locus, *Qste.ocs-1BL, Qste.ocs-2D* (associated with the *Ppd-D1* locus) and *Qste.ocs-6A* {1010}. In 2007 the respective R^2 values were 0.289, 0.155, 0.067 and 0.058. Jagger alleles on chromosome 5A, 1B and 6A promoted stem elongation whereas the allele on chromosome 2D had a delaying effect {10722}.

66. Restorers for Cytoplasmic Male Sterility

66.1. Restorers for *T. timopheevi* cytoplasm

Minor restorer effects were associated with *Xbarc330-5A* in R18 and *Xgdm130-7D* in R9034

{10222}. The relationships of these QTL with previously located restorers in chromosomes 5A {860} and 7D (*Rf2*) are unknown.

66.2. Restorers for *Aegilops longissima* cytoplasm

66.3. Restorers for photoperiod-sensitive *Aegilops crassa* cytoplasm

Morai & Tsunewaki {1047} described photoperiod sensitive CMS caused by *Ae. crassa* cytoplasm in wheat cv. Norin 26. Almost complete sterility occurred when plants were grown in photoperiods of 15h or longer.

67. Ribosomal RNA

The *5S-Rrna-1* loci were physically mapped in 1AS, 1BS, and 1DS and the *5S-Rrna-2* loci were physically mapped in 5AS, 5BS and 5DS of Chinese Spring using deletion lines {1043}. Table 1 in {276} lists the chromosome or chromosome arm locations of rRNA loci in 12 Triticeae species.

67.1. 5S rRNA genes

Within the Triticeae there are basically two sets of 5S rRNA loci. One set, identified by repetitive units 320-468 bp in length, is located on group 1 chromosomes. The other set, identified by repetitive units 469-500 bp in length, is on group 5 chromosomes. Within species the repetitive units at a locus are extremely uniform in size and sequence. They remain stable in foreign genetic backgrounds.

68. Seedling Leaf Chlorosis

69. Segregation Distortion

See also, Gametocidal Genes.

70. Soft Glumes

71. Sterol Esterification in Kernels - Synthesis of b-Sitosterol Esters

Two sterol-ester phenotypes, p-L (palmitate + linoleate) and L (linoleate) are inherited as alleles at a single locus.

72. Stem solidness

Solid stem, caused by increased pith in normally hollow stem regions, is associated with resistance to wheat stem sawfly, *Cephus cinctus*. Solid stem confers resistance to wheat stem sawfly. See also Reaction to *Cephus* spp.

73. Temperature-Sensitive Winter Variegation

This phenotype involves reduced vigour and chlorotic patches on leaves of certain genotypes in *Ae. umbellulata* cytoplasm when grown at low temperatures {1596}.

74. Tenacious Glumes

Tg1 and *Tg2* were considered to be homologues of *sog* for soft glumes in *T. monococcum*. See Soft glumes.

A QTL analysis of the relationship of glume tenacity (*Gt*) with threshability (*Ft*) and the size of the glume base scar (*Gba*) after glume detachment in two crosses, viz. the ITMI population and CS*/CS (*Ae. tauschii* 2D), was undertaken {10497}. In the first cross *QFt.orst-2D.1* and *QGt.orst-2D.1* were closely associated with *Xgwm261-2D*, and *XFt.orst-2D.2* and *XGt.orst-2D* were associated with *Xgwm455-2D*, in the second population only the first pair along with *Xba.orst-2D* were detected; these appeared to correspond with *Tg1* {10497}.

75. Tiller Inhibition

A QTL of large effect on spike number per plant in a DH population of Fukuho-Komugi/Oligoculm mapping to the *Hg - Xpsp2999(Glu3)-1A* region {10218} probably corresponds to *Tin1*.

76. Uniculm Stunt

Stunting is favoured by a combination of long days and low night temperatures {581}. Caused by duplicate recessive genes, *us1* and *us2*, located in chromosomes 4A and 5B, respectively {200}.
Genotypes: Normal **v**: *Us1 us2*: Alfa {581}; Jaral {581}.
Normal **v**: *us1 Us2*: Mabruk {581}.
Stunted **v**: *us1 us2*: Line 492 {581}.

77. Variegated Red Grain Colour

78. Yield and Yield Components

78.1. Grain weight

78.1.1. 50-grain weight

78.1.2. 1000-grain weight

QTL: Two QTLs for 1,000-kernel weight were assigned to chromosome 3A in RSLs from Cheyenne*7/Wichita 3A {0025}. QTLs for grain size were identified on chromosome arms 1DS, 2DL and 6BL in a RIL population from RS111/CS {0236}. Eight QTLs for 1,000-kernel weight (54 % of the variation) were mapped in Forno/ Oberkulmer spelt {0280}.

78.1.3. Test weight

78.2. Grain weight/ear

78.3. Grain number per spike

QTL: Three QTLs for kernel number per spike were assigned to chromosome 3A in RSLs from Cheyene*7/Wichita {0025}.

78.4. Grain yield

Non-glaucous (virescent) lines from a Shamrock/Shango DH population had higher yields than glaucous sibs {10543}; see Glaucousness, subsection Epistatic inhibitors of glaucousness.

Grain yield under drought stress

QTL: Dharwar Dry (drought tolerant)/Sitta: SSR locus *Xwmc89-4AL* was the marker most closely associated with QTL for grain yield, grain fill rate, spike density, grains/m^2, biomass and drought susceptibility index covering a genetic distance of 7.7 cM {10488}.

78.5. Spikelet number/ear

78.6. Spike number per square metre

QTL: A QTL for spike number per square metre was assigned to chromosome 3A in RSLs from Cheyenne*7/Wichita 3A {0025}.

78.7. Spike length

78.8. Tiller number/plant

78.9. Kernel number per square metre

78.10. Grain volume weight

79. Yellow Berry Tolerance

QTL : A QTL for yellow berry tolerance, contributed by RS111, was associated with *Xgwm190-5D* and *Xgwm174-5D* in a RIL population from RS111/CS {0237}. A tolerance QTL contributed by CS, the susceptible parent, was detected on 6B {0237}.

80. Proteins

80.1. Grain protein content

Thirteen QTLs for grain protein content were identified in a RI population from the cross WL711 (low protein content) and PH132 (high grain content) {10055}. The QTLs that were identified using more than one method or in more than one environment are listed below. Also listed is a QTL that was identified in the mean over the four environments and was therefore deemed important {10055}.

QTLs for grain protein content were detected on chromosome arms 6AS (associated AFLP marker, *XE38M60*$_{200}$) and 1BL (associated RFLP marker, *Xcdo1188-1B*) in Courtot/Chinese Spring {0141}.
Nine QTLs (51% of the variation) were mapped in cross 'Forno'/ 'Oberkulmer' spelt {0280}.
A QTL for grain and flour protein content, contributed by CS, was associated with *XTri-1D*/Centromere in a RSL population from the cross Cheyenne (high quality wheat)/CS (low quality wheat) {0251}.
For QTLs conferring grain protein content detected in the cross Renan/Recital {10071}, only QTLs stable over at least 4 of 6 locations are presented. Renen contributed the four alleles for high grain protein content.

Ning 7840/Clark: RILs: QTLs from Ning 7840 were detected on chromosomes 3AS (*Xwmc749-3AS* - *Xgwm369-3AS*; R^2=0.09-0.11) and 4B (*Xgwm368-4B* - *Xwmc617-4B*, R^2=0.08-0.11) {10702}.
Durum: In 3BIL-85 (high protein introgressed from *T. dicoccoides*/Latino QTL were detected in chromosomes 2AS (associated with *Xcfa2164-2A*, R^2=17%), 6AS (*Xp39M37*$_{250}$*-6A*, R^2=17%) and 7BL (*Xgwm577-7B*, R^2=9%) {10338}.

80.2. Enzymes
80.2.1. Acid phosphatase
80.2.2. Alcohol dehydrogenase (Aliphatic)

Three *Adh* genes were identified in *Hordeum vulgare* and *H. spontaneum* {144,490,493,520}. Two of these were tightly linked at the *Adh-H1* locus {144}. The third gene was tentatively located in 5H {490}.
A low-level of aliphatic alcohol dehydrogenase activity is commonly observed on zymograms in the absence of added substrate {513}; this may account for the observation of wheat lactate dehydrogenase that was reported in {1465}.
The gene series formerly designated *Adh-2* and *Adh-3* appear under Aromatic Alcohol Dehydrogenase

80.2.3. Aminopeptidase
80.2.4. Alpha-amylase
80.2.5. Beta-amylase
80.2.6. Endopeptidase
80.2.7. Esterase

Genetic control of esterases [carboxylic ester hydrolases (E.C.3.1.1.1)] was the subject of a comparative study {814}.

EST-2, EST-5 and EST-8 are controlled by genes on 3L and where a recombination test was possible between *Est-D5* and *Est-D8*, no segregation was observed. The different gene symbols were retained because of the different tissue specificities and polymerisation profiles of the enzymes. The same arguments surround the EST-1 and EST-6 genes located in the 3S arms {814}.
The *Est-6* gene of rye was mapped {249}. The *Est-6* genes of wheat were mapped

comparatively in the proximal regions of chromosomes 2S {256}. The *Est-2, Est-5 and Est-8* were mapped to the extreme distal regions in the 3L arms {247}.

80.2.7.1. EST-1

EST-1 is a dimeric enzyme that electrofocuses around pH4.0 and is expressed in all tissues except endosperm {814}.

80.2.7.2. EST-2

EST-2 is a coleoptile-specific monomeric enzyme that electrofocuses at low pI.

80.2.7.3. EST-3

EST-3 is a monomeric enzyme that is expressed in young seedlings (this enzyme was not observed in {814}.

80.2.7.4. EST-4

EST-4 is a monomeric, leaf-specific enzyme that electrofocuses around pH 4.5.

80.2.7.5. EST-5

EST-5 consists of 20 or more monomeric, grain-specific isozymes that electrofocus between pH 5.6 and 7.0.

80.2.7.6. EST-6

EST-6 is a dimeric enzyme that electrofocuses around pH 7.6 and is specific to endosperm.

A group of leaf esterase isozymes controlled by the long arms of the homoeologous group 3 chromosomes were reported {919}. The relationship of these esterases to EST-2 and to the leaf esterase designed EST-6 reported in {629} has not been determined.

80.2.7.7. EST-7

EST-7 is a monomeric enzyme that electrofocuses in the same region as EST-6 but is specific to green tissues.

80.2.7.8. EST-8

EST-8 consists of about 10 isozymes that electrofocus between pH 4.5 and 6.5 and are expressed only in vegetative tissues. EST-8 is likely to be the enzyme previously described in {919} and {629}.

80.2.7.9. EST-9

EST-9 is a monomeric enzyme that electrofocuses around pH 5.0 and is expressed only in embryos.

80.2.8. Glucosephosphate isomerase

80.2.9. Glutamic oxaloacetic transaminase

Wehling {1559} identified a GOT locus designated *Got1* in 4RL of *S. cereale*.

80.2.10. Hexokinase

Allelic variation was observed in three of 55 hexaploid accessions {006}.

80.2.11. Lipoxygenase

The wheat *Lpx-1* gene in wheat corresponds to barley *LoxA* (GenBank L35931). The *Lpx-B1* locus is duplicated, with the *Lpx-B1.1* and *Lpx-B1.2* loci corresponding to GenBank sequences DQ474240 and DQ474241, respectively. The *Lpx-B1b* allele corresponds to a deletion associated with a 4.5-fold reduction in lipoxygenase activity. The *Lpx-2* gene in wheat corresponds to the barley *LoxC* gene (GenBank L37358) whereas the *Lpx-3* gene in wheat corresponds to the barley *LoxB* gene (GenBank L37359).

80.2.12. Malate dehydrogenase

80.2.13. Peroxidase

Peroxidase (EC1.11.1.7) isozymes have high tissue specificity. Staining and electrophoretic systems are reviewed in {118}. PER-1, -2, -3, -4 and -5 are all reported in {816}.

80.2.13.1. PER-1

PER-1 is expressed in leaf {012} and coleoptile {816} tissues.

80.2.13.2. PER-2

PER-2 is expressed in young leaf {118}, coleoptile and root {816} tissues.

80.2.13.3. PER-3

PER-3 is expressed in embryo {119,816} and scuteller {119} tissues.

80.2.13.4. PER-4

PER-4 is expressed in endosperm tissue {086,119}.

80.2.13.5. PER-5

PER-5 is expressed in roots {816}.

80.2.14. Phosphodiesterase

80.2.15. Phosphogluconate dehydrogenase

Loci were also identified in 6B {1435}, 1EL {1435}, 1HL {147,1072}, $1H^{ch}$ {352} and 1RL {779}.

80.2.16. Phosphoglucomutase

80.2.17. Shikimate dehydrogenase

80.2.18. Superoxide dismutase

80.2.19. Triosephosphate isomerase

80.2.20. Aromatic alcohol dehydrogenase

The *Aadh-1* and *Aadh-2* loci were designated with the synonyms *Adh-2* and *Adh-3*, respectively, in a number of publications in addition to {508,518,584}. These include: {510,509,511,519,517,587,1066,1139}.

80.2.21. Aconitase

80.2.22. NADH dehydrogenase

80.2.22.1. Ndh-1

Based on the correspondence of the electrophoretic patterns, isoelectric points (pIs) and chromosomal location, it was proposed that the *Ndh1* (NADH dehydrogenase) and *Dia3* (diaphorase) represent the same locus {0356}.

80.2.22.2. Ndh-2

Based on the correspondence of the electrophoretic patterns, isoelectric points (pIs) and chromosomal location, it was proposed that the *Ndh-2* (NADH dehydrogenase) and *Dia2* (diaphorase) represent the same locus {0356}.

80.2.22.3. Ndh-3

Based on the correspondence of the electrophoretic patterns, isoelectric points (pIs) and chromosomal location, it was proposed that *Ndh-3* (NADH dehydrogenase), *Dia1* (diaphorase) and *Mnr1* (menadione reductase) represent the same locus {0356}.

80.2.22.4. Ndh-4

80.2.23. Dipeptidase

80.2.24. Malic enzyme

A dimeric enzyme extractable from mature grains.

80.2.25. Adenylate kinase

80.2.26. Glutamate-pyruvate transaminase

80.2.27. Catalase

A catalase locus, designated *Cat2*, was mapped 6 cM proximal to *Aco-D2* in an *Ae. tauschii* F_2 population derived from VIR-1954/VIR-1345 cross {10046}. This locus may be orthologous to *Cat-B1* {10046}.

80.2.28. Beta-glucosidase

80.2.29. Starch branching enzyme I

80.2.30. Starch branching enzyme II

80.2.31. Benzoxinones

The putative role of benzoxinones sets *Bx-1* to *Bx-5* is to catalyze the pathway Indole-3-glycerol phosphate to DIBOA. Primers designated from maize sequences were used to generate RT-PCR products utilised to screen a cDNA library from CS seedlings. Full-length cDNAs were heterologously expressed in yeast and the *Bx* gene products had enzymatic action. The *Bx* genes located by Southern analysis of CS deletion stocks occurred as clustered groups in homoeologous groups 4 (*Bx-1, Bx-2*) and 5 (*Bx-3.1, .2, Bx-4, Bx-5*) {10103}.

80.2.32. Acetohydroxyacid synthase (EC 4.1.3.18)

An orthologous series was mapped as the active target sites of imidazolinone herbicides. See section: Herbicide Response: Imidazolinone resistance.

80.2.33. Phytoene synthase

Phytoene synthase, which condenses two molecules of geranyl geranyl diphosphate to produce phytoene, is the first of the specific enzyme necessary for carotene biosysthesis in plants.

80.2.33.1. Phytoene synthase 1 (EC 2.5.1.32)

Homology with the same gene in rice (*Psy1*) {10230}.

Phytoene synthase is involved in the carotenoid biosynthetic pathway and influences yellow pigment content in grain (See Flour colour and Grain quality parameters: Flour, semolina and pasta colour). The gene *Psy-A1* was cloned and a functional marker developed from the sequence distinguishing Chinese common wheats with high and low pigment contents {10501}. Most hexaploid wheat cultivars have a 676-bp insertion in intron four that is absent in Australian cultivars Dundee, Raven, and Aroona with high yellow pigment. The *Psy-B1b* allele from tetraploid wheat Kofa is the result of a B-A intergenomic conversion event that probably occurred in Cappelli *ph1c* mutant 1 {10530}. An EMS mutation in the *Psy-E1* gene is associated with whiter endosperm in lines carrying the *Th. elongatum* 7EL translocation.

80.2.33.2. Phytoene synthase 2 (EC 2.5.1.32)

Homology with the same gene in rice (*Psy2*) {10230}.

80.2.34. Polyphenol oxidase

High PPO activity in kernels and flour leads to a time-dependent discolouration of end products such as noodles, pasta and breads.

Primers different from those in {10386} were developed in {10504}, but their ability to distinguish phenotypic groupings (alleles) were similar. A null allele of *Ppo-D1* was identified for this locus using primer pair WP3-2 {10504}.

80.2.35. Protein disulfide isomerase (EC 5.3.4.1)

The genes for PDI and their promoters were sequenced in {10423}. A related sequence on 1BS was shown to be a partial, non-expressed copy in {10424}, but not detected in {10409}. PCR-RFLP markers for [*TaPDI-4A*] and [*TaPDI-4B*] were designated [*Xvut(PDI)-4A*] and

[*Xvut(PDI)-4B*] in {10409}. These were also closely associated with Germin (oxalate oxidase {10441}) genes {10409}.

80.2.36. Isoamylase 1

80.2.37. Polygalacturonase-inhibiting proteins

PGIPs are leucine-rich repeat (LRR) proteins involved in plant defence.

80.3. Endosperm storage proteins

80.3.1. Glutenins

These are heterogeneous mixtures of proteins comprising subunits linked by disulfide bonds. 'A' are high-molecular-weight (HMW) and 'B', 'C' and 'D' are low-molecular-weight (LMW) subunits.

Using proteomic analysis of 2D gels of seed storage proteins in 39 ditelocentric lines of cv. CS, 105 protein spots were resolved {03129}. Locations of structural genes controlling 26 spots were identified in 10 chromosomal arms (4 on 1BL, 5 on 1BS, 4 on 1DL, 4 on 1DS, 2 on 6AS, 3 on 6BS, 1 on 6DL, 1 on 6DS, 1 on 3BS and 1 on 3BL). Multiple regulators of the same protein located on various chromosome arms were observed. Two novel subunits, named 1Bz and 1Dz, were found to have very similar structures to HMW glutenin subunit 12 (encoded by *Glu-D1-2a* - see the relevant list below) and were located to chromosome arms 1BL and 1DL, respectively.

PCR amplification of genomic DNA was used to isolate three LMW glutenin genes in cultivar Chinese Spring, named LMWG-MB1, LMWG-MB2 and LMWG-MB3 {01101}. The deduced amino-acid sequences showed a high similarity between these ORFs and with those of other LMW glutenin genes. The authors state that the study provided direct evidence that insertions and/or deletions provide a mechanistic explanation for the allelic variation, and hence the resultant evolution, of prolamin genes, and comment on relationships with gamma-secalins and beta-hordein families. Single-base substitutions at identical sites generate premature stop codons in both LMWG-MB2 and LMWG-MB3, indicating that these clones are pseudogenes.

80.3.1.1. Glu-1

The *Glu-1* loci, all of which are compound, encode HMW glutenin subunits.
Each *Glu-1* locus in hexaploid wheat contains two genes, the products of which were described as 'x-type' and 'y-type' based on differences in molecular weight and isoelectric point {1118}.

Other evidence has shown that these gene products differ in electrophoretic fingerprint pattern {1124} and cysteine content {1028}, and the genes themselves differ in nucleotide sequence {1470,1433,373}.

Although early evidence suggested up to 6 genes in total at each locus {1471,373], it appears likely that only a single copy of each gene is present at the 1AL, 1BL, and 1DL loci {495}.

No 'y-type' protein from the *Glu-A1* locus has been demonstrated in hexaploid wheat {1118}, although they are found in diploid wheats {1535,798}, and sequencing experiments have shown the presence of two stop codons in the transcribed portion of the gene {10088}. Definitive evidence that subunit 21^{*} {602}, which has a mobility close to that of subunit 21, is a 'x-type' protein rather than a 'y-type' protein has not been obtained. The gene coding for 'x-type' proteins within *Glu-A1* is also often silent {1118,420}.

The symbols for the genes within the *Glu-1* loci coding for 'x-type' and 'y-type' proteins will be *Glu-1-1* and *Glu-1-2*, respectively, rather than *Glu-1x* and *Glu-1y* {1470}. The genes are closely linked but recombination has been observed between *Glu-B1-1* and *Glu-B1-2* with a frequency of 3 in 3,450 {1117}. The gene order, relative to the centromere, has not been ascertained.
The subunit nomenclature used is that devised in {1116}; however, an alternative system based upon molecular weight was proposed in {1068}. A system of naming the *Glu-A1-1*, *Glu-A1-2*, *Glu-B1-1* and *Glu-B1-2* alleles in *T. turgidum* var. *dicoccoides* is given in {796}.

In {00116}, a comparison between spelt wheats (*T. spelta*) and bread wheat was carried out for the glutenins using a nomenclature system described in {00117}.
The *Glu-1* loci may be recognised by the DNA probe pTag1290 {1471} and probe pwhe1(Dy10) {030}. Individual *Glu-1-1* loci on 1A, 1B and 1D and the *Glu-1-2* loci may be recognised by specific primers {263}.
In {00105}, the evolution of the high molecular weight glutenin loci of the A, B, D and G genomes of wheat was explored; 30 partial allele sequences were compared, designated by Greek letters (alpha, beta, gamma, etc.) (5 of which were cited as Schlumbaum, pers. comm.; the remaining 25 were deposited as GenBank, accession nos. X98583-X98592, X98711-X98715 and Y12401-Y12410). These partial alleles derive from all six *Glu-1-1* and *Glu-1-2* loci in current-day samples taken from seven species of wheat, as well as from DNA extracted from charred grain of two samples from archaeological excavations, dated 3000 and 5000 years old, respectively.

Following the first listing which considers the *Glu-1* set for hexaploid wheat as a single locus, there is a provisional listing based on x- and y- type glutenins. These are not referenced.

The importance of the HMW glutenin subunits for bread-making quality was first noted from observations in wheat cultivars of related pedigree on the effects of the presence of subunit 1 encoded by *Glu-A1a* {0197}, effects that have repeatedly been confirmed since (for example {0198,0199,01100}).

A nomenclature system for prolamin banding patterns of triticale was proposed in {03139}. Extensive allelic variation in triticale at *Glu-A1*, *Glu-B1*, *Glu-R1* and *Gli-R2* loci was reported in {03121}.

80.3.1.2. Glu-2

80.3.1.3. Glu-3

The *Glu-3* loci are defined as the cluster of LMW glutenin genes previously considered a component of the compound *Gli-1* loci.
More than 30 LMW glutenin complete genes, partial genes or pseudogenes have been sequenced from *Triticum* species (reviewed in {0245}).
In *T. aestivum*, only *Glu-B3* was shown to recombine with the gliadin genes (1.7 +/- 0.8) {1355,1358}. However, in *T. durum*, recombination was observed for both *Glu-A3* and *Glu-B3* with their respective *Gli-1* loci: the map distance between *Glu-A3* and *Gli-A1* has been estimated as 1.3 +/- 0.4 cM {1242}, and that between *Glu-B3* and *Gli-B1* as 2.0 +/- 0.8 in {1144} and as 2.0 +/- 0.4 in {1242}. It appears that *Glu-B3* is proximal to *Gli-B1*, and there is some evidence, albeit only tentative as the authors acknowledge, that *Glu-A3* is proximal to *Gli-A1* {1242}.
Whereas hitherto it has been widely thought that all the LMW subunits of glutenin were encoded by genes located on the chromosomes of homoeologous group 1, it has been demonstrated that, although the majority of the subunits are indeed controlled by genes on

this group, some of the C subunits must be controlled by loci elsewhere in the genome {482}. A novel type of polymeric protein (M_r approx. 71,000) was reported in the Australian advanced breeding line DD118 {03125}. It participates in the polymeric structure of glutenin (possibly as a chain terminator), and with an M_r of approximately 71,000, could be considered as a D-subunit of LMW glutenin. However, N-terminal sequencing suggests it to be a *Gli-B1* type omega-gliadin that has acquired a cysteine residue through mutation.

In an electrophoretic survey of 51 primary tritordeums {03113}, 20 distinct whole banding patterns (a-t), each consisting of between one and three bands, were observed for D-zone prolamins exhibiting glutenin-like solubility characteristics.

In 85 Japanese common wheat cultivars and 61 elite F_6 breeding lines, 3 alleles were observed at each of *Glu-A3* and *Glu-B3*, and 2 alleles at *Glu-D3* were named according to their parental origins in three doubled haploid mapping populations {03135}.

C-type LMW glutenin subunits in CS were assigned to chromosome groups 1 and 6, and shown to have sequences very similar to those of alpha- and gamma-gliadins {03134}. The authors suggest that they may be encoded by novel genes at loci tightly linked or present within the *Gli-1* and *Gli-2* loci, unlike other LMW glutenin subunits encoded by the *Glu-3* loci.

The HMW and LMW glutenin subunits carried by chromosome $1A^m$ of *T. monococcum* accession G1777 were characterised electrophoretically and evaluated for quality characteristics using recombinant chromosome substitution lines with chromosome 1A of CS {03142}. The HMW subunits from G1777 are promising for bread-making quality, whereas its LMW subunits are promising for biscuit-making quality.

The bread wheat cv. Salmone has been shown to carry two DNA fragments designated as SF720 and SF750 located on the chromosome 1B satellite and associated with the presence of two LMW glutenin subunits {03143}. However, the authors suggest that they occur at a locus other than *Glu-B3* due to their relatively high frequency of recombination with *Gli-B3*.

A naming system in which roman numerals are assigned to whole banding patterns for the LMW glutenin subunit is given in {03131} as an alternative to the LMW-1/-2 system described in {03136}. A further system naming whole banding patterns from LMW-1 to LMW-23 in emmer wheat is described in {03137}.
In {00111}, in a study of common and durum wheats from Portugal, the authors used the nomenclature system described in {00113} for the LMW subunits in common wheat, and that described in {00114} for the LMW subunits in durum wheat. The latter system was updated according to {02110}, but has been changed herein to new alleles with the earlier durum designation {00114} given as synonyms.In {03116}, it was suggested that *Glu-B3d* (common wheat standard genetic stock) is equivalent to *Glu-B3r* (durum wheat standard genetic stock), and that (referring to article {03127}) LMWsubunits observed in some Portugese triticales could be of the durum type.

A novel storage protein gene with chimerical structure was isolated from the old Hungarian cultivar Bankuti 1201, containing gamma-gliadin sequences in the 5' region, LMW-glutenin sequences in the 3' region and a frameshift mutation leading to a completely new polypeptide in the C-terminal region. A further seven recombinant prolamin genes were subsequently isolated. The eight genes, designated *Ch1* to *Ch8*, seem to derive from four gamma-gliadin and three LMW-glutenin sequences and are probably the result of crossing over between the

loci *Gli-1* and *Glu-3*. However, the precise recombinational mechanism that gave rise to them has yet to be elucidated {10307}.

80.3.1.4. Glu-4

The following loci, *Glu-D4* and *Glu-D5*, encoding low molecular weight subunits of glutenin (30-32 kDa) were described in {02111}; the proteins encoded by them were first observed earlier {02114, 02115}, and the former was later tentatively assigned the symbol *Glu-4* {02116}, before its chromosomal location was established and the locus definitively named as *Glu-D4* in {02111}. While this locus is located on chromosome 1D (in accordance with the position on the group 1 chromosomes of the remaining glutenin encoding loci found to date), the locus *Glu-D5* is located on chromosome 7D. In SDS-PAGE, the proteins from both loci are detected only in the presence of 4-vinylpyridine added to the sample extract. Their amino acid compositions do not match those of the major prolamin groups; nonetheless, they classify as glutenins based upon solubility, immunological behaviour and N-terminal amino acid sequence (the latter suggesting an evolutionary link with the major (B and C) low molecular weight glutenin subunits).

80.3.1.5. Glu-5

A collection of 173 *Ae. tauschii* accessions were analysed for low molecular weight glutenin subunits by SDS-PAGE {02112}. Thirty three different patterns for B-subunits and 43 for C-subunits were identified, some of which were of identical electrophoretic mobility to those observed in common wheat. Also observed were subunits with the same mobilities as the D-subunits and as the subunits encoded by the *Glu-D4* and *Glu-D5* loci. This variation represents a source of novel germplasm of potential value for breeding programmes aimed at improving the D-genome of common wheat in the context of bread-making quality.

80.3.2. Gliadins

These are heterogeneous mixtures of alcohol-soluble polypeptides without quaternary structure. The *Gli-1* loci are compound and are now considered to comprise the omega-gliadin and gamma gliadin {982,1415} multigene families {494}, which in some circumstances may be divided into *Gli-1-1* and *Gli-1-2*, respectively. The LMW glutenin multigene families, which are closely linked to the *Gli-1* loci {588}, are listed separately as the *Glu-3* set {1358}; information on map distance and gene order in relation to *Glu-3* and the centromere is given in the preamble for the *Glu-3* loci. There is evidence that a few of the omega-gliadin genes are separated from the main omega-gliadin gene cluster {993}. Variation at the *Gli-1* loci was described earlier {634,996,1126} and applied in mapping experiments {1243,1125,196,422,1120}. A rational system of naming the alleles was produced by Dr. E.V. Metakovsky{988}. This nomenclature is reproduced below. A considerable number of alleles were added to the original list given in {988}, and referenced here accordingly. A few alleles have been deleted, because, following much detailed comparison, there is now doubt that they can be reliably distinguished from existing alleles {9981}. The allelic letter in these cases has not been reused. To facilitate practical use of the list, the aim was to give at least three standard cultivars from a range of countries for each allele {9981}. This was achieved for the vast majority of entries and is a change from the original list compiled from {988}, where up to two standards were given. While the three or more standards described almost always include the original standards, some have been replaced for various reasons, such as international awareness of the cultivar, availability of seed, or the ease with which an allele can be identified in a particular genetic background {9981}. In the original list, where two cultivars were given as prototypes for an allele, the first named was from the USSR and the second from elsewhere; this is no longer the case,

although care was taken to include a Russian cultivar where possible, to maintain a wide base of germplasm in which the alleles are available, as well as to acknowledge the research groups in the country where much of the pioneering work was carried out.
For discussion of null alleles at the *Gli-1* and *Gli-2* loci, see {9984}.
Recombination was observed within the gliadin multigene family at *XGli-A1* {277}. These closely linked genes may correspond to *Gli-A1* and *Gli-A5*, but they were temporarily designated *XGli-A1.1* and *XGli-A1.2* until orthology with *Gli-A1* and/or *Gli-A5* is established.

Note: The catalogue entries reproduced here only refer to alleles in *T. aestivum*; there is, however, enormous variation in the gliadins in the close relatives of wheat; see, for example, {989} for studies in *T. monococcum* (more than 80 gliadin electrophoretic patterns observed in 109 accessions), {990} for studies in *T. boeoticum* (more than 50 electrophoretic patterns in 60 accessions), and {1076} studies in *T. durum* (19 electrophoretic patterns, referring only to variation in the omego-gliadins, in 243 accessions).
In {00110}, variants for omega-gliadins were reported from study of twenty-four accessions of einkorn wheat (*T. monococcum* ssp. *monococcum*). In {00111}, in a study of common wheat and durum from Portugal, the authors used the nomenclature system described in {00112} for the omega-gliadins. In {00116}, a comparison between spelt and common wheat was carried out for the gliadins using a nomenclature system described in {00118}.
The *Gli-1*loci may be recognised by probes pcP387 {372} and pTag1436 {065}, and by specific microsatellites primers {252}. Furthermore, it was shown that probe pTag1436 differentiates gliadin alleles rather well; using this probe, families of gliadin alleles and some of their relationships were described {9988}.

Twenty eight gamma-gliadin gene sequences from GenBank were grouped into nine subgroups in {10063}. Primers were developed against some of the subgroups and the chromosomal locations of the gamma-gliadin genes were determined {10063}.

Based upon morphological observation and RFLP analysis, it was proposed that the cultivar 'Chinese Spring' is a strain of the landrace 'Chengdu-guangtou' from the Chengdu Plain, Sichuan Province; this proposal is supported by the observation that CS and the landrace share the same alleles at all nine *Gli-1*, *Gli-2* and *Glu-1* loci {see 01102}.
PCR primers GAG5 and GAG6 were applied to 35 cultivars of closely related spelt and hexaploid wheat, and to eight cultivars of durum, to yield products originating from two gamma-gliadin genes mapped to chromosomes 1B (termed GAG56B) and 1D (termed GAG56D) {01103}. Two alleles for GAG56D (differing in a 9 bp deletion/duplication and single nucleotide polymorphism) were found, one a new allele and the other previously published {01104}. Meanwhile two alleles found for GAG56B among the durum wheats correlated with the presence of gluten quality markers, gamma-gliadins 42 or 45.

1B and 1D sulphur-poor omega-gliadins in cultivar Butte 86 were characterised by RP-HPLC, SDS-PAGE, two-dimensional PAGE, amino acid composition determination and sequencing, matrix assisted laser desorption ionisation-time of flight mass spectrometry and circular dichroism spectroscopy to reveal the detailed nature of the peptides belonging to the two groups, and showing that the complexity of mixtures of the peptides of the 1B group was greater than that of the 1D group {01105}. Although circular dichroism spectra were similar for the two groups of peptides, and suggested a mainly flexible random structure, there was evidence for a significant amount of left-handed polyproline II helical conformation in the case of the 1D components. The authors placed some of the results in the context of the possible ancestor of the B-genome and relationships with the barley C-hordeins and rye omega-secalins.

Eleven new gliadin alleles were found in a collection of 52 Spanish landraces of common wheat {03141}. These will be added to the *Gli-1* and *Gli-2* allelic lists in a later Supplement.

A new family of low-molecular-weight gliadin genes located on groups 4 and 7 were reported in {10117}. They appear to influence rheological properties and seem to be closely related to the 17kDa epsilon hordein, important in beer foam stability.

A novel storage protein gene with chimerical structure was isolated from the old Hungarian cultivar Bankuti 1201, containing gamma-gliadin sequences in the 5' region, LMW-glutenin sequences in the 3' region and a frameshift mutation leading to a completely new polypeptide in the C-terminal region. A further seven recombinant prolamin genes were subsequently isolated. The eight genes, designated *Ch1* to *Ch8*, seem to derive from four gamma-gliadin and three LMW-glutenin sequences and are probably the result of crossing over between the loci *Gli-1* and *Glu-3*. However, the precise recombinational mechanism that gave rise to them has yet to be elucidated {10307}.

Transcriptome analysis showed the presence of proteins called avenin-like a and b. The former contained a duplicated sequence of about 120 residues and corresponded to the LMW-gliadins. The latter was not previously characterized, but may form part of the glutenin fraction and hence influence quality. These avenin-like proteins showed higher expression levels in three *Aegilops* species (*Ae. caudata, Ae. cylindrica* and *Ae. tauschii*) than in common wheat {10321}.

Four new classes of low molecular weight proteins related to gliadins, though not sufficiently similar to be classified as such, were reported in {02113}. One of the classes has no close association to previously described wheat endosperm proteins.

80.3.2.1. Gli-1

In barley, the B and C hordeins are controlled by the *Hor2* and *Hor1* loci, respectively, which are linked {1341} on chromosome 1HS {1063,1153}. The map distances and homology of the proteins indicate that *Hor1,* the locus closest to the centromere, is equivalent to the omega-gliadins (*Gli-1-1*) in *Gli-1* {1338}.
Three alleles at each of the *Gli-1-1* (omega gliadin) loci were noted {1358}. The complexity of the *Gli-1* compound loci is further emphasized by a report of individual genes being separable by recombination, where *G1d-1A* (a block of gamma and omega genes) is separable by 0.3% from *Gld4-1A* (omega gliadins) which is in turn, separable by 1.5% from *Gld3-1A* (omega gliadins) {1103}.
Elsewhere, variation was described {634,996,1126} and applied in mapping experiments {107,196,422,1120,1125,1243}. Sixteen combinations of *Gli-B1* and 4 combinations of *Gli-D1* subunits are listed in {420}. Multiple alleles described in {996}, number 15 at *Gli-A1*, 18 at *Gli-B1*, and 8 at *Gli-D1*.
The *Gli-1* alleles present in 57 Yugoslav wheat varieties were reported in {994}.

80.3.2.2. Gli-2

Prior to the publication of {988}, allelic variation was demonstrated at all of the wheat *Gli-2* loci, including 13 alleles at *Gli-A2*, 11 at *Gli-B2*, and 10 at *Gli-D2*, in a study of 39 cultivars {996}.
The *Gli-2* alleles present in *57* Yugoslav wheat varieties were determined {994}.

80.3.2.3. Gli-3

A *Gli-3* set of loci coding for omega-type gliadins are located 22 to 31 cM proximal to *Gli-1* on the short arms of group 1 chromosomes {422,1403,589}.

80.3.2.4. Gli-4

It is not clear how *Gli-S^{l}4* and *Gli-S^{l}5* relate to the *Gli-4* and *Gli-5* sets described below.
A locus designated *Gli-A4* controlling omega-gliadins in cv. Perzivan biotype 2 was mapped at 10 cM proximal to *Gli-A1* on the short arm of chromosome 1A {1205}.
However, Metakovsky *et al.* {9983} have since shown that this locus and *Gli-A3* are, in fact, the same locus. Furthermore, Dubcovsky *et al.* {277} did not find evidence for the simultaneous presence of both *Gli-A3* and *Gli-A4* in five 1A or 1A^{m} mapping populations and concluded that *Gli-A4* should be considered to be *Gli-A3* until conclusive evidence for the former is obtained. For these reasons, the locus *Gli-A4* is deleted from the catalogue.

80.3.2.5. Gli-5

A locus designated *Gli-5* controlling omega-gliadins was mapped to the short arms of chromosomes 1A and 1B, distal to *Gli-1* {1147}. The map distance between *Gli-B5* and *Gli-B1* was estimated as 1.4 cM (recombination value of 1.4 +/- 0.4%), although there was significant variation in recombination values over crosses, ranging from 0 % to 5.9 % over the six crosses analysed. This variation was attributed to genotypic influence on the frequency of recombination.

80.3.2.6. Gli-6

80.3.2.7. Gli-7

80.3.3. Other endosperm storage proteins

80.3.3.1. Triticin proteins

The triticin proteins {1360} or [Triplet proteins {1357}] are storage globulins with homology to pea legumins and related proteins in oats, rice and several dicotyledonous species {1360}. Triticin gene segments including its hypervariable region were PCR-amplified, with preferential amplification of *Tri-D1* for the only pair of primers giving consistent results {10322}.

80.4. Enzyme Inhibitors

80.4.1. Trypsin inhibition

80.4.2. Subtilisin inhibition

Considerable genetic variation for *Si-2* was noted in {701}. A chromosome location for *Si-H2* on 1HL was inferred in {528} but questioned in {701}.
Three subunits of the wheat tetrameric inhibitor of insect a-amylase, CM1, CM3 and CM16, with homology to the dimeric and monomeric a-amylase inhibitors and the trypsin inhibitors, were located by Southern analysis of cDNAs pCT1, pCT2, and pCT3 to 4A, 4B, 4D; 7A, 7B, 7D; and 4A, 4B, 4D, respectively {427}.
Genes encoding proteins which inhibit the action of mammalian and insect, but not cereal, a-amylases, were located in chromosomes 3BS, 3DS and 6DS of Chinese Spring {1260}. Also, genes encoding inhibitors of insect a-amylases were located in *H. chilense* chromosomes 4H^{ch} and 7H^{ch} {1262}.

80.4.3. Inhibitors of alpha-amylase and subtilisin

Orthologous genes were identified in *Ae. speltoides* and *T. timopheevii* {908}. All durum wheats investigated had the genotype *Isa-A1b, Isa-B1b*.

80.4.4. Inhibitors (dimeric) of heterologous alpha-amylases

Chromosome 3BS has duplicated loci controlling two dimeric inhibitors of exogenous a-amylases, one known as 0.53 or Inh I {1260}, and the other as WDA I-3 {1260}. Chromosome 3DS has a homoeologous locus controlling a dimeric inhibitor of exogenous a-amylases, known as 0.19 or Inh III {1260,0124}, that is closely related to 0.53/Inh I. Intervarietal polymorphism for the WDA-3 protein was identified by isoelectric focussing of water-soluble endosperm proteins {0124}. This was interchromosomely mapped on 3BS using both a DH population of Cranbrook/Halberd, and a set of RILs of Opata 85/W-7984 (ITMI population) {0125}.

Three genome allele specific primer sets were designed for the 3BS and 3DS alpha-amylase inhibitors in cv. Chinese Spring, based upon SNPs. Their validity was confirmed in 15 accessions of *Triticum urartu, Triticum monococcum, Aegilops tauschii* and *Triticum dicoccoides*. The results offered support that the 24kDa dimeric alpha-amylase inhibitors in cultivated wheat are encoded by a multigene family {10323}, previously proposed in {10324}, as the result of phylogenetic analysis of sequences characterized by cSNPs.

80.5. Other proteins

80.5.1. Lipopurothionins

80.5.2. Lectins

80.5.3. Iodine binding factor

A monomeric water soluble protein from mature grain which preferentially binds iodine {818}.

80.5.4. Water soluble proteins

WSP-1 are monomeric grain endosperm proteins identified by their high pI's {817}.

80.5.5. Salt soluble globulins

GLO-1 are endosperm proteins (23-26 kDa) soluble in salt but not in water {455}.

80.5.6. Waxy proteins

Waxy protein (granule-bound starch synthase = ADP glucose starch glycosyl transferase, EC 2.4 1.21 = GBSSI) is tightly bound within endosperm starch granules and is involved in the synthesis of amylose {1616}. Waxy variants, characterised by starch granules containing increased amylopectin and reduced amylose, are preferred for Japaness white salted or "udon" noodles {1650}. Similar waxy phenotypes are controlled by orthologous genes in barley, maize and rice but are not known to occur in rye {725}. All combinations of the null alleles were produced in Chinese Spring {0018}. Partial genomic clones of various diploid, tetraploid, and hexaploid wheats were sequenced {0278,0279}.

A multiplex PCR assay for identifying waxy genotypes is described in {10032}.

Lists of cultivars, lines and landraces of tetraploid and hexaploid wheats with different, mostly null, alleles at the *Wx* loci are given in {9910,9911,9912,1053,1054,9913,9915, 9916,1650,9917}.
The complete genomic sequence for *Wx-D1a* from CS {0073} and the cDNA sequence for the *Wx-D1b* allele from Bai Huo {0075} were determined.
Isolation of a wheat cDNA encoding *Wx-A1* and *Wx-D1* was reported in {0123} and {0167}, respectively. Isolation of genomic sequences for the genes encoding granule-bound starch synthase (*GBSSI* or *Wx*) in *T. monococcum, Ae. speltoides* and *Ae. tauschii* was reported in {0168}. Cloning of a second set of *GBSSI* or *waxy* genes, *GBSSII*, which were shown to be located on chromosomes 2AL, 2B and 2D, was reported in {0167}.
Various hard and soft wheats with the alleles *Wx-A1b, Wx-B1b* and *Wx-D1b* are listed in {0304}. Fifteen percent of Chinese wheats possessed *Wx-B1* null alleles {10357}.

80.5.7. Starch granule proteins

The proteins, designated SGP-1, are starch synthases, encoded by *SsII-A1, SsII-B1* and *SsII-D1* {0042}.

A triple null stock (SGP-1 null wheat) is reported in {0137}. Deletion mapping indicated that the gene order on the 7S arms is; centromere - *Sgp-1* - *Sgp-3* - *Wx*{1615}.

80.5.8. Puroindolines and grain softness protein

Puroindolines a and b are the major components of friabilin, a protein complex that is associated with grain texture (see 'Grain Hardness'). The name 'puroindoline' and the complete amino acid sequence of puroindoline a were given in {0382} from cv Camp Remy. Hard grain texture in hexaploid wheat results from unique changes in the puroindoline amino acid sequence or, currently, four null forms {0295} of the completely linked genes (max. map distance 4.3 cM) {452}. Tetraploid (AABB, AAGG) wheats lack puroindolines and are consequently very hard {03103}. A searchable database of wheat varieties and their puroindoline genotype is available at http://www.wsu.edu/~wwql/php/puroindoline.php. Grain softness protein-1 is a closely related gene which is closely located to the puroindoline genes {03111,1185}. 'GenBank' and 'dbEST' refer to sequence databases available at NCBI (also available throught EMBL and DDB).

Recent reviews {10522, 10523} provide comprehensive descriptions of the molecular genetics and regulation of puroindolines. Morris and Bhave {10524} reconciled the D-genome puroindoline alleles with DNA sequence data. Bonafede et al. {10525, 10526} developed a CS line (PI 651012) carrying a $5A^{m}S.5AS$ translocation from *T. monococcum*; the translocated chromatin carries A-genome *Pina, Pinb* and *Gsp-1* alleles that confer softer kernel texture.

Pinb-D1b, Pinb-D1c, Pinb-D1d, Pinb-D1e, Pinb-D1f, or *Pinb-D1g* are present in hard hexaploid wheats not carrying the *Pina-D1b* (null) mutation {452,1035,0082,0204}.

Wheats with *Pinb-D1b* were slightly softer and a little superior to those with *Pina-D1b* in milling and bread-making characteristics although there was considerable overlap {0206}.
Transgenic rice with the *Pina-D1a* and *Pinb-D1a* alleles possessed softer grain {0207}.

Genotypes for a selection of North American wheats are given in {0204}.

In *T. monococcum* the gene order was reported to be : tel - *Gsp-1* - *Pina* - *Pinb* {0083, 10122} whereas in *Ae. squarrosa* it was : tel - *Gsp-1* - *Pinb*- *Pina* {10037}.

Ikeda et al. {10305} reported a double-null with apparently no *Pina-D1* or *Pinb-D1* genes present in **v:** Bindokku, Cheyenne 'A', Chosen 68, Saiiku 18, Saiiku 44, and tentatively assigned it *Pina-D1b/Pinb-D1h(t).* How this deletion compares with the double null mutation reported by Tranquili et al. {10077} which was assigned *Pina-D1k/Pinb-D1q* is unknown.

80.5.9. Grain softness protein

80.5.10. Starch synthase

80.5.11. Histone H1 Proteins

The relationship of this gene series with a *Hst-A1, Hst-B1, Hst-D1* series in group 5 chromosomes {0216} based on DNA hybridization studies was not established.

81. Reaction to Barley Yellow Dwarf Virus

Disease: Cereal yellow dwarf

82. Reaction to *Bipolaris sorokiniana*

Diseases: Spot blotch and common root rot.

Spot blotch

QTL

Yangmai 6 (R)/Sonalika (S): RIL population: AUDPC was controlled by four QTLs derived from Yangmai 6, viz. *QSb.bhu-2AL* (*Xbarc353-2A* - *Xgwm445-2A*, R^2=0.148), *QSb.bhu-2BS* (*Xgwm148-3B* - *Xgwm375-2B*, R^2=0.205), *QSb.bhu-5BL* (*Xgwm67-5BL* - *Xgwm371-5BL*, R^2=0.386) and *QSb.bhu-6DL* (*Xbarc173-6D* - *Xgwm732-6DL*, R^2=0.225) {10719}.

83. Reaction to *Blumeria graminis* DC.

Disease: Powdery Mildew.

Resistance genes and their molecular associations are reviewed in {10141}.

83.1. Designated genes for resistance

Note: Chancellor, used as a susceptible genetic background, for some near-isogenic lines probably carries *Pm10* and *Pm15* {1479}.
33 NILs, including 22 resistance genes and 3 genetic backgrounds are listed in {10389}.

A further gene derived from *T. monococcum* PI 427772 was identified in BCBGT96A = PI 599036 = Saluda*3/PI 427772 {10479}.
A single resistance gene was identified on chromosome 7AL in hexaploid germplasms NC96BGT4 (a *T. monococcum* derivative). This gene was proximal to *Pm1* and considered to be different from *Pm37*, although possibly allelic {10274}.
Genotype lists:Chinese wheats{1608,572}; Finnish wheats {0028}; French wheats{1629}; Hungarian wheats {02104}; Western Siberian wheats{1101}
Complex genotypes:
Drabent {heterogeneous} *Pm2 Pm4bPm9/Pm1 Pm2 Pm4b Pm9* {1287};
Nemares *Pm1 Pm2Pm4b Pm6 Pm9* {1287};
Planet, Sappo & Walter *Pm1 Pm2 Pm4b Pm9* {096,097,540,1287,1428}

Scandinavian wheats {10681}.

83.2. Suppressors of *Pm*

Some wheats which, on the basis of cytological and rust tests carry 1RS from Petkus rye, do not express resistance due to presence of a suppressor {385}. Zeller & Hsam {1625} located a suppressor of *Pm8* and *Pm17* in chromosome 7D of Caribo. Mildew resistance was suppressed in Florida, Heinrich, Ikarus, Olymp and Sabina, which are derivatives of Caribo with 1BL.1RS. According to Ren *et al*. {1209}, *SuPm8* does not suppress *Pm17*. Hanusova *et al*. {492} listed 16 wheats that carry a suppressor of *Pm8*; 111 wheats did not carry the suppressor. In contrast, a high frequency of suppression occurred in CIMMYT wheats {108,1208}. Further genotypes are identified in {491}. Although Line 81-7241 carries *Pm8* as well as *Pm23*, evidence was presented to indicate that *Pm8* was suppressed in Line 81-7241{1618} and , by inference, indicated that Chinese Spring possessed *SuPm8*.

83.3. Temporarily designated genes for resistance to *Blumeria graminis*

83.4. QTLs for resistance to *Blumeria graminis*

QTL: Several QTLs were detected in two RE714/Hardi populations when tested at two growth stages and with different cultures over three years. The most persistent and effective QTL was located in the vicinity of *Xgwm174-5D* {0272}. Three QTLs, *QPm.vt-1B, QPm.vt-2A* and *QPm.vt-2B*, with additive gene action, accounted for 50% of the variation in a population developed from Becker/Massey{0284}.
These QTLs were confirmed by the addition of extra markers to the Becker/Massey map and in a separate analysis of USG 3209 (A Massey derivative)/Jaypee (susceptible) {10505}. USG 3209 possessed *Pm8* (1BL.1RS) and an unknown specific resistance factor and their combination had a positive effect on APR even though neither was effective against the races used to identify the QTL {10505}.
QTLs on chromosomes 1A, 2A, 2B, 3A, 5D, 6A and 7B were detected in a RE714/Festin population in multiple locations and over multiple years. The QTL on chromosome 5D was detected in all environments and all years and was associated with markers *Xgwm639-5D* and *Xgwm174-5D*. Resistance was contributed by RE714. A QTL coinciding with *MlRE* on 6A was also detected in all environments. The QTL on chromosome 5D and 6A accounted for 45% to 61% of the phenotypic variation {0354}.
Avocet R(S)/Saar (R) F6 RILs: QTL located on chromosomes 1BL (close to *Xwmc44-1B*) (*Pm39*), 7DS (*Xgwm1220-7D*) (*Pm38*) and 4BL (*XwPt-6209*) (resistance allele from Avocet R {10481}.

Fukuho-Komugi/Oligoculm, DH population. QTL for adult plant resistance located on 1AS (R^2=22%, *Pm3* region, *Xgdm33 - Xpsp2999*), 2BL (R^2=8%, *Xwmc877.1-Xwmc435.1)* and 7DS (R^2=10%) derived from Fukuho-komugi, and 4BL (R^2=6% at one of two sites, *Xgwm373-Xgwm251*) from Oligoculm {10335}. The QTL on 7DS, flanked by *Xgwm295.1-7D* and *Ltn*, is likely to be *Lr34/Yr18*.

CI 13227(S)/Suwon 92(R), SSD population: APR (field resistance) was closely associated with *Hg, Xpsp2999-1A* and *Xpm3b.1* and *Xpm3B.2* designed from the *Pm3b* sequence {10340}.

RE9001(R)/Courtot(S) RIL population:*QPm.inra-2B* (R^2=10.3-36.6%), in the vicinity of *Pm6,* was consistent over environments {10360}. Eleven QTL, detected in at least one environment were identified by CIM {10360}.

Bainong 64 (R)/Jingshuan 16 (S), DH lines: Four QTL from Bainong 64: *Qpm.caas.1A, Xbarc148-1A - Xgwmc550-1A* interval, R^2=0.074-0.099; *QPm.caas-4DL* proximal to *Xwmc331-4D*, R^2=0.15-0.23; *QPm.caas-6BS*, proximal to *Xbarc79-6BS*, R^2=0.09-0.13; and *QPm.caas-7AL*, proximal to *Xbarc174-7AL*, R^2=0.067-0.071 {10680}.

Lumai 21 (R)/Jingshuang 16 (S), F_3 lines: Three QTLs from Lumai 21: *QPm.caas-2BS, Xbarc98-2BS - Xbarc1147-2BS* interval, R^2=0.106-0.206; *QPm.caas-2BL, Xbarc1139-2BL - Xgwm47-2BL* interval, R^2=0.052-0.101; and *QPm.caas-2DL, Xwmc18-2DL - Xcfd233-2DL* interval, R^2=0.057-0.116 {10707}.

84. Reaction to *Cephus* spp.

Pest: Wheat stem sawfly. North American species *C. cinctus*; European species *C. pygmeus*. Resistance to wheat stem sawfly is associated with solid stem (see also: Stem solidness).

Tetraploid wheat

85. Reaction to *Cochliobolus sativus* Ito & Kurib.

Disease: Cochliobolus root rot.

86. Reaction to *Diuraphis noxia* (Mordvilko)

Insect pest: Russian aphid, Russian wheat aphid.

QTL: QTLs for antixenosis were associated with *Xpsr687-7D* (7DS) and *Xgwm437-7D* (7DL) in CS/CS (Synthetic 7D) {10136}. Separate antibiotic effects were demonstrated for the same chromosome {10136}.

A QTL, *QDn.unlp.6A*, for antixenosis was associated with *Xgwm1393-6AL* and *Xgwm1150-6AL* in a CS/CS(Synthetic 6A) DH population {10216}.

87. Reaction to *Fusarium* spp.

87.1. Disease: Fusarium head scab, scab

Type II resistance. Whereas much of the recent genetic work involved FHB caused by *F. graminearum*, according to {10514}, *F. culmorum* is more damaging than *F. graminearum* in terms of FHB severity, kernel damage, yield reduction and DON/NIV contamination.

Patterson (mod sus)/Fundulea 201R RILS: QTLs accounting for 19% and 13% of phenotypic variation were found on chromosomes 1BL (*Xbarc8-1BS* - *Xgwm131-1BL* region) and 3AS (*Xgwm674-3A/Xbarc67-3A* region) {10114}. Two weak QTLs were possibly associated with chromosomes 3D (Patterson allele) and 5AS {10114}.

Arina(R)/Forno(S): Three QTLs, *QFhs.fal-6DL* (R^2=22%), *QFhs.fal-5BL.1* (in Forno, R^2=14%) and *QFhs.fal.4AL* (R^2=10%) and 5 minor QTLs in 2AL, 3AL, 3BL, 3DS and 5DL were detected {10172}.

Arina/Riband DH lines: QTL affecting ADUPC were identified in 1BL(2), 2B, 4DS, 6BL and 7AL (Arina), and 7AL and 7BL (Riband). The most effective was the 4DS QTL that appeared to be an effect of *Rht-D1a* rather than height *per se* {10464}.

Cansas (moderately resistant)/Ritmo (susceptible): Map based analysis across environments revealed seven QTL, *QFhs.whs-1BS* (1RS), *QFhs.whs-3B* (not *Fhb1*), *QFhs.whs-3DL, QFhs.whs-5BL, QFhs.whs-7AL* and *QFhs.whs-7BL* (cumultatively, R^2 = 0.56). The chromosome 1D gene was primarily involved in resistance to fungal penetration and the others in resistance to spread {10503}. There were significant correlations of FHB response with height and heading date {10503}.

More detailed mapping led to the relocation of the 5B QTL to chromosome 1BL. The renamed *Qfhs.lfl-1BL* reduced FHB severity by 42% relative to line lacking it {10698}. This gene was also present in Biscay, History and Pirat {10698}.

Three RGA sequences putatively assigned to chromosome 1A explained 3.37-12.73% of the phenotypic variation in FHB response among F7 and F10 populations {10364}. STS marker FHBSTS1A-160 was developed from one of the RGA.

Dream(R)/Lynx(S) RIL population. Following inoculation with *F. culmorum* 4 QTL for AUDPC were identified on chromosomes 6AL (R^2=19%), 1B (12%), 2BL (11%) and 7BS (21%). The resistance allele in 1B came from Lynx and was associated with T1BL.1RS {10260}.

Dream*4/Lynx lines were developed by selection of QTL on chromosomes 6AL, 7BS and 2BL. Lines carrying *QFhs.lfl-6AL* and *QFhs.lfl-7BS* were more resistant than lines lacking them; the 2BL QTL effect was not verified {10470}.

Frontana(R)/Remus(S): Major QTLs in chromosomes 3AL (*Xgwm270-3AL - Xdupw227-3A* region) and 5A (*Xgwm129-5A - Xbarc-5A* region) accounted for 16% and 9% of the phenotypic variation (mainly type 1 resistance) over 3 years {10174}.

Frontana(MR)/Seri82(S), F3 and F3:5 populations: QTLs were located in chromosomes 1BL (R^2=7.9%), flanked by AFLP markers, 3AL (R^2=7.7%), flanked by *Xgwm720-3A* and *Xgwm121-3A*, 7AS (R^2=7.6%), flanked by an AFLP and *Xgwm233-7A* {10349}.

Veery (S) / CJ9306 (R): Four QTLs, *XQFhs.ndsu-3BS* (*Xgwm533b - Xgwm493*), *QFhs.nau-2DL* (*Xgwm157 - Xwmc-041*), *QFhs.nau-1AS* (*Xwmc024 - Xbarc148*) and *QFhs.nau-7BS* (*Xgwm400 - Xgwm573*) accounted for 31, 16, 10 and 7%, respectively, of the average phenotypic variation over three years {10490}

Type I resistance and DON accumulation: Hobbit Sib/*T. macha* 4A DH population: Both traits were assigned to a small region distal to *Xgwm601-4A* and cosegregating with *Xgwm165-4A* {10254}.

DH181(R)(Sumai 3/HY 386 Seln.): QTL identified in 2DS, 3AS, 3BS, 3B Cent. region, 4DL, 5AS, 6BS {10213}.

Field resistance: Wuhan-1/Maringa, QTLs were located on chromosomes 2DS, 3BS (Proximal) and 4B {10020}.

Resistance to DON accumulation: Wuhan-1/Maringa, QTLs were located on chromosomes 2DL and 5DS {10020}.

Veery/CJ 9306 (R): Four QTLs contributed to resistance; *QFhs.ndsu-3BS* nearest marker *Xgwm533b* (R^2 = 0.23), *QFhs.nau-2DL, Xgwm539* (R^2 = 0.2), *QFhs.nau-1AS, Xbarc148* (R^2 = 0.05) and *QFhs.nau-5AS, Xgwm425* (R^2 = 0.05) {10496}.
Haplotype diversity among a large number of FHB resistant and susceptible (mainly Canadian) germplasms indicated similarities in Asian, Brazilian and other materials {10173}. Brazilian cv. Maringa was more similar to Asian than to other Brazilian lines {10173}.

For review see{0283}.

Mesterhazy et al.{0006} reported a strong genetic correlation in resistance to different species of *Fusarium*.

Bobwhite plants transformed with AtNPR1, an *Arabidopsis thaliana* gene that regulates activities of SAR, displayed a heritable type II response equal to that of Sumai 3 {10237}.

In cross Patterson (open)/Goldfield (closed) RILs, narrow flower opening which was correlated with FHB resistance. The major QTL effect associated with narrow flower opening and low FHB incidence occured in map interval *Xbarc200 - Xgwm210* (29% of variation in

FHB incidence); these genes were probably located in chromosome 2BS {10243}.

Wangshuibai/Annong8455:RIL population: CIM analysis over 2 years detected QTL for FHB response on chromosome 3B (R^2=0.17) and 2A (R^2=0.12) and for DON levels in 5A (R^2=0.13), 2A (R^2=0.85) and 3B (R^2=0.06) {10447}. The regions involved were *Xgwm533-3B* - *Xbarc133-3B, Xgwm425-2A*, and *Xgwm186-5A* - *Xgwm156-5A* {10447}.

In a reciprocal backcross analysis of Chris monosomics/Frontana, Frontana chromosomes 3A, 6A and 4D reduced visibly diseased kernels, kernel weight and DON content, whereas Frontana chromosomes 2A, 2B, 4B and 7A increased the same traits {10398}.

Soissons (relatively resistant)/Orvantis (susceptible): Soissons carried *QFhs.jic-4D* (R^2=0.106-0.161) associated with *Rht-D1a* (tall allele) {10718}. FHB susceptibility tended to be associated with the *Rht-D1b* allele {10718}. Supporting studies with NILs indicated that the presence of *Rht-B1b* led to reduced type 2 resistance relative to presence of *Rht-B1b* or the tallness alleles at both loci {10718}.

87.2. Disease: Crown rot caused by *Fusarium pseudograminearum, F. culmorum* and other *Fusarium* species.

QTL: Kukri(R)/Janz(S) DH population. Simple interval mapping in the region Pst1 ACG.Mse1 CAC - *Xgwm251-4B* accounted for 48% of the variation in crown rot response {10034}.

Lang (S)/CSCR6(R):RIL population: tested under controlled conditions with *F. pseudograminearum* and *F. graminearum*: *Qcrs.cpi-3BL* from CSCR6, R^2=0.49 and *Qcrs.cpi-4B* from Lang R^2=0.23 {10703}.
2-49 (partially Resistant) / Janz(susceptible) DH population: Analysis of partial seedling resistance indicated major QTL in chromosomes 1D (R^2=0.21) and 1A (R^2=0.09) and minor QTL in 2A, 2B (from Janz), 4B and 7B {10132}.
W21NMT70/Mendos: DH population: three consistent QTLs for seedling resistance were identified with CIM; these were located in chromosome 5D and 2D (resistance alleles from W21NMT70) and 2B (resistance allele from Mendos) {10358}.

88. Reaction to *Heterodera avenae* Woll.

Cereal root eelworm; cereal cyst nematode.

QTL: *Qcre.src-1B* was located to the *Xwmc719-1B* (R^2=12%) - *Xgwm140-1B* (R^2=12%) region in Trident/Molineux {10343}.

89. Reaction to *Magnaporthe grisea* (Herbert) Barr

M. grisea is a pathogen of blast on many graminaceous species, the best known of which is rice. In Brazil it has become a pathogen of wheat. The wheat pathotype(s) is different from those attacking other species such as rice, oat, millets and weeping lovegrass.

A second gene designated *Rwt3* {0302} was present in CS and Norin 4. Genes *Rwt3* and *Rwt4* were detected using hybrids of *Triticum*-virulent and *Avena*-virulent pathogen isolates.

90. Reaction to *Mayetiola destructor* (Say) (*Phytophaga destructor*) (Say)

Insect pest: Hessian fly.

A recombination value of 12.0% between leaf-rust reaction {possibly *Lr10*} and Hessian-fly reaction in Selection 5240 was reported {018}.

91. Reaction to *Meloidogyne* spp.

Root rot nematode, root knot eelworm

92. Reaction to *Mycosphaerella graminicola* (Fuckel) Schroeter

Disease: Septoria tritici blotch

QTL: Four QTLs for resistance to *Mycosphaerella graminicola* were identified in replicated field experiments in a double haploid population from Savannah (susceptible)/Senat(resistant). Senat contributed all the alleles providing resistance {10067}

QStb.riso-2B was mapped on chromosome arm 2BL linked to SSR marker *Xwmc175-2B* (LOD>5, R^2>17%) {10067}.

QStb.riso-3A.2 was mapped on chromosome arm 3AS linked to SSR markers *Xwmc489-3A*, *Xwmc388-3A* and *Xwmc505-3A* (LOD>4, R^2>18%). Also detected at the seedling stage {10067}. *Xgwm369-3A* is present on chromosome arm 3AS {0187}. A resistance gene from Senat located at or near the *Stb6* locus was mapped 5 cM from microsatellite *Xgwm369-3A* on chromosome arm 3AS {10067}.

QStb.riso-6B was mapped on the centromeric region between SSR markers *Xwmc494-6B* and *Xwmc341-6B* (LOD>16, R^2>68%). Also detected at the seedling stage {10067}.

QStb.riso-7B was mapped on chromosome 7B close to SSR marker *Xwmc517-7B* (LOD>4, R^2>11%) {10067}.

ITMI Population: Three QTL, ***QStb.ipk-1DS, QStb.ipk-2DS*** and ***QStb.ipk-6DS*** conferred seedling-stage resistance to 2 isolates, whereas 2 QTL ***QStb.ipk-3DL*** and ***QStb.ipk-7BL*** conferred separate adult-stage resistances to each isolate {10151}.

A weak QTL, ***QStb.psr-7D.1***, giving partial resistance to Portuguese isolate IPO92006, was detected in the *Xcdo475b-7B* - *Xswm5-7B* region in chromosome 7DS {10341}.

93. Reaction to *Phaeosphaeria nodorum* (E. Muller) Hedjaroude (anamorph: *Stagonospora nodorum* (Berk.) Castellani & E.G. Germano).

Disease: Septoria nodorum blotch, Stagonospra nodorum blotch.

93.1. Genes for resistance

QTL

A QTL analysis of SNB response in the ITMI population found significant effects associated with chromosome 1B (probably *Snn1*) and 4BL, with an interactive effect involving the 1BS region and a marker on chromosome 2B {10009}. An additional QTL on 7BL was effective at a later stage of disease development {10009}.

Four QTLs, on chromosomes 2B (proximal part of long arm), 3B (distal part of short arm), 5B and 5D, were mapped in a Liwilla / Begra doubled haploid population. Longer incubation period and lower disease intensity were contributed by Liwilla {10045}.

Two QTLs for glume blotch resistance under natural infection were identified on chromosomes 3BS and 4BL in Arina / Forno RILs {10065}. The 3BL QTL, designated *QSng.sfr-3BS*, was associated with marker *Xgwm389-3B* and explained 31.2% of the

variation. The resistance was contributed by Arina {10065}. The 4BL QTL, *QSng.sfr-4BL*, was associated with *Xgwm251-4B* and explained 19.1% of the variation. Resistance was contributed by Forno {10065}. A QTL on 5BL, *QSng.sfr-5BL*, overlapped with QTLs for plant height and heading time {10065}. *QSng.sfr-3BS* peaked 0.6 cm proximal to *Xsun2-3B* {10465}. Association mapping involving 44 modern European cultivars indicated that the association was retained in a significant proportion of genotypes {10465}.

A QTL, *QSnl.ihar-6AL*, identified in DH lines of Alba (R) / Begra (S) accounted for 36% of the phenotypic variance in disease severity and 14% of the variance in incubation period {10143}.

Forno (S) / Oberkulmer spelt (R). Among 204 RILs leaf and glume response were genetically different but correlated (R^2=0.52). Ten QTLs for glume blotch (SNG) resistance were detected, 6 from Forno. A major QTL (R^2=35.8%) was associated with q. Eleven QTLs (4 from Forno) affected leaf blotch; 3 of these (chromosome 3D, 4B and 7B) with R^2>13% were considered potential candidates for MAS {10250}.

ITMI population: A major QTL, coinciding with *Snn1*, was located in chromosome 1BS (R^2 = 0.58, 5 days after inoculation), minor QTL were found in 3AS, 3DL, 4AL, 4BL, 5DL, 6AL and 7BL {10009}.

Br34 / Grandin: Three QTLs with resistance effects from BR34; *Qsnb.fcu-5BL.1* (*Tsn1*), R^2 = 0.63, *Qsnb.fcu5BL.2*, R^2 = 0.06, and *Qsnb.fcu-1BS* (vicinity of *Snn1*), R^2 = 0.10 {10458}. QTL analysis of the RIL population with Culture Sn6 revealed four QTLs, *Qsnb.fcu-2DS* (R^2 = 0.3 - 0.49) associated with *Snn2*, *Qsnb.fcu-5BL* (R^2 = 0.14 - 0.2) associated with *Tsn1*, *Qsnb.fcu-5AL* (R^2 = 0 - 0.13) associated with *Xfcp13-5A*, and *Qsnb.fcu-1BS* (R^2 = 0 - 0.11) associated with *Xgdm125-1BS* {10507}.

P91193D1 (partially resistant) / P92201D5 (partially resistant) RIL populations were tested in Indiana and Western Australia for glume resistance. Two QTL were identified: *Qng.pur-2DL.1* from P91193D1 (R^2 = 12.3 in Indiana and 38.1% in WA, respectively; *Xgwm526.1-2D* - *Xcfd50.2-2D*) and *QSng.pur-2DL.2* from P99201D5 (R^2 = 6.9% and 11.2%, respectively; *Xcfd50.3-2D* - *wPT9848*) {10471}.

HRWSN125(R)/WAWHT2074(S): Constant detection of *QSnl.daw-2DL* for flag leaf resistance, and *QSng.daw-4BL* for glume resistance over two years {10584}.

Tetraploid wheat

Langdon/Langdon (*T. turgidum* ssp. *dicoccoides* Israel-A 5B): *QSnb.ndsu-5B* located 8.3 cM proximal to *tsn1* for tan spot resistance; R^2 = 0.38 {10597}.

93.2. Sensitivity to SNB toxin

Australian cultivars with *Tsn1* and *tsn1* are listed in {10540}.

Tetraploid wheat

In a reevaluation of this work Faris and Friesen {10688} attributed all of the variation in SNB response to the presence or absence of SnTox1.

ma: *Xbcd183-5B* - 1.2 cM - *Tsn1/Xbcd1030-5B* - 2.4 cM - *Xrz575-5B* {10688}.

QTL: ITMI population: A major QTL, coinciding with *Snn1*, was located in chromosome 1BS (R^2=0.58, 5 days after inoculation), minor QTLs were found in 3AS, 3DL, 4AL, 4BL, 5DL, 6AL and 7BL {10009}.

94. Reaction to *Pratylenchus* spp.

Root lesion nematode; prats

94.1. Reaction to *Pratylenchus neglectus*

94.2. Reaction to *Pratylenchus thornei*

QTLs were located on chromosomes 2BS and 6DS {0122}.

95. Reaction to *Puccinia graminis* Pers.

Disease: Black rust; black stem rust; stem rust.
Note: Some near-isogenic lines are based on Marquis. The genes present in the Marquis background are not listed for those NILs.

Additional temporary designations are listed in {1230}.
Genotype lists: {323,970,10270,10511,10697}.

Complex genotypes:

AC Taber: *Sr2, Sr9b, Sr11, Sr12*{9905}.
Centurk: *Sr5* {979}, *Sr6* {979}, *Sr8a, Sr9a* {979}, *Sr17* {979}.
Chris: *Sr5* {679,1371}, *Sr7a* {1371}, *Sr9g* {1371}, *Sr12* {1371}.
Egret: *Sr5* {939}, *Sr8a* {939}, *Sr9b* {939}, *Sr12* {939}.
FKN: *Sr2, Sr6, Sr7a, Sr8a* {791}, *Sr9b* {791}.
H-44: *Sr2, Sr7b* {677}, *Sr9d* {677}, *Sr17*.
Hartog: *Sr2* {127}, *Sr8a, Sr9g, Sr12* {939}.
Hope: *Sr2* {677}, *Sr7b* {677}, *Sr9d* {677}, *Sr17*.
Kenya Plume: *Sr2* {1370}, *Sr5* {1370}, *Sr6* {1370}, *Sr7a* {1370}, *Sr9b* {1370}, *Sr12* {1370} *Sr17* {1370}.
Khapstein: *Sr2, Sr7a, Sr13* {674}, *Sr14* {674}.
Lawrence: *Sr2, Sr7b* {939}, *Sr9d, Sr17*.
Lerma Rojo 64: *Sr2, Sr6, Sr7b* {979}, *Sr9a* {979}.
Madden: *Sr2, Sr9b, Sr11, Sr13* {842}.
Manitou: *Sr5* {679}, *Sr6* {679}, *Sr7a, Sr9g* {965}, *Sr12* {939}.
Mendos: *Sr7a* {939}, *Sr11* {879}, *Sr17, Sr36*.
Pasqua: *Sr5, Sr6, Sr7a, Sr9b, Sr12*. Gene *Lr34* acted as an enhancer of APR{9905}.
PI 60599: *Sr7a* {689}, *Sr8a, Sr9b, Sr10*.
Selkirk: *Sr2* {499}, *Sr6* {468}, *Sr7b* {499}, *Sr17, Sr23* {950}.
Redman: *Sr2, Sr7b* {939}, *Sr9d* {939}, *Sr17*.
Reliance: *Sr5* {1308}, *Sr16* {1238}, *Sr18, Sr20*.
Renown: *Sr2, Sr7b* {939}, *Sr9d* {939}, *Sr17*.
Roblin: *Sr5, Sr7a? Sr11, Sr12*.
Timgalen: *Sr5* (heterogeneous) {1555}, *Sr6* {1555}, *Sr8a, Sr36*.
Thatcher: *Sr5* {1308}, *Sr9g* {965}, *Sr12* {939}, *Sr16* {1308}.
WW15 = Anza = Karamu = T4: *Sr5* {939}, *Sr8a* {939}, *Sr9b* {939}, *Sr12* {939}.

QTL:

Arina / Forno:*Qsr.sun-5BL* {10565}; resistance contributed by Arina, associated with

Xglk356-5B, R^2 = 11-12% {10565}. *Qsr.sun-7DS* {10565}; resistance contributed by Forno, associated with markers *XcsLV34* and *Xswm10* diagnostic for *Lr34/Yr18* {0828}.

HD2009/WL711 RILs: Three of several QTLs gave consistent effects across environments, viz. *QSr.sun-3BS*, R^2 = 0.09-0.15, probably *Sr2*, *QSr.sun-5DL*, R^2 = 0.2-0.44, probably *Sr30*, and *QSr.sun-7A*, R^2 = 0.07-0.13, nearest marker *wPT-4515* {10632}.

96. Reaction to *Puccinia striiformis* Westend.

Disease: Stripe rust, yellow rust.

96.1. Designated genes for resistance to stripe rust

Sources of additional genes for seedling (designated "12") and adult resistances ("13", "14", "15") are listed in {1430}.

Genotype list: Chinese common wheats {10369}. European wheats {10579}. U.K. wheats {10697}.

96.2. Temporarily designated genes for resistance to stripe rust

North American workers {181,186,184} allocated a number of temporary designations to uncatalogued genes detected with North American *P. striiformis* accessions. Druchamp, Yamhill and Stephens were reported to carry '*Yr3a* or *Yr4a*" because these genes could not be distinguished with the cultures that were used.

96.3. Stripe rust QTLs

Two QTLs in Camp Remy/Michigan Amber were located on chromosome 2BL (*QYR1*, LOD score 12) and 2AL (*QYR2*, LOD 2.2) {0287}. Four QTLs were scored in the ITMI population. The most effective (*QYR3*, LOD 7.4) on chromosome 2BS was probably *Yr27*, the others were located in 7DS (*QYR4*, LOD 3.4), 5A (*QYR5*, LOD 2.8), 3D (*QYR6*, LOD 2.8) and 6DL(*QYR7*, LOD 2.4) {0287}.

Camp Remy/Recital: 217 RILs. Six QTLs for APR were detected over 4 years. *QYr.inra-2BL* (R^2=0.42-0.61) corresponded largely to seedling resistance gene *Rsp* and possibly *Yr7*. The other genes were *Qyr.inra-2AL, QYr.inra-2BL, QYr.inra-2DS* (perhaps *Yr16*), *QYr.inra-5BL.1* and *QYr.inra-5BL.2* {10279}.

Seven QTLs were identified for stripe rust severity in a joint analysis of five datasets from a Fukuhokomugi/Oligoculm doubled haploid population {10060}. Their location, associated marker, percentage variation explained, and genotype contributing to enhanced resistance at that locus, are listed below.

3BS; *Xgwm389-3B*; 0.2-4.9%; Oligoculm {10060}.
4BL; *Xgwm538-4B*; 1.8-12.3%; Oligoculm {10060}.
4DL; *Xwmc399-4D*; 2.5-8.0%; Oligoculm {10060.}
5BL; *Xwmc415-5B*; 2.4-16.1%; Oligoculm {10060}.
6BS(centromeric); *Xgwm935-6B*; 0.5-3.8%; Oligoculm {10060}.
7BS; *Xgwm935-7B*; 1-5.2%; Oligoculm {10060}.
7DS; *Xgwm295-7D*; 10.7-23.7%; Fukuho {10060}; the 7DS QTL was probably *Yr18* {10060}.
Four QTLs were identified for stripe rust infection in a joint analysis of three datasets from a Fukuhokomugi/Oligoculm doubled haploid population {10060}. Their location, associated marker, percentage variation explained and parent contributing to enhanced resistance at that

locus are listed below.

2DL; *Xgwm349-2D*; 6.5-9.6%; Fukuho {10060}.
3BS; *Xgwm389-3B*; 15.1-24.5%; Oligoculm{10060}. The 3BS QTL may be *Yr30* {10060}.
5BL; *Xwmc415-5B*; 6.4-12.7%; Oligoculm {10060}.
7BL; *Xwmc166-7B*; 2.5-9%; Oligoculm {10060}.

Otane (R)/Tiritea (S) DH population: QTL in 7DS (probably *Yr18*), 5DL (from Otane) and 7BL (Tiritea) {10150}. Interval mapping of 7DS indicated that the presumed *Yr18* was 7 cM from *Xgwm44-7D* {10150}.

Kariega/Avocet S DH population: Two QTLs ***QYr.sgi-7D*** (probably *Yr18*) and ***QYr.sgi.2B.1*** accounted for 29 and 30 %, respectively, of the phenotypic variation for stripe rust response. The nearest marker to the latter was *Xgwm148-2B* {10184}.

Four QTLs were detected in a multiple cross analysis {10283}: Chromosome 2AL (probably *Yr32* in Deben, Kris and Soloist), 2AS (probably *Yr17* in Kris), 2BL (*Xwmc149-2B* - *Xwmc317a-2B* in Deben) and 6BL (*Xwmc397-6B* - *Xwmc105b-6B* in Soloist and Kris).

Avocet S/Pavon 76: QTL identified in 1BL (*Xgwm259*), 3BS (PstAATMseCAC2), 4BL (*Xgwm495*), 6AL (*Xgwm617*), 6BL (PstAAGGMseCGA1) {10443}.

T. monococcum PAU14087 (resistant)/*T. boeoticum* PAU5088 (resistant): RIL population: One adult plant resistance QTL identified in each parent and named *QYrtm.pau-2A* (in a 3.6 cM interval between *Xwmc407-2A* and *Xwmc170-2A*; $R^2 = 0.14$) and *QYrtb.pau-5A* (in a 8.9 cM interval between *Xbarc151-5A* and *Xcfd12-5A*; $R^2 = 0.24$) {10518}.

Luke (R) /Aquileja (R): Two QTLs for high-temperature adult plan resistance, *QYRlu.cau-2BS.1* (distal, flanked by *Xwmc154-2B* and *Xgwm148-2B*, $R^2 = 0.366$) and *QYrl.cau-2BS.2* (proximal, flanked by *Xgwm148-2B* and *Xbarc167-2B*, $R^2 = 0.415$) from Luke, and *QYraq.cau-2BL* (flanked by *Xwmc175-2B* and *Xwmc332-2B*, $R^2 = 0.615$) in Aquileja for stripe number {10582}.

Acocet S / Attila: QTLs were located on chromosomes 2BS (probably *Yr27*), 2BL (a race-specific effect) and 7BL (*XP32/M59* - *Xgwm344-7B* {10586}.

Guardian / Avocet S: F3 lines. One major QTL, *QPst.jic-1BL* (*Xgwm818-1* - *Xgwm259-1B*, R^2 up to 0.45), and two minor resistance QTLs on chromosomes 2D and 4B originating from Guardian {10589}. The major QTL was in the region of *Yr29*.

Stephens / Michigan Amber: Two QTLs for high temperature APR were located in chromosome 6BS; *QYrst.wgp-6BS.1* located in a 3.9 cM region flanked by *Xbarc101-6B* and *Xbarc136-6B* and *QYrst.wgp-6BS.2* located in a 17.5 cM region flanked by *Xgwm132-6B* and *Xgdm113-6B* {10602}.

Pingyuan 50 (R) / Mingxian 169 (S): DH population: APR: *QYrcaas-2BS* (*Xbarc13-2BS)* - *Xbarc230-2BS*, R^2=0.05-0.09), *QYr.caas-5AL*(*Xwmc410-5AL* - *Xbarc261-5AL*, R^2=0.05-0.2), *QYrcaas-6BS*(*Xgwm361-6BS* - *Xbarc136-6BS*, R^2=0.05-0.08) {10693}.

Renan (R) / Recital (S) RIL population: Tested for AUDPC in 1995/6 and 2005/6 with pathogen isolates avirulent and virulent, respectively, for *Yr17*:*QYr.inra-2AS.2*, (=*Yr17*),

R^2=0.45, 1995/6; *QYr.inra-2AS.1*, R^2=0.9, 2005/6; *QYr.inra-2BS*, R^2=0.11 & 0.13, *QYr.inra-3Bcent*, R^2=0.06 in 2005/6; *QYr.inra-6B*, R^2=0.04 & 0.06; from Renan; and *QYr.inra-2AS.1*, R^2=0.09; *QYr.inra-3DS*, R^2=0.08 & 0.12 from Recital. Other QTLs were effective only at certain growth stages {10689}.

Express / Avocet S: RIL population: Relative AUDPC for high temperature APR was controlled by *QYrex.wgp-6AS*, R^2=0.326, interval *Xgwm334-6A* - *Xgwp56-6A*; *QYrex.wgp-3BS*, R^2=0.274, interval *Xgwm299-3B* - *Xwgp66-3B*, *QYrex.wgp.1BL*, R^2=0.094, interval *Xwmc631-1B* - *Xwgp78-1B* {10672}. When rust phenotyping was based on infection type only the 6S and 3BL QTLs were evident {10672}.

97. Reaction to *Puccinia triticina*

Disease: Brown rust, leaf rust.

97.1. Genes for resistance

A series of temporary designations for seedling and adult plant resistance genes in six durums is given in {1648}.
A potentially novel resistance gene was located in chromosome 5BS of Iranian landrace PI 289824. *Xgwm234-5B* - 8.9 cM - *Lr* - 2.3 cM - STS $Xtxw_{200}$ {10253}.

Complex genotypes:

AC Domain: *Lr10 Lr16 Lr34* {820}.
Alsen: *Lr2a Lr10 Lr13 Lr23 Lr34* {10223}.
Benito: *Lr1 Lr2a Lr12 Lr13* {1256}.
Buck Manantial: *Lr3 Lr13 Lr16 Lr17 Lr34?* {300}.
Era: *Lr10 Lr13 Lr34* {342}.
Grandin: *Lr2a Lr3 Lr10 Lr13 Lr34* {821}.
Mango: *Lr1 Lr13 Lr26 Lr34* {1374}.
MN7529: *Lr1 Lr2a Lr10 Lr16* {976}.
Opata 85: *Lr10 Lr27+Lr31 Lr34* {1058}.
Pasqua: *Lr11 Lr13 Lr14b Lr30 Lr34* {304}.
Prospect: *Lr1 Lr2a Lr10 Lr13* {197}.
Roblin: *Lr1 Lr10 Lr13 Lr34* {303,713}.
Trap: *Lr1 Lr3 Lr10 Lr13 Lr34* {1374}.
AC Splendor: *Lr1 Lr16 Lr34* {10179}
AC Teal: *Lr1 Lr13 Lr16* {821}
Alsen: *Lr2a Lr19 Lr13 Lr23 Lr34* {10152}
Norm: *Lr1 Lr10 Lr13 Lr16 Lr23 Lr34* {10152, 10223}

Genotype lists:Australian cultivars {0288}; Chinese cultivars {0013, 10682}; Combinations with *Lr34*{1361}; Cultivars from the former USSR {1380}; Czechoslovakian cultivars{855,0102}; European cultivars {0229,0260,0288,0337,10345}; Indian cultivars {1365,1345}; Indian Subcontinent{1365}; Mexican cultivars{1373}; U.S.A. cultivars {1219,978,0334,10111,10146,10152}, see also {970}.

97.2. Suppressor of genes for resistance to *P. triticina*

See also evidence for specific suppression in {948}.

97.3. QTLs for reaction to *P. triticina*

Two QTLs, located distally on chromosome arm 1BL and on chromosome 7DS, were mapped for leaf rust severity in a Fukuho-komugi/Oligoculm doubled haploid population {10060}. The resistance on 1BL was contributed by Oligoculm and explained 15% of the variation. The 1BL QTL may correspond to *Lr46* and was associated with marker *Xwmc44-1B* {0460}. The resistance on 7DS was contributed by Fukuho-komugi and explained 41% of the variation. The 7DS QTL corresponds to *Lr34* and was associated with marker *Xgwm295-7D* {10060}.
Two major QTL, located on chromosomes 7D and 1BS, for leaf rust resistance were mapped in an Arina/Forno RIL population {10066}. The resistance on 7D was contributed by Forno and explained 32% of the variation. This QTL most likely corresponds to *Lr34* {10066}. The resistance on 1BS (*QLr.sfr-1BS*) was associated with *Xgwm604-1B* and was contributed by Forno {10066}. Additional minor QTLs were identified on chromosome arms 2DL, 3DL, 4BS and 5AL {10066}.
QTLs for leaf rust resistance were identified in {0050} and were named by the catalogue curators as follows:

Beaver/Soissons DH population: QTL for resistance to Australian pathotypes were located on 4-6 chromosomes over 3 years; the most consistent being 1B(1BL.1RS), 4BS (proximal to *Xbarc20-4B*) and 5AS (*QTLBvr5AS,* proximal to *Xbarc10-5A*) and in the vicinity of *wPt-8756* and *wPt-1931* {10687}.

QTLs: Two QTLs for slow leaf rusting, located on chromosomes 2B and 7BL, were mapped for final severity, area under disease progress curve, and infection rate in a CI 13227 (resistant)/Suwon (susceptible) SSD population {10211}. ***QLr.osu-2B*** was associated with microsatellite markers *Xbarc18-2B* and *Xbarc167-2B* (R^2 = 9-18%). ***QLr.osu-7BL*** was associated with microsatellite marker *Xbarc182-7B* (R^2 = 12-15%) {10211}. CI 13227 constributed the resistant alleles for both QTLs. ***QLrid.ocu-2D***, linked to *Xgwm261-2D,* affected the duration of infection {10211}.

Avocet S/Pavon 76: QTL identified included: 1BL (PstAFAMseCAC1&2), 4BL (*Xgwm368*), 6AL (*Xgwm617*), 6BL (PstAGGMseCGA1) {10443}.
Avocet S/Attila: At least two additive genes for slow rusting {10586}. In addition to *Lr46* there were small effects on chromosomes 2BS, 2BL and 7BL {10586}.
Tetraploid wheat
Colosseo/Lloyd: A major QTL, *QLr.ubo-7B.2*, for seedling and adult plant resistance from Colosseo, was located between *Xgwm344.2-7B* and DART 378059, bin 7BL 10-0.78-1.00 {10600}.

TA4152-60/ND 495 DH population: Four QTLs for APR, *QLr.fcu-3AL*(*Xcfa2183-3AL - Xgwm666-3AL*, R^2=0.18), *Qlr.fcu-3BL*(*Xbarc164-3BL - Xfcp544-3BL*, R^2=0.19), *Qlr.fcu5BL*, and *Qlr.fcu-6BL*(*Xbarc5-6BL - Xgwm469.2-6BL*, R^2=0.12) were from TA4152-60 and *Xlr.fcu-4DL*(*Xgdm61-4DL - Xcfa2173-4DL*, R^2=0.13) was from ND495 {10717}. The 3AL QTL conferred seedling resistance to all 3 races, and the 3BL gene gave race-specific seedling resistance to one race. *Xlr.fcu-3BL* was effective only in the presence of an allele associated with *Xgwm359-5DS* {10717}.

98. Reaction to *Pyrenophora tritici-repentis* (anomorph: *Drechlera tritici*-repentis)

Disease: Tan spot, yellow leaf spot.
Virulence in the pathogen is mediated by host-specific toxins and host resistance is characterized at least in part by insensitivity to those toxins. Three toxins, Ptr ToxA, Ptr

ToxB and Ptr ToxC have been identified (see {10153}). Toxin sensitivity determined by use of toxins extracted from pathogen strains and resistance determined by infection experiments are treated as different traits, although common genes may be involved.

A review is provided in {10690}.

98.1. Insensitivity to tan spot toxin (necrosis)

In Kulm/Erik, toxin response accounted for 24% of the variation in disease response, which was affected by 4-5 genes {10030}.

98.2. Insensitivity to tan spot toxin (chlorosis)

QTLs: 'ITMI population': In addition to *tsc2* which accounted for 69% of the phenotypic variation in response to race 5, a QTL in chromosome 4AL (*Xksu916(Oxo)-4AS*, W-7948) accounted for 20% of the phenotypic variation {10015}.

Introgressions of genes for insensitivity to Ptr ToxA and Ptr ToxB are outlined in {10153}.

Grandin(S)/BR34(R) RILs: QTL in 1BS, *QTs.fcu-1BS*, (13-29% of variation depending on race) and 3BL, (13-41%) were involved in resistance to 4 races. Five other QTL showed race specific responses {10248}.

98.3. Resistance to tan spot

QTL

QTsc.ndsu-1A {9924}. Resistance is likely recessive {344}. [*Tsc1* {344}]. 1AS {344}. **v:** Synthetic W7984 {344}. **ma:** Association with *Gli-A1* {344, 0040, 0264}. *QTsc.ndsu-1A*, or a closely associated gene, confers insensitivity to Ptr ToxC, see {0315}. Inoculation with purified toxin Ptr ToxC was used to map this locus. *QTsc.ndsu-1A* confers resistance in both seedlings and adult plants.

QTsc.ndsu-4A. 4AL {0090}. **v:** Opata 85/W-7984 (ITMI) RI mapping population; resistance was contributed by W-7984 {0090}; In W-7976/Trenton resistance was contributed by W-7976 {0264}. **ma:** Association with *Xksu916(Oxo2)-4A* and *Xksu915(14-3-3a)-4A* {0090}; In W-7976/Trenton there was association with *Xwg622-4A* {0264}; Minor QTLs in chromosomes 1AL, 7DS, 5AL and 3BL were associated with resistance in adult plants {0264}.

QTLs: ITMI population: In addition to *tsc2* which accounted for 69% of the phenotypic variation in response to race 5, a QTL in chromosome 4AL (*Xksu916(Oxo)-4AS*, W-7948) accounted for 20% of the phenotypic variation {10015}.

Grandin (S) / BR34 (R) RILs: QTL in 1BS, *QTs.fcu-1BS*, (13-29% of variation depending on race) and 3BL, *QTs.fcu-3BL*, (13-41%) were involved in resistance to 4 races. Five other QTLs showed race specific responses {10248}.

Introgressions of genes for insensitivity to Ptr ToxA and Ptr ToxB are outlined in {10153}.
QTL:
TA4152-60(R)/ND495(S)DH population. Five QTLs for resistance, all from TA4152-60 {10580}, viz., *QTs.fcu-2AS* and *QTs.fcu-5BL.1* conferring resistance to all races used,

QTs.fcu-5AL conferring resistance to races 1, 2 and 5, *QTs.fcu-5B.2* conferring resistance to races 1 and 2, and *QTs.fcu-4AL* conferring resistance to race 3.

WH542(R)/HD29(S) RIL population: SIM indicated QTL on chromosomes 1B, 3AS, 3BL, 5B and 6BS, but only two were confirmed by CIM, *Qts.ksu-3AS* flanked by *Xbarc45-3A* and *Xbarc86-3A* (LOD 5,4, $R^2 = 0.23$) and *Qts.ksu-5BL* (probably *Tsn1*) flanked by *Xgwm499-5B* and *Xest.stsbe968-5B* (LOD 6,5, $R^2 = 0.27$) {10552}.

99. Reaction to *Sitodiplosis mosellana* (Gehin)

Insect pest: Orange blossum wheat midge, Wheat midge. This pest should not be confused with *Contarinia tritici*, the yellow blossom wheat midge.

100. Reaction to *Schizaphis graminum* Rond. (*Toxoptera graminum* Rond.)

Insect pest: Greenbug

QTL: Antibiosis was associated with several markers, including *Rc3* (7DS) in chromosome 7D {10167}. ***QGb.unlp.6A***, for antixenosis was associated with *Xgwm1009-6A* and *Xgwm1185-6A* in a CS/CS(Synthetic 6A) DH population {10216}.

101. Reaction to Soil-Borne Cereal Mosaic Virus

Syn.: Soilbome wheat mosaic. Vectored to the roots by the fungus, *Polymyxa graminis*

A major QTL, ***QSbv.ksu-5D***, (R^2=0.38) was found in Karl 92*2/TA4152-4 {10273}; the resistance was contributed by Karl 92.

102. Reaction to *Tapesia yallundae*. (Anomorph: *Pseudocerosporella herpotrichoides* (Fron) Deighton)

Disease: eyespot, strawbreaker footrot.

103. Reaction to *Tilletia caries* (D.C.)Tul., *T. foetida* (Wallr.) Liro, *T. controversa*

Disease: Bunt, dwarf smut, stinking smut.

104. Reaction to *Tilletia indica* Mitra

Disease: Karnal bunt.

105. Reaction to *Ustilago tritici* (Pers.) Rostrup

Disease: Loose smut.

106. Reaction to Wheat Spindle Streak Mosaic Bymovirus (WSSMV)

QTL : 79% of the variation between Geneva (resistant) and Augusta (susceptible) was associated with markers *Xbcd1095-2D* and *Xcdo373-2D* located 12.4 cM apart in chromosome 2DL {0131}. WSSMV is soil-borne and vectored by the fungus *Polymxa graminis*. This virus has some sequences similarity to Wheat Yellow Mosaic {10285}.

107. Reaction to Wheat Streak Mosaic Virus

Vectored by wheat curl mites, *Eriophyes tulipae* and *E. tosichella*. See: Resistance to colonization by *Eriophyes tulipae*. According to {10226} WSMV may also be see-borne.

108. Reaction to *Xanthomonas campestris* pv. *undulosa*

Disease: Bacterial leaf streak

109. Resistance to Colonization by *Eriophyes tulipae* (*Aceria tulipae*)

Mite pest: Wheat curl mite.
Eriophyes tulipae is the vector of wheat streak mosaic virus (WSMV) and the wheat spot mosaic agent (WSpM).

110. Reaction to Wheat Yellow Mosaic Virus

WYMV is soil-borne and vectored by the fungus *Polymxa graminis*. This virus has some sequence similarity to Wheat Spindle Streak Mosaic {10258}.