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* 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

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 head, four-rowed spike, supernumerary spikelet, tetrastichon spikelet.

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

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

5.Anthocyanin Pigmentation

5.1. Purple anthers.

A single, dominant factor was reported {1326}.

5.2. Purple/Red auricles. Purple leaf base

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.

5.4. Purple/red culm/straw/stem.

Purple or red colour is dominant.

5.5. Purple grain/pericarp

Genes for purple pericarp have been 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.

6.Awnedness

6.1. Dominant inhibitors

6.1.1. Hooded

6.1.2. Tipped 1

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 supporting 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

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)

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.

QTLs: Two QTLs for narrow-sense earliness were detected on chromosome 2B in a CS/*T. spelta* var. *duhamelianum* KT19-1 RI population{10057}. These QTLs were associated with

markers *Xpsr135-2B* and *Xabc451-2B* {10057}. For both QTLs, earliness was conferred by the CS allele.

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}.

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

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.

27.Glume Colour and Awn Colour

27.1. Red (brown/bronze) 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 1A. See {1640} for review. A 1A gene, *Rg3*, was eventially identified by linkage with *Gli-A1* {1405} and shown to cosegregate with *Hg* {624}.

27.2. Black glumes

Bga and *Bgb* are dominant and cause a solid black glume and a black line at the margins of the glume, respectively. *bg* is recessive and confers non-black glumes.
A single factor for black glumes was reported in diploid, tetraploid and hexaploid wheats {1347}. Linkage with *Hg* was demonstrated at all levels of ploidy, indicating a common gene on chromosome 1A; *Bg* is epistatic to *Rg*.

27.3. 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.

27.4. Black-striped glumes

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

27.5. Inhibitor of glume pigment

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

27.6. Chocolate chaff

27.7. 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) {0380}, 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}.
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.

29.Grain Quality Parameters

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 21. Flour Colour *Lr19* and *Sr25*.

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

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}.

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}.

32.Hairy/Pubescent Auricles

33.Hairy Glume

34.Hairy Leaf

35.Hairy Leaf Sheath

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

36.Hairy Neck/Pubescent Peduncle

37.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.

38.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}.

39.Height

Ht is the general symbol.

39.1. Reduced Height : GA-insensitive

39.2. 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 gene. 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}.

39.3. Reduced Height : QTL

In Courtot/CS:

40.Herbicide Response

40.1. Difenzoquat insensitivity

40.2. 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.

40.3. Chlortoluron Insensitivity

40.4. 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.

41.Hybrid Weakness

41.1. 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.

41.2. Hybrid chlorosis type 1

41.3. Hybrid chlorosis (type 2) {1511}.

42.Iron Deficiency

43.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; 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.

44.Leaf Erectness

45.Leaf Tip Necrosis

46.Lodging

47.Male Sterility

47.1. Chromosomal

47.2. Sterility in hybrids with wheat

48.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}.

49.Megasporogenesis

49.1. Control of megasporogenesis

50.Meiotic Characters

50.1. Low-temperature pairing

50.2. Pairing homoeologous

50.3. Inhibitor of pairing homoeologous

51.Nitrate Reductase Activity

52.Nuclear-Cytoplasmic Compatability Enhancers

53.Nucleolus Organizer Regions

53.1. 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*.

54.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.

55.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).

56.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}

57.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

QTL: 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}.

58.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,Myb-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*.

59.Reaction to Black-Point of Grain

Black-point 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).

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}.

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}.

60.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".

61.Response to Salinity

61.1. K+/Na+ discrimination

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

62.Response to Tissue Culture

63.Response to Vernalization

Winter cultivars carry recessive alleles at all *Vrn* loci. Differences among winter wheats with respect to vernalization requirements seem to be due to multiple recessive alleles {1173,0202}. Two genes may determine differences between winter wheats requiring 20 days and 60-65 days of vernalization {461,1173,9902}.

New combinations of *vrn* alleles from Mironovskaya 808 with a high vernalization requirement and Bezostaya 1 with a lower requirement gave progenies with higher and lower vernalization requirements than the respective parents {9902}. The allelic variants were designated with subscripted letters $vrn1^B$, $vrn2^B$, $vrn3^B$ and $vrn1^M$, $vrn2^M$, $vrn3^M$. Spring and

intermediate genotypes carry dominant alleles leading to no or reduced vernalization response.

64.Restorers for Cytoplasmic Male Sterility

64.1. Restorers for *T. timopheevi* cytoplasm

64.2. Restorers for *Aegilops longissima* cytoplasm

64.3. 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.

65.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.

65.1. 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.

66.Seedling Leaf Chlorosis

67.Segregation Distortion

68.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.

69.Stem solidness

70.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}.

71.Tenacious Glumes

72.Tiller Inhibition

73.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}.

74.Variegated Red Grain Colour

75.Yield and Yield Components

75.1. Grain weight

75.1.1. 50-grain weight

75.1.2. 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}.

75.2. Grain weight/ear

75.3. Grain number per spike

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

75.4. Grain yield
75.5. Spikelet number/ear
75.6. 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}.

75.7. Spike length
75.8. Tiller number/plant
75.9. Grain yield
75.10. Kernel number per square metre
75.11. Grain volume weight

76.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}.

77.Proteins

77.1. 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.
For QTLs conferring grain protein content detected in the cross Renan/Recital {10071}, only QTLs stable over at least 4 of the 6 locations are presented. Renan contributed the four alleles for high grain protein content.

77.2. Enzymes
77.2.1. Acid phosphatase
77.2.2. 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 2.20. Aromatic Alcohol Dehydrogenase

77.2.3. Aminopeptidase
77.2.4. Alpha-amylase
77.2.5. Beta-amylase
77.2.6. Endopeptidase
77.2.7. 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}.

77.2.7.1. EST-1

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

77.2.7.2. EST-2

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

77.2.7.3. EST-3

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

77.2.7.4. EST-4

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

77.2.7.5. EST-5

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

77.2.7.6. 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.

77.2.7.7. EST-7

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

77.2.7.8. 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}.

77.2.7.9. EST-9

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

77.2.8. Glucosephosphate isomerase
77.2.9. Glutamic oxaloacetic transaminase

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

77.2.10. Hexokinase

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

77.2.11. Lipoxygenase
77.2.12. Malate dehydrogenase
77.2.13. 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}.

77.2.13.1. PER-1

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

77.2.13.2. PER-2

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

77.2.13.3. PER-3

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

77.2.13.4. PER-4

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

77.2.13.5. PER-5

PER-5 is expressed in roots {816}.

77.2.14. Phosphodiesterase

77.2.15. Phosphogluconate dehydrogenase

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

77.2.16. Phosphoglucomutase
77.2.17. Shikimate dehydrogenase
77.2.18. Superoxide dismutase
77.2.19. Triosephosphate isomerase
77.2.20. 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}.

77.2.21. Aconitase
77.2.22. NADH dehydrogenase
77.2.22.1. 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}.

77.2.22.2. 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}.

77.2.22.3. Ndh-3

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

77.2.22.4. Ndh-4

77.2.23. Dipeptidase

77.2.24. Malic enzyme

A dimeric enzyme extractable from mature grains.

77.2.25. Adenylate kinase

77.2.26. Glutamate-pyruvate transaminase

77.2.27. 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}.

77.2.28. Beta-glucosidase

77.2.29. Starch branching enzyme

77.2.30. Benzoxinones

The putative role of benzoinones 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}.

77.2.31. 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.

77.3. Endosperm storage proteins

77.3.1. 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 1BDz, 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.

77.3.1.1. 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}.

77.3.1.2. Glu-2

77.3.1.3. 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.

77.3.1.4. 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).

77.3.1.5. 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.

77.3.2. 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 location 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.

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.

77.3.2.1. 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}.

77.3.2.2. 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}.

77.3.2.3. Gli-3

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

77.3.2.4. 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.

77.3.2.5. 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.

77.3.2.6. Gli-6

77.3.3. Other endosperm storage proteins

Triticin proteins {1360} [Triplet proteins {1357}].

Storage globulins with homology to pea legumins and related proteins in oats, rice and several dicotyledonous species {1360}.

77.4. Enzyme Inhibitors

77.4.1. Trypsin inhibition

77.4.2. 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}.

77.4.3. 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*.

77.4.4. 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}.

77.5. Other proteins

77.5.1. Lipopurothionins

77.5.2. Lectins

77.5.3. Iodine binding factor

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

77.5.4. Water soluble proteins

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

77.5.5. Salt soluble globulins

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

77.5.6. 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 cutivars, 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}.

77.5.7. 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}.

77.5.8. 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).

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}.

77.5.9. Grain softness protein
77.5.10. Starch synthase
77.5.11. 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.

78.Reaction to Barley Yellow Dwarf Virus

Disease: Cereal yellow dwarf

79.Reaction to *Blumeria graminis* DC.

Disease: Powdery Mildew.

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

79.1. Designated genes for resistance

Note: Chancellor, used as a susceptible genetic background, for some near-isogenic lines probably carries *Pm10* and *Pm15* {1479}.

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}

79.2. 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*.

79.3. Temporarily designated gene for resistance to *Blumeria graminis*

79.4. 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}.
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}.

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

Disease: Cochliobolus root rot.

81.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}.

82.Reaction to *Fusarium graminearum*

Disease : Fusarium head scab.

82.1. Fusarium head scab, scab

Type II resistance.

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}.

Frontant(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}.

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

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

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.*

82.2. Disease: Crown rot cuased by *Fusarium pseudograminearum, F. culmorum* and other *Fusareum* species.

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

83.Reaction to *Heterodera avenae*Woll.

Cereal root eelworm; cereal cyst nematode.

84.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.

85.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}.

86.Reaction to *Meloidogyne* spp.

Root rot nematode, root knot eelworm

87.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}.

88.Reaction to *Pratylenchus* spp.

Root lesion nematode; prats

88.1. Reaction to *Pratylenchus neglectus*

88.2. Reaction to *Pratylenchus thornei*

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

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

Disease: Septoria nodorum blotch, Stagonospra nodorum blotch.

89.1. 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 x 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 x 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}.

A QTL, *QSnl.ihar-6A-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}.

89.2. Sensitivity to SNB toxin

90.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.

91.Reaction to *Puccinia striiformis* Westend.

Disease: Stripe rust, yellow rust.

91.1. 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}.

91.2. 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.

91.3. 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}.

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}.

92.Reaction to *Puccinia triticina*

Disease: Brown rust, leaf rust.

92.1. Genes for resistance

A series of temporary designations for seedling and adult plant resistance genes in six durums is given in {1648}.

Complex genotypes:
AC Domain: *Lr10 Lr16 Lr34* {820}.

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}

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

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

92.3. QTLs for reaction to *P. triticina*

QTLs for leaf rust resistance were identified in {0050} and were named by the catalogue curators.

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: 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 {101211}.

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

Disease: Tan spot, yellow leaf spot.
Virulance in the pathogen is mediated by host-specific toxins and host resistance is characterized by insensitivity to those toxins. Three toxins, Ptr, ToxA, Ptr, ToxB and Ptr ToxC have been identified (see {10153}).

93.1. Insensitivity to tan spot toxin

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

93.2. Resistance to chlorosis induction

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}.

94.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.

95.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}.

96.Reaction to Soil-Borne Cereal Mosaic

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

Disease: eyespot, strawbreaker footrot.

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

Disease: Bunt, dwarf smut, stinking smut.

99.Reaction to *Tilletia indica* Mitra

Disease: Karnal bunt.

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

Disease: Loose smut.

101.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 12.4cM apart in chromosome 2DL {0131}.

102.Reaction to Wheat Streak Mosaic Virus

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

Disease: Bacterial leaf streak

104.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).