

1. Gross Morphology: Spike characteristics

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

1. Common wheat *Q c SI* v: vulgare group.
2. Club wheat *Q C SI* v: compactum group.
3. Shot wheat *Q c sI* v: sphaerococcum group.
4. Spelt wheat *q c SI* 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 c SI* {1049}.

1.1. Squarehead/spelt

1.2. Club

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

Synonymns: 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 <i>vulgare</i>	---- <i>QQ Bs Bs</i>	0.00
Speltoids	StFF <i>qq Bs Bs</i>	0.00
	StF <i>qq Bs Bs</i>	0.08

St1A	<i>qq Bs Bs</i>	0.39
St1	<i>qq Bs Bs</i>	0.96
St2	<i>qq bs bs</i>	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.

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 *CICl.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.

20. Flowering Time

21. Flour Colour

Loci controlling flour colour were identified and mapped in a recombinant inbred population derived from hexaploid wheat cultivars Schomburgk and 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.

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 independent 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 (*wal*) {725} and maize (*gl2*) {211}.

A gene for spike glaucousness, *Ws*, was mapped distally on the short arm of chromosome 1B 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 eventually 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 other varieties mentioned. A similar study using CS (CNN5D) x 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.

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}.

QTL: 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 level of yellow pigment. Two additional small QTLs were detected on 7AL {0365}.

Other references to flour colour are given under *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 the cross Cranbrook (*Wx-B1a*) x 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 α -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

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

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 Hermesen {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}. One gene at the tetraploid level is allelic with one of those in the hexaploid {939}. 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}.

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 Compatibility 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-RI* 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 *TaqI* 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 *BamHI/EcoRI* 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. Pollen Killer**56. 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}.

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}.

57. Red Grain Colour

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*.

58. 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".

59. Response to Salinity

59.1. K⁺/Na⁺ discrimination

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

60. Response to Tissue Culture**61. 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.

62. Restorers for Cytoplasmic Male Sterility**62.1. Restorers for *T. timopheevi* cytoplasm****62.2. Restorers for *T. longissimum* cytoplasm****62.3. 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.

63. 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.

63.1. 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.

64. Seedling Leaf Chlorosis**65. Segregation Distortion****66. 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.

67. 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}.

68. Tenacious Glumes**69. Tiller Inhibition****70. 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}.

71. Variegated Red Grain Colour

72. Yield Components

72.1. Grain weight

72.1.1. 50-grain weight

72.1.2. 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}.

72.2. Grain weight/ear

72.3. Grain number per spike

72.4. Plant yield

72.5. Spikelet number/ear

72.6. 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}.

72.7. Spike length

72.8. Tiller number/plant

73. 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}.

74. Proteins

74.1. Grain protein content

QTLs for grain protein content were detected on chromosome arms 6AS (associated AFLP marker, *XE38M60₂₀₀*) 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}.

74.2. Enzymes

74.2.1. Acid phosphatase

74.2.2. 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

74.2.3. Aminopeptidase

74.2.4. Alpha-amylase

74.2.5. Beta-amylase**74.2.6. Endopeptidase****74.2.7. 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}.

74.2.7.1. EST-1

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

74.2.7.2. EST-2

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

74.2.7.3. EST-3

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

74.2.7.4. EST-4

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

74.2.7.5. EST-5

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

74.2.7.6. 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.

74.2.7.7. EST-7

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

74.2.7.8. 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}.

74.2.7.9. EST-9

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

74.2.8. Glucosephosphate isomerase**74.2.9. Glutamic oxaloacetic transaminase**

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

74.2.10. Hexokinase

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

74.2.11. Lipoxygenase

74.2.12. Malate dehydrogenase

74.2.13. 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}.

74.2.13.1. PER-1

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

74.2.13.2. PER-2

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

74.2.13.3. PER-3

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

74.2.13.4. PER-4

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

74.2.13.5. PER-5

PER-5 is expressed in roots {816}.

74.2.14. Phosphodiesterase

74.2.15. Phosphogluconate dehydrogenase

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

74.2.16. Phosphoglucomutase

74.2.17. Shikimate dehydrogenase

74.2.18. Superoxide dismutase

74.2.19. Triosephosphate isomerase

74.2.20. 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}.

74.2.21. Aconitase

74.2.22. NADH dehydrogenase

74.2.22.1. 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}.

74.2.22.2. 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}.

74.2.22.3. 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), *Dial* (diaphorase) and *Mnr1* (menadione reductase) represent the same locus {0356}.

74.2.22.4. Ndh-4

74.2.23. Dipeptidase

74.2.24. Malic enzyme

A dimeric enzyme extractable from mature grains.

74.2.25. Adenylate kinase

74.2.26. Glutamate-pyruvate transaminase

74.2.27. Catalase

74.2.28. Beta-glucosidase

74.2.29. Starch branching enzyme

74.3. Endosperm storage proteins

74.3.1. 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 has been 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.

74.3.1.1. 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 a terminating sequence inside the transcribed portion of the gene {373}. 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 prolamins 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}.

74.3.1.2. Glu-2

74.3.1.3. 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}) LMW subunits observed in some Portuguese triticales could be of the durum type.

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).

74.3.1.5. *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.

74.3.2. 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 omega-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-I* 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}.

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 the next Supplement.

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

74.3.2.1. Gli-1

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 *Gld-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}.

74.3.2.2. *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}.

74.3.2.3. *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}.

74.3.2.4. *Gli-4*

It is not clear how *Gli-S⁴* and *Gli-S⁵* relate to the *Gli-4* and *Gli-5* sets described below.

74.3.2.5. *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.

74.3.2.6. *Gli-6*

74.3.3. 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}.

74.4. Enzyme Inhibitors

74.4.1. Trypsin inhibition

74.4.2. 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 α -amylase, CM1, CM3 and CM16, with homology to the dimeric and monomeric α -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, α -amylases, were located in chromosomes 3BS, 3DS and 6DS of Chinese Spring {1260}. Also, genes encoding inhibitors of insect α -amylases were located in *H. chilense* chromosomes 4H^{ch} and 7H^{ch} {1262}.

74.4.3. 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*.

74.4.4. Inhibitors (dimeric) of heterologous alpha-amylases

Chromosome 3BS has duplicated loci controlling two dimeric inhibitors of exogenous alpha-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 alpha-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 Opatá 85/W-7984 (ITMI population) {0125}.

74.5. Other proteins

74.5.1. Lipopurothionins

74.5.2. Lectins

74.5.3. Iodine binding factor

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

74.5.4. Water soluble proteins

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

74.5.5. Salt soluble globulins

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

74.5.6. 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 Japanese 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}.

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 *T. 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}.

74.5.7. 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}.

74.5.8. 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 through 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}.

74.5.9. Grain softness protein

74.5.10. Starch synthase

74.5.11. 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.

75.Reaction to Barley Yellow Dwarf Virus

76.Reaction to *Blumeria graminis* DC.

Disease: Powdery Mildew.

76.1. 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}

76.2. 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*.

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

76.4. 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 QTLs on chromosome 5D was detected in all environments and all years and is associated with markers *Xgwm639-5D* and *Xgwm174-5D*. Resistance was contributed by RE714. A QTL coinciding with *MIRE* 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}.

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

Disease: Cochliobolus root rot.

78.Reaction to *Diuraphis noxia* (Mordvilko)

Insect pest: Russian aphid, Russian wheat aphid.

79.Reaction to *Fusarium graminearum*

Disease : Fusarium head scab.

80.Reaction to *Heterodera avenae*Woll.

Cereal root eelworm; cereal cyst nematode.

81.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.

82.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}.

83.Reaction to *Meloidogyne* spp.

Root rot nematode, root knot eelworm

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

Disease: Septoria tritici blotch

85.Reaction to *Pratylenchus* spp.

Root lesion nematode; prats

85.1. Reaction to *Pratylenchus neglectus*

85.2. Reaction to *Pratylenchus thornei*

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

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

Disease: Septoria nodorum blotch.

87.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.

88.Reaction to *Puccinia striiformis* Westend.

Disease: Stripe rust, yellow rust.

88.1. Designated genes for resistance to stripe rust

88.2. Temporarily designated gene for resistance to stripe rust

88.3. Stripe rust QTLs

QTL: In the ITMI mapping population, QTLs were found in 2BS, 7DS, and possibly 5A, 3D and 6D {0287}. The 2BS gene is likely to be *Yr27*. In Camp Remy/Michigan Amber, QTLs were found in 2AL and 2BL {0287}.

Two QTLs in Camp Remy/Michigan Amber were located on chromosome 2BL (*QYR1*, LOD score 12) and 2AL (*QYR2*, LOD 2.2) {0304}. 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) {0304}.

89.Reaction to *Puccinia triticina*

Disease: Brown rust, leaf rust.

89.1. 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}.

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}, see also {970}.

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

89.3. QTLs for reaction to *P. triticina*

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

90. Reaction to *Pyrenophora tritici-repentis*

Disease: Tan spot, yellow leaf spot.

Tan spot produces two types of genetically determined symptoms, viz. extensive chlorosis and tan necrosis. Pathotypes with the ability to inflict tan spot necrosis (TSN) produce a host gene-specific toxin in culture.

90.1. Insensitivity to tan spot toxin

90.2. Resistance to chlorosis induction

91. Reaction to *Sitodiplosis mosellana* (Gehin)

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

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

Insect pest: Greenbug

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

Disease: eyespot, strawbreaker footrot.

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

Disease: Bunt, dwarf smut, stinking smut.

95. Reaction to *Tilletia indica* Mitra

Disease: Karnal bunt.

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

Disease: Loose smut.

97. 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}.

98. Reaction to Wheat Streak Mosaic Virus

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

Disease: Bacterial leaf streak

100. 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).

