



Australian Government

Department of Health and Ageing

Office of the Gene Technology Regulator

**The Biology and Ecology of Bread Wheat
(*Triticum aestivum* L. em Thell.) in
Australia**

TABLE OF CONTENTS

TABLE OF CONTENTS	2
Preamble.....	3
1. Origin and Distribution.....	3
2. Taxonomy and Genetics	5
3. uses of bread wheat	8
3.1 IMPORTANCE OF BREAD WHEAT	8
3.2 COMMERCIAL USES	8
4. biology.....	9
4.1 GROWTH AND DEVELOPMENT OF THE WHEAT PLANT	10
4.1.1 VEGETATIVE DEVELOPMENT	10
Germination of the wheat seed	10
Leaf development	11
Stem development	11
Tiller development.....	11
4.1.2 REPRODUCTION	11
4.2 BREEDING BREAD WHEAT.....	13
4.3 MOLECULAR GENETICS OF WHEAT	15
Figure 2. Stained wheat chromosomes (from left to right) by N-banding, modified C banding, and C-banding (whole and telosomic chromosomes) (chromosomes 1A and 3D to 6D do not show any N-bands, and were not identified). 17	
5. Diseases and Pests of wheat.....	21
5.1 DISEASES OF WHEAT IN AUSTRALIA	21
5.2 PESTS OF BREAD WHEAT.....	21
6. Toxicity and Allergenicity of bread wheat.....	23
6.1 ANTI-NUTRITIONAL FACTORS AND TOXICITY	23
6.1.1 Enzyme inhibitors.....	23
6.1.2 Lectins	23
6.1.3 Phytic acid	23
6.1.4 Nitrate poisoning	24
6.2. ALLERGENICITY OF WHEAT	24
6.2.1 Coeliac Disease.....	24
7. weediness.....	25
7.1 FACTORS AFFECTING WEEDINESS OF WHEAT	25
7.1.1 Taxonomy.....	25
7.1.2 Dormancy	26
8. gene transfer	27
8.1 GENE TRANSFER TO OTHER TRITICUM SPECIES, INCLUDING TRITICUM AESTIVUM	27
8.2 GENE TRANSFER TO OTHER SEXUALLY COMPATIBLE SPECIES	30
8.2.1 Interspecific hybridisation requiring artificial conditions.....	30
8.2.2 Interspecific hybridisation under natural conditions.....	32
8.3 GENE TRANSFER TO OTHER PLANTS.....	33
8.4 GENE TRANSFER TO OTHER ORGANISMS.....	33
9. previous releases of GM wheat	34
9.1 GM WHEAT RELEASES IN AUSTRALIA.....	34
9.2 INTERNATIONAL RELEASES OF GM WHEAT	36
10. references	39

PREAMBLE

This document is a resource document for dealings involving the intentional release (DIR) into the Australian environment of genetically modified (GM) wheat either for the purpose of field trials or commercial release. This document has been prepared to summarise information on conventional (non-genetically modified) wheat (*Triticum aestivum* L. em. Thell.) that may be relevant to assessing any risks to the health and safety of people and the environment posed by GM wheat. It will also support the detailed risk assessment and risk management plan prepared for each DIR application involving GM wheat. Particular genetic modifications, and how the Regulator assesses their associated risks would be detailed in the risk assessment and management plan prepared for each application. Two important companion documents include the Consensus Document on the Biology of *Triticum aestivum* (Bread Wheat) (Environment Directorate OECD Series on Harmonization of Regulatory Oversight in Biotechnology No. 9 1999) and The Biology of *Triticum aestivum* L. (Wheat) (Canadian Food Inspection Agency, Plant Biotechnology Office, Regulatory Directive Dir1999-01 1999).

1. ORIGIN AND DISTRIBUTION

“The precise origin of the wheat plant as we know it today is not known. Wheat evolved from wild grasses, probably somewhere in the Near East. A very likely place of origin is the area known in early historical times as the Fertile Crescent - a region with rich soils in the upper reaches of the Tigris-Euphrates drainage basin” (Briggle & Curtis 1987). Naked wheat was cultivated between the late fifth and early fourth millennium B.C in the southern Caucasus in neolithic settlements. Evidence also shows that naked wheat was found at several sites in the Crimea (1000-900 B.C.) which matches archaeological findings of wheat in Israel from the same period (Korber-Grohne 1988). As European civilisation spread to north and south America, wheat was carried both as edible grain and as seed.

Wheat cultivation in Australia

Wheat was introduced into Australia in 1788 at the time of European settlement. William Farrer developed wheat varieties adapted for Australian conditions in the early 20th century. The most famous of the varieties that he developed was ‘Federation’ (Simmonds 1989). Early maturity was a key selection criterion which gave his selections disease escape, rather than disease resistance. A substantial increase in wheat production started in the mid-1950s and continues (Table 1). The wheat growing areas of Australia (wheat belt) are shown in Figure 1.

In Australia, bread wheat is grown as a winter crop. However, true winter wheats require a period of cold stimulus (vernalisation) to initiate floral development. Spring wheats do not have a vernalisation requirement. Normally the winter wheats are planted in April- May in Australia and spring wheats are planted in May – June. However, planting time is determined by soil moisture availability. Sowing rates vary from 20 – 100 kg/ ha in dryland conditions. Phosphorus fertiliser application is most important and dressings can vary from 6 – 25 kg/ha (Sims 1990).

Grain harvest commences when moisture content reaches 13 %. This occurs in October-November in the northern parts of the wheat belt and in December in the southern regions.

Sims (1990) noted that in the cooler regions of the wheat belt harvest can continue into February.

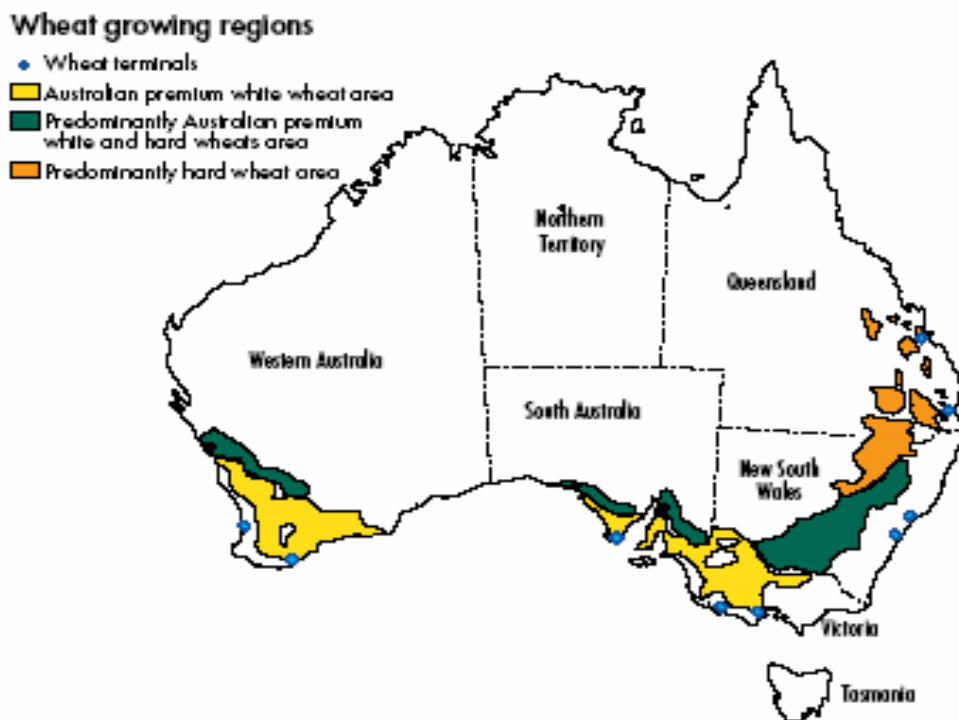


Figure 1. Wheat growing areas in Australia (ABARE 2003).

Yields in Australia have improved substantially, through the introduction of semi-dwarf genes and also improved resistance to diseases. However, drought conditions are a frequent impediment to maximised production. In Western Australia, the wheat belt has undergone a significant expansion in the last 20 years and has increased in area from 2.275m ha (10 year average 1961-70) to 4.174m ha (10 year average 1981-90) (Australian Wheat Board 2004).

Table 1. Wheat production statistics for Australia, 1939-2003 (Australian Wheat Board 2004).

Period	10 year average area (1000ha)	10 year average yield (t/ha)	10 year average production (1000t)
1939-50	4596	0.86	3962
1951-60	3907	1.22	4754
1961-70	7681	1.23	9415
1971-80	8734	1.3	11361
1981-90	11174	1.3	15022
1991-2000	8688	1.76	17254
2001-03	11160	1.6	18483

2. TAXONOMY AND GENETICS

Bread wheat is a segmental hexaploid (6x), which regularly forms 21 pairs of chromosomes ($2n = 42$) during meiosis. These chromosomes are subdivided into 3 closely related (homoeologous) groups of chromosomes, the A, B, and D genomes. Each of these homoeologous groups normally contains 7 pairs of chromosomes (AABBDD). Sears (1966) established that each chromosome in hexaploid wheat has a homoeologue in each of the other 2 genomes.

This homoeology in hexaploid wheat and also in tetraploid wheat (AABB) allows a range of chromosomal abnormalities (aneuploidy) to survive, which cannot survive in diploid species such as barley (*Hordeum vulgare* L.) and maize (*Zea mays* L.). Sears (1954) described the effects of aneuploidy for each wheat chromosome, including the nullisomics, monosomics, telocentrics and isochromosomes. An important aspect of wheat aneuploidy is the study of the evolutionary basis of bread wheat. At present it is understood that hexaploid wheat is the product of two unique hybridisation events.

In the first hybridisation event, the A genome progenitor combined with the B genome progenitor to form a primitive tetraploid wheat ($2n=28$, AABB). This hybrid occurred in the cytoplasm of the B genome. The second event involved hybridisation between the tetraploid (AABB) form and the D genome progenitor (Kimber & Sears 1987) to form the basic hexaploid configuration, AABBDD, again in the B genome cytoplasm (Tsunewaki 1988). McFadden and Sears (1946) identified the D genome progenitor as *Triticum tauschii* (Coss.) Schmal. (formerly *Aegilops squarrosa*). The processes of interspecific hybridisation and the ubiquitous nature of the B genome cytoplasm have been reviewed by Tsunewaki (1991). The progenitors and relevant wild species are listed in Table 2.

The A genome progenitor has been identified as *Triticum boeoticum* L. Synonyms for this species are *T. urartu*, *T. monococcum* and *T. thaoudar* (Kimber & Sears 1987). Differences between the C-banding patterns of chromosome 4A of *T. monococcum* and chromosome 4A of *T. turgidum* were attributed to structural rearrangements that occurred in the tetraploid form (Friebe et al. 1990).

More recently, Gonzalez et al. (1993) studied meiotic pairing in the F₁ progeny of the substitution line 'Courtot' ('Norin 61' 5B) and an F₂ plant of the cross 'Roazon/'Norin 61' pollinated by *T. monococcum*. Meiotic pairing was observed between the *T. monococcum* chromosomes (A^a) 1A, 2A, 3A and 7A and their respective wheat homoeologues. Pairing also occurred at low frequencies between the related wheat chromosomes and 5A^a and 6A^a. However, *T. monococcum* chromosome 4 did not pair with any wheat chromosomes.

The specific identity of the B genome donor remains unclear. It was originally proposed that the B genome donor was based upon *T. speltoides* (Tausch) (Sarkar & Stebbins 1956). Feldman (1979) concluded that *T. longissimum* (Schweinf. and Muschli in Muschli) Bowden and *T. searsii* (Feldman and Kislev) Feldman, comb. nov. (Feldman & Kislev 1977) were candidates for the B genome progenitor. Nath et al. (1983) concluded that *T. searsii* was the possible source of the B genome after studying several likely progenitors with DNA hybridisations

Table 2. Chromosome number and genome(s) of the species of the tribe *Triticeae* (Dewey (1984); Kimber and Sears (1987)).

Species	Synonyms	Chromosome number	Genome code	Species	Synonyms	Chromosome number	Genome code
<i>Triticum boeoticum</i> L.		14	A	<i>T. zhukovskyi</i> Men & Er.		42	A.A.G
<i>Triticum speltooides</i>	<i>Aegilops speltooides</i>	14	S	<i>Triticum timopheevii</i> (Zhuk.) Zhuk.	<i>T. araraticum</i>	28	A.G
<i>Triticum tauschii</i> (Coss.) Schmal.	<i>Aeg. squarrosa</i>	14	D	<i>T. crassum</i> (4x) (Boiss.) Aitch. & Hensl.	<i>Aegilops crassa</i>	28	D.M
<i>Triticum bicornis</i> Forsk.	<i>Aeg. bicornis</i>	14	S ^b	<i>T. ventricosum</i> Ces.	<i>Aegilops. ventricosa</i>	28	D.Un
<i>T. longissimum</i> (Schweinf. & Muschli in Muschli) Bowden	<i>Aeg. longissima</i>		S ^l	<i>T. crassum</i> (6x) (Boiss.) Aitch. & Hensl.	<i>Aeg. crassa</i>	42	D.D.M
<i>T. searsii</i> (Feldman & Kislev) Feldman, comb. nov.		14	S ^s	<i>T. syriacum</i> Bowden	<i>Aeg. crassa</i> ssp. <i>vavilovii</i>	42	D.M.S
<i>T. tripsacoides</i> (Jaub & Spach) Bowden	<i>Aeg. mutica</i>	14	Mt	<i>T. juvenile</i> Thell.	<i>Aeg. juvenalis</i>	42	D.M.U
<i>T. comosum</i> (Sibth. & Sm.) Richter	<i>Aeg. comosa</i>	14	M	<i>T. kotschyi</i> (Boiss.) Bowden	<i>Aeg. kotschyi</i>	28	U.S
<i>T. uniaristatum</i> (Vis.) Richter	<i>Aeg. uniaristata</i>	14	Un	<i>T. ovatum</i> (L.) Raspail	<i>Aeg. ovata</i>	28	U.M
<i>T. dichasians</i> (Zhuk.) Bowden	<i>Aeg. caudata</i>	14	C	<i>T. triaristatum</i> (4x) (Willd.) Godr. &Gren.	<i>Aeg. triaristata</i>	28	U.M

Species	Synonyms	Chromosome number	Genome code	Species	Synonyms	Chromosome number	Genome code
<i>T. umbellulatum</i> (Zhuk.) Bowden	<i>Aegilops</i> <i>umbellulata</i>	14	U	<i>T. triaristatum</i> 6x) (Willd.) Godr. &Gren.	<i>Aeg. triaristata</i>	42	U.M.Un
<i>T. zhukovskyi</i> Men & Er.		42	A.A.G	<i>T. machrochaetum</i> (Schuttl. & Huet. Ex Duval-Jouve) Richter	<i>Aeg. biuncialis</i>	28	U.M
<i>Triticum timopheevii</i> (Zhuk.) Zhuk.	<i>T. araraticum</i>	28	A.G	<i>T. columnare</i> (Zhuk.) Morris & Sears	<i>Aeg. columnaris</i>	28	U.M
<i>T. crassum</i> (4x) (Boiss.) Aitch. & Hensl.	<i>Aegilops crassa</i>	28	D.M	<i>T. triunciale</i> (L.) Raspail		28	U.C
<i>T. ventricosum</i> Ces.	<i>Aegilops ventricosa</i>	28	D.Un	<i>T. cylindricum</i> Ces.	<i>Aeg. cylindrica</i>	28	C.D
<i>T. crassum</i> (6x) (Boiss.) Aitch. & Hensl.	<i>Aegilops crassa</i>	42	D.D.M	<i>Thinopyrum ponticum</i>		70	J-E
<i>T. syriacum</i> Bowden	<i>Aegilops crassa</i> ssp. <i>vavilovii</i>	42	D.M.S	<i>Thinopyrum intermedium</i>		42	E1.E2.S
<i>T. juvenile</i> Thell.	<i>Aegilops juvenalis</i>	42	D.M.U	<i>Triticum turgidum</i>		28	A.B
<i>T. kotschyi</i> (Boiss.) Bowden	<i>Aegilops kotschyi</i>	28	U.S	<i>Triticum aestivum</i>		42	A.B.D
<i>T. ovatum</i> (L.) Raspail	<i>Aegilops. ovata</i>	28	U.M	<i>Secale</i> spp. (ryes)		14	R
<i>T. triaristatum</i> (4x) (Willd.) Godr. &Gren.	<i>Aegilops triaristata</i>	28	U.M	<i>Hordeum</i> spp. (barleys)		14	H

Worldwide, three species of wheat are commonly grown. *T. aestivum*, or bread wheat, forms the classes hard red winter, hard red spring, soft red winter, hard white and soft white. *T. compactum* includes club wheats. The third, *T. turgidum* ssp. *durum*, includes the durum and red durum wheat classes (macaroni wheats).

In Australia, production is limited to bread wheat and durum wheat and bread wheat is exclusively white and does not have the red colour which typifies most bread wheat grown in the northern hemisphere.

3. USES OF BREAD WHEAT

3.1 Importance of bread wheat

Bread wheat is the widely grown food crop in the world (585 x10⁶ metric tonnes of grain produced in 1996, relative to 562 x10⁶ mt of rice). World wheat production doubled during the 25 year period to 1984-85 (Briggle and Curtis 1987) and in absolute terms, more than half of this increase occurred in the developed world.

Whilst the consumption of wheat products is long-standing in developed countries, in developing countries, it represents a valuable source of calories and protein. The consumption of wheat in developing countries increased by 73% in the 10 year period 1972-82 (Briggle and Curtis 1987).

The primary use of bread wheat is for bread manufacture. Pomeranz (1987) estimated that 'national average (per capita per year) bread consumption ranges from about 40 to 300 kg'. Wheat flour is also used to produce biscuits, confectionary products, noodles and vital wheat gluten.

3.2 Commercial uses

Bread wheat is the source of flour for breads, rotis, chapattis, semolina, biscuits and other confectionary products. Wheat grain is also used to manufacture alcoholic beverages. Bran from flour milling is used in livestock feed and the germ is a valuable addition to feed concentrate. Grains are fed to livestock whole or coarsely ground. The wheat plant is also used as a pasture feed before stem elongation and this practice permits plant regeneration and grain harvest. Wheat straw is also used as a source of fibre.

The comparatively high protein content of wheat grain makes it a most important source of human nutrition. Several by-products of wheat from the food industry have created outlets for technical and industrial applications. These are wheat germ oil, wheat gluten and wheat starch.

4. BIOLOGY

The stages of growth and development of a wheat plant are represented in Figure 2.

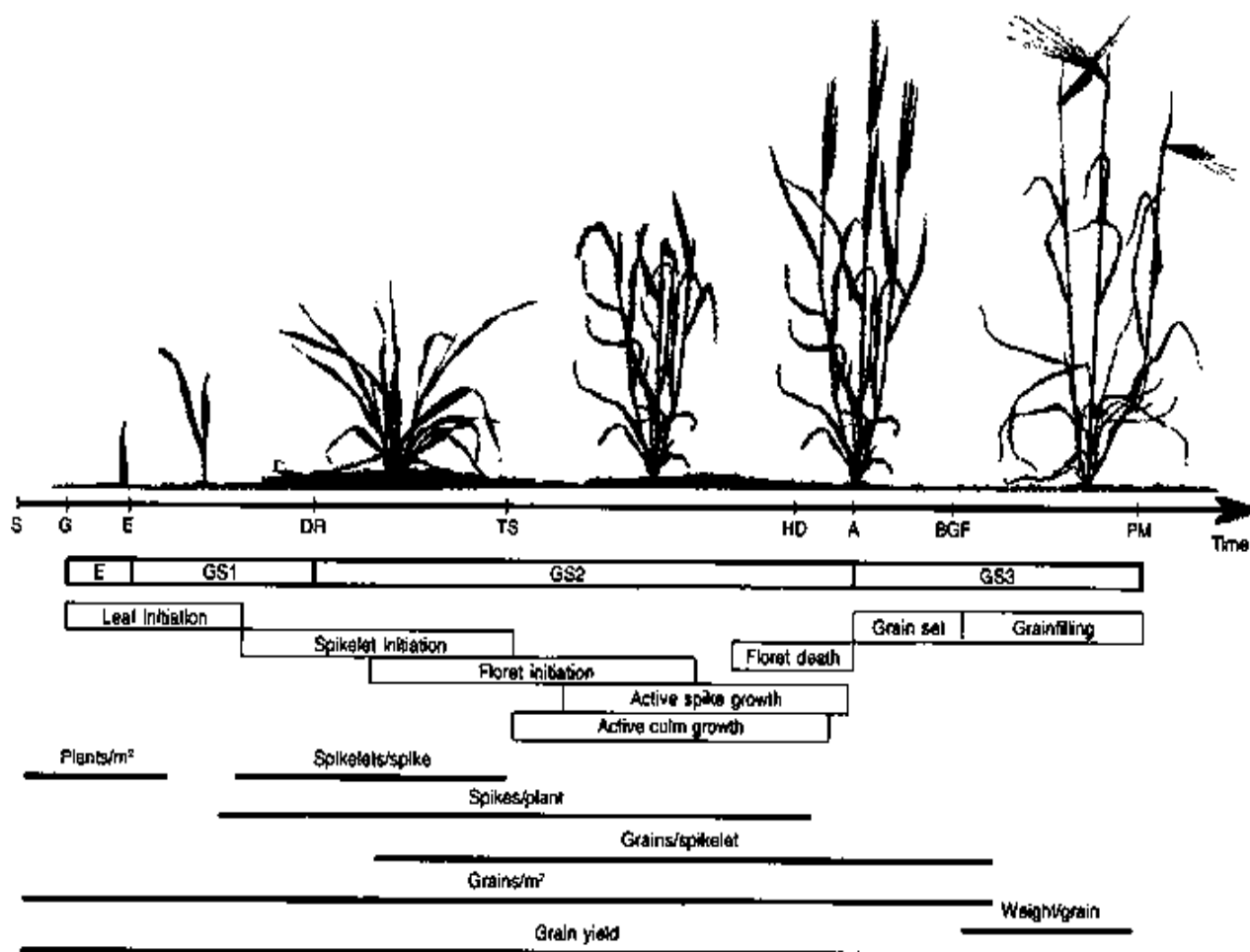


Figure 2. Schematic diagram of wheat growth and development stages, periods of initiation or growth of specific organs and periods of different components of grain yield (Acevedo et al. 2002).

Key: S=sowing; G=germination; E=emergence; DR=double ridge appearance; TS=terminal spikelet initiation; HD=heading; A=anthesis; BGF=beginning of grain filling period; PM=physiological maturity; GS=growth stage

4.1 Growth and development of the wheat plant

Bread wheat is a cereal of temperate climates. Its various growth stages and their durations are listed in Table 3.

Table 3. Duration of growth stages of wheat.

Plant growth stage	Temperature requirements (°C)	Duration (days)
Germination	3-4 (minimum); 12-25 (optimum)	4-10
Flowering	14 (minimum)	
Vegetative: winter		280-350
Vegetative: spring		120-145

Winter wheat is planted in the autumn and it requires a period of below-freezing temperatures before it can form inflorescences (vernalisation). Spring wheat does not require cold weather to form inflorescences or spikes. In Australia, spring wheats can be planted in May and June, ideally before the middle of June, to maximise vegetative growth and to ensure that flowering does not coincide with late frosts.

4.1.1 Vegetative development

Germination of the wheat seed

Minimum moisture for germination in wheat is 35 to 45% of kernel dry weight (Evans et al. 1975). During germination, the seminal root extends first, followed by the coleoptile. Adventitious roots are produced in association with the coleoptile node. When the coleoptile emerges from the soil its growth stops and the first true leaf pushes through its tip. The seedling is dependent upon energy and nutrients provided by the endosperm until its first leaf becomes photosynthetically functional (Simmons 1987).

Root development

One or more nodes may develop below the soil surface depending on the depth of sowing, each bearing roots (Hadjichristodoulou et al. 1977). Root axes are produced at predictable times in relation to shoot development, and the total number of roots formed is associated with the number of leaves on a tiller (flowering stem) and the degree of tillering (Klepper et al. 1984).

Roots originating from tillers generally develop after a tiller has formed three leaves. Root growth of a genotype is proportional to its top growth (Mackey 1973). Lupton (1974) concluded that more extensive root growth was seen in semidwarf cultivars of winter wheat than in taller cultivars. Cholick et al. (1977) compared tall and

semidwarf winter wheat genotypes and concluded that no correlation existed between cultivar height and rooting depth.

Leaf development

After germination the vegetative shoot apex initiates additional leaf primordia. The number of leaf primordia can vary from 7 to 15 (Kirby 1983) and is affected by genotype, temperature, light intensity, and nutritional status of the plant. Temperature has a major influence on leaf appearance and extension. The minimum temperature for leaf extension is approximately 0°C, the optimum 28°C and the maximum greater than 38°C (Kirby et al., 1983).

Stem development

Stem elongation coincides with the growth of leaves, tillers, roots and the inflorescence (Patrick 1972). Elongation of the stem begins when most florets on the developing spike have initiated stamen primordia, which corresponds closely to the formation of the terminal spikelet. In spring wheat the fourth internode is the first to elongate, possessing nine leaves, while the lower internodes of the stem remain short (Kirby & Appleyard 1981).

When an internode has elongated half its final length, the internode above it begins to elongate. This sequence continues until stem elongation is complete, usually near anthesis. The peduncle is the final segment to elongate (Evans et al. 1975). The height of the wheat plant ranges from 30 -150 cm and is determined by the genotype and the growing conditions. Differences in plant height are mostly attributable to variation in internode length rather than internode number (Austin & Jones 1975).

Tiller development

The first tillers to emerge are the ones formed between the axils of the coleoptile and the first true leaf. In general, three phyllochrons separate the emergence of a leaf and its subtended tiller (phyllochron is the interval between two successive leaves) (Kirby 1983).

In winter wheat, a few tillers may form in autumn or winter if conditions are mild. A rapid increase in tiller number occurs with warmer spring temperatures. The main shoot and early formed tillers complete development and form grains in winter or spring wheat (Kirby et al., 1983). Later formed tillers usually senesce prematurely.

4.1.2 REPRODUCTION

Wheat is predominantly self-pollinating. However, outcrossing rates up to 10% or higher depending on the population density, genotype and environmental conditions (Jain 1975). Wind-borne cross fertilisation depends heavily on physical factors like warm weather and high humidity. Warm, dry weather can contribute to higher (3.7 to 9.7%) cross fertilisation rates when compared to minimal (0.1%) cross fertilisation rates under high humidity (OECD 1999).

Poehlmann (1959) reported that cross-fertilisation in wheat may be as high as 1 to 2%. Hucl (1996) studied 10 Canadian spring wheat cultivars and reported that the cross-pollination frequency (which was always lower than 9%) varied according to the genotype. Cultivars which had low pollen staining, tapered spikes at the extremities and greater spikelet opening at anthesis had the highest outcrossing rates. Martin (1990) reported outcrossing rates of 0.1-5.6% among winter wheat cultivars and concluded that the semi dwarf stature of plants did not affect these rates.

The time and duration of flowering is dependent upon geographical location. Sunny weather and temperatures of at least 11 - 13°C are required for flowering (Mandy 1970; Garcke 1972). Florets on the spike of the main tiller open first and flowering commences in the middle of each spike and proceeds synchronously towards the tip and the base.

Pre-anthesis spike development

The shift to reproductive development occurs more closely to elongation of the apical dome when the main shoot has about three full leaves. Floret differentiation begins in the lower central portion of the spike and proceeds both upward and downward when the spikelet initiation comes to an end. This establishes a development hierarchy within the spike that persists through anthesis and grain growth. Initiation of the terminal spikelet marks the end of spikelet formation (Austin and Jones 1975; Kirby et al. 1981; Kirby et al. 1983).

During pre-anthesis there is a synchronisation of various developmental phases. Kirby (1974) reported that a difference of several weeks in initiation of various shoots on a plant is reduced to only a few days by the time of spike emergence. Similarly the difference in time of initiation between the first two florets in a spikelet may be more than two days, but the time differential between these florets at meiosis may be only 6 hours (Kirby 1974). When the anthers are green and 1 mm long, meiosis occurs simultaneously in the anthers and carpel (Kirby & Appleyard 1981).

The lemmas and paleas open to an angle of 20 - 35° at flowering (anthesis). The duration of time that wheat flowers remain open ranged from 8-60 minutes depending on genotype and environmental conditions (de Vries 1971). Mandy (1970) reported that an unfertilised spikelet can remain open for several hours or even days, whereas under favourable weather conditions, a floret will complete the flowering cycle in 13 to 18 minutes.

Heslop-Harrison (1979) reported that after release, wheat pollen attaches to the stigmatic branches through a brief electrostatic force followed by absorption of water by the pollen grain through gaps in the stigma cuticle. This process enables the pollen tube to grow, which in turn facilitates fertilisation. The wheat stigma is receptive for 6-13 days although this may be influenced by environmental conditions. Kirby (2002) noted that when florets are not pollinated, the stigmas can remain receptive for up to 5 days after anthesis and the floret may open again, by the swelling of part of the ovary.

In field conditions, the viability of pollen grains may be less than 30 minutes (OECD 1999). Pollen tube growth is initiated 1-2 hours after pollination and fertilisation takes place after an additional 30-40 hours (de Vries 1971). However, pollen grains

can germinate within minutes after landing on the stigmatic surface with fertilisation taking place in less than one hour Canadian Food Inspection Agency (CFIA) (1999). In wheat, the stamens are smaller and produce fewer pollen grains (1000-3800 per anther; 450,000 per plant) than other cereal grasses. This compares to 4 million for rye (*Secale cereale* L.) and 18 million for maize (*Zea mays* L.) (de Vries 1971).

Nearly 80% of pollen from an anther, which protrudes from the spikelet, is dispersed into the air. Laboratory experiments have shown that pollen travels about 60m distance at a height of 1 m (D'Souza 1970). In field experiments, Wilson (1968) found 10% seedset on male sterile wheat plants 30m from the pollen donor plants.

Pollen formation

Each lobe of an anther contains a cylindrical column of microspore mother cells. These columns are each surrounded by a tapetum, which is a nutritive layer (Lersten 1987). Meiosis in the microspore mother cells takes 24 hours and a cell plate is formed after each division. The resultant tetrad is appressed to the tapetum. Throughout meiosis, the tapetal nuclei divide mitotically and these tapetal cells become binucleate. After meiosis, the callose that has isolated each meiocyte dissolves but the microspores remain appressed to the tapetum. This situation remains until the pollen is mature and each pollen grain has formed a single pore at the point of tapetal contact. This continued contact between tapetum and pollen is unique to grasses.

Kernel development

The rate of endosperm cell division is influenced by light intensity, water stress, temperature and genotype (Wardlaw 1970; Brocklehurst et al. 1978). Starch deposition begins 1-2 weeks after anthesis and initiates a 2-4 week period of linear increase in kernel dry weight. This process is also influenced by water stress, temperature and genotype (Simmons 1987). The growth and final weight of an individual kernel depends on the spikelet and floret position, kernels formed in central spikelets and proximal florets within an individual spikelet are usually largest (Kirby, 1974; Simmons, 1987).

When rain coincides with harvest, pre-harvest sprouting can occur. Kernels that mature under cool conditions are more dormant than those ripened under warm conditions (Austin and Jones, 1975). In Australia, rising temperatures late in the development of the wheat crop, particularly after heading, are considered an important yield-limiting factor. However, wheat cultivars vary in their response to high temperature (14.7-26.7°C) during kernel filling (Austin & Jones 1975). Wardlaw and Moncur (1995) reported a significant drop in kernel dry weight at maturity, with significant variation in response, ranging from a 30-60% decrease in kernel dry weight at maturity for a rise of temperature from 18/13°C (day / night) to 30/25°C (day / night).

4.2 Breeding bread wheat

Gale and King (1988) reviewed Australian wheat germplasm and observed that most Australian wheat cultivars derived from 'Condor' carried the semi-dwarfing (or

gibberellic acid insensitive gene) gene *Rht1*. Cultivars (cv.) ‘Hartog’ (Pavon 76), ‘Suneca’ and ‘Kite’ selections carried the semi-dwarfing *Rht2* gene.

In Australia, great emphasis has been placed upon the release of varieties which combine high yield, acceptable quality characteristics and resistance to the three rust diseases and other diseases. Australian wheat is exported to Japan, South-east Asia, China and the Middle East.

4.2.1 QUALITY CHARACTERISTICS OF AUSTRALIAN WHEATS

Quality characteristics of different wheat classes are described in Table 4.

Table 4. Australian wheat classes.

Wheat class	Protein (%)	Dough strength	Grain quality	End use
Prime hard	>13	High	Hard, excellent milling qualities	Bread, high protein flour
Aust hard	>11.5	Good	Good milling and good dough qualities	Bread
ASW	10-12	Varies because of range of collection sites	Varies because of range of collection sites	Bread, chinese noodles
Soft	8.4	Weak	Low protein, weak extensible doughs	Biscuit wheat

4.2.2 DEVELOPMENT OF NEW CULTIVARS

The primary methods of wheat breeding are the pedigree method and bulk breeding method. Single Seed Descent is also used to develop new germplasm, but in Australia, the importance of disease resistance has focussed most breeding strategies on pedigree methods of selection. Backcrossing is the principle method of introducing new forms of disease resistance into wheat germplasm. However, subsequent selection is largely based on pedigree methods.

Excellent reviews of plant breeding methodologies are presented by (Simmonds 1986) and also by (Allard 1999). A collection of winter cereals, including wheat varieties and advanced breeding lines from Australian and international breeding programs is held at the Australian Winter Cereals Collection, Tamworth. This collection also includes wild relatives of wheat.

4.2.3 MODIFICATIONS TO THE WHEAT GENOME THROUGH CONVENTIONAL BREEDING

The bread wheat genome has been subject to many alterations through homoeologous recombination with wild wheat (alien) species. This procedure has been used to introduce disease resistance to wheat cultivars. More recently, mutagenesis has been applied to wheat to introduce tolerance to herbicides.

Introduction of foreign DNA by homoeologous recombination

Wheat-alien translocations involve the transfer of chromosomal material between wheat chromosomes and their wild wheat or alien homoeologues. Wild wheats have provided an important source of new disease resistance in wheat breeding. The 'Agent' source of resistance has provided both leaf rust (*Lr24*) and stem rust resistance (*Sr24*) genes to bread wheat. This was a spontaneous translocation between chromosome 3D of hexaploid wheat and the alien homoeologue derived from *Thinopyrum ponticum* (Smith et al. 1968).

The modified translocation, 3*Ag*#3, is present in cultivar (cv.) 'Torres' (Mackay 1983); another modified translocation, 3*Ag*#14 is present in cultivars 'Skua', 'Sundor' and 'Vasco' (Mackay 1984a; Mackay 1984b; Mackay 1987).

Hybrid wheat

The production of hybrid wheat occurs on a limited scale in Australia and the female parents of all hybrids are alloplasmic and male sterile. Male sterility is a function of the interaction between the *T. aestivum* nucleus and the *T. timopheevii* cytoplasm. In the hybrid, male fertility is restored by the presence of a chromosomal segment from the *T. timopheevii* genome. This segment is normally present in a chromosomal translocation in the male parent (male fertility restorer) of the hybrid (Wilson & Ross 1962).

Herbicide tolerance

'Clearfield' is the production system comprising herbicide-tolerant wheat and Beyond TM herbicide. This system was developed by the chemical company Badische Anilin- & Soda-Fabrik AG (BASF). 'Clearfield' wheats carry a mutation to the acetohydroxyacid synthase (AHAS) gene and confers tolerance to imidazolinone herbicides (Health Canada 2004).

BASF used the chemical mutagens, Ethylmethane Sulfonate (EMS) and Diethyl Sulfate (DES) to induce mutants in the wheat cultivar 'Fidel' (Johnson et al. 2004). The mutant gene has been introduced to commercial germplasm in North America to develop the cultivars 'Above' and AP502CL.

4.3 Molecular genetics of wheat

The chromosomes of bread wheat (21 pairs) can be readily identified by their heterochromatic (C) bands (Figure 1, Figure 2.) (Li et al. 2004). Although other banding techniques exist (Figure 2), C-banding provides an effective method of identifying each of the 21 wheat chromosomes. Erayman et al. (2004) reported that wheat chromosomes have regions of high gene density interspersed by vast expanses of unpopulated regions consisting of repeated DNA. A comparison of the genetic distances among C-bands revealed that distribution of recombination is also uneven along wheat chromosomes (Erayman et al. 2004).

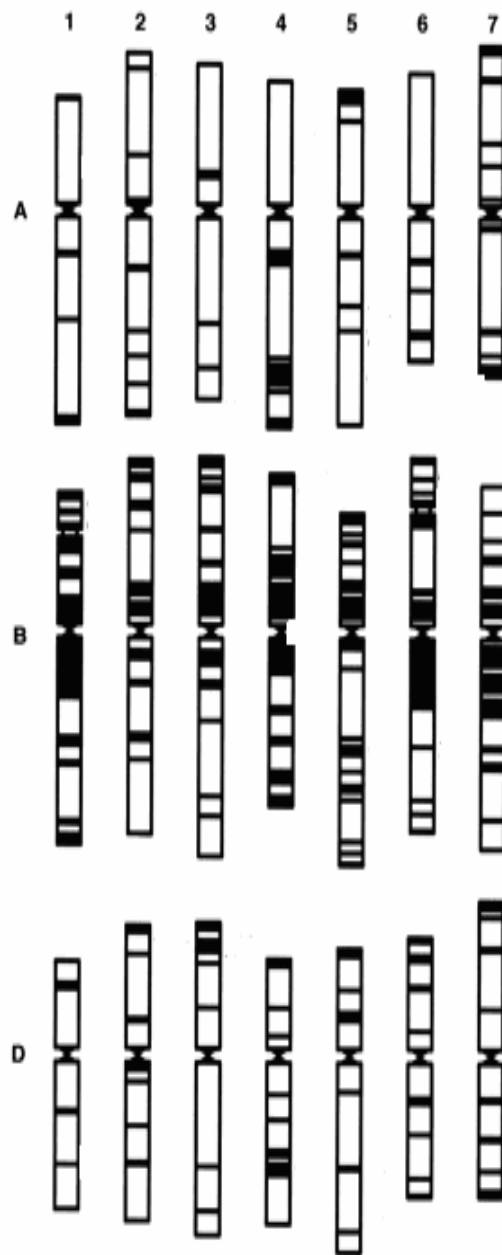


Figure 1. Heterochromatic C bands of the 21 bread wheat chromosomes

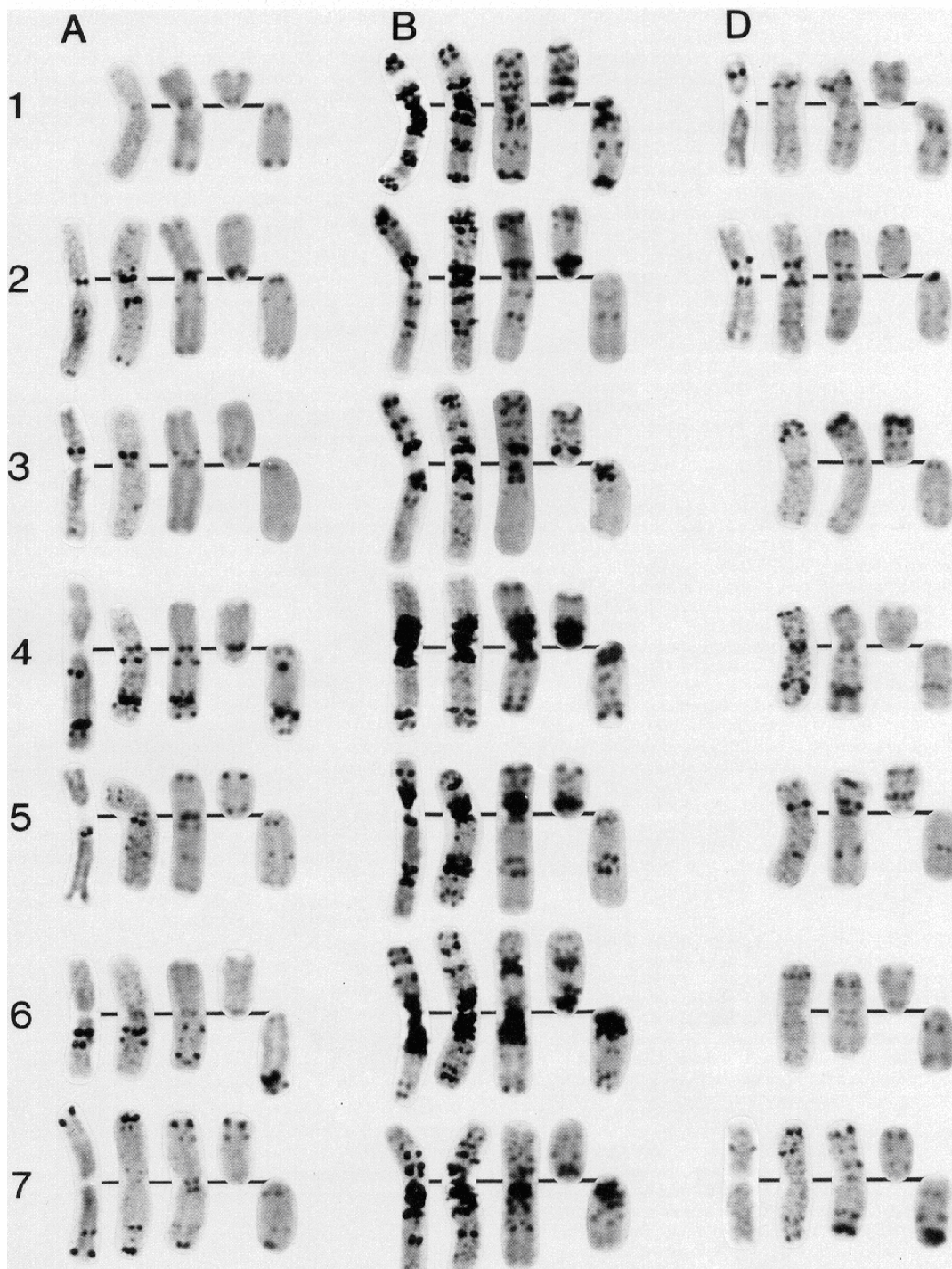


Figure 2. Stained wheat chromosomes (from left to right) by N-banding, modified C banding, and C-banding (whole and telosomic chromosomes) (chromosomes 1A and 3D to 6D do not show any N-bands, and were not identified).

Bread wheat genes appear to be concentrated in certain regions of the chromosomes. Sandhu and Gill (2002) reported that more than 85 % of wheat genes are present in less than 10 % of chromosomal regions. In general, gene density in the distal regions of chromosomes is higher as compared with the proximal regions.

More specifically, Li et al. (2004) reported that in the short arms of the chromosome 1 group, 70 % of genes and 82 % of total recombination distance were contained within 2 major gene rich regions (GRRs) that physically encompassed 14 % of the arms. Similarly, a sampling of 3025 gene loci of the bread wheat genome found that 29 % of the genome contained 94 % of the genes. Forty-eight GRRs were identified and 18 of these were considered major regions, spanning 11 % of the genome and accounting for 60 % of genes. These major GRRs occurred in the distal 35 % of chromosomes and the long arms of chromosomes contained twice as many genes as the short arms. Of the 94 % of genes in the GRRs, 59 % were in the 27 GRRs in the long arms of chromosomes, the remaining 21 GRRs occurred in the short arms (Erayman et al 2004).

The approximate size of the GRRs in wheat chromosomes ranges from 3-71 Mb and GRRs have not been observed in the centromeric regions of chromosomes. The regions around eukaryotic centromeres and in some cases telomeres have been reported to suppress recombination rates. Recombination occurs mainly in these GRRs (Erayman et al. 2004). The gene density in the GRRs in grasses is comparable with average gene density in *Arabidopsis*, which is 1 gene/ 4-5 kilobases (Sandhu and Gill 2002).

The tribe Triticeae has 300 species and bread wheat has the largest genome in the tribe (16000 Mb). Table 1 lists the genome size and DNA content of selected members of the Poaceae. Most large plant genomes consist of repeated sequences with a small fraction belonging to genes. Transposable elements (TE's) dispersed in the intergenic regions form dominant components of repeated sequences. Transposable elements account for 13.3% of the wheat genome, but only 1.22% in maize (Li et al. 2004).

The gene containing fraction of the genome is expected to be the same in all Poaceae species (Sandhu & Gill 2004). The best estimates for the gene containing regions of selected species are: wheat (7 %), barley (12 %), maize (17 %) and rice (24 %).

Table 1. DNA content and genome size of different members of family Poaceae

Plant	Chromosome No.	Genome Size	DNA Content 2C
	<i>n</i>	<i>Mb</i>	<i>pg</i>
Rice	12	415	<u>0.9</u>
Sorghum (<i>Sorghum bicolor</i>)	10	750	<u>1.6</u>
<i>Pennisetum americanum</i>	7	2,410	<u>4.8b</u>
Maize	10	2,500	5.6
Barley	7	5,000	<u>10.1</u>
<i>Aegilops tauschii</i>	7	4,000	<u>10.3</u>
<i>Triticum monococcum</i>	7	5,750	<u>11.9</u>
Wheat	21	16,000	<u>33.1</u>

At lower resolution, genes in cereal genomes appear to be clustered in small chromosomal regions separated by large blocks of repeat retrotransposon-like sequences. At higher resolution, gene-rich regions appear to consist of mini-gene-rich regions interspersed by non-transcribing repeat (NTRs). At the sequence level, genes present in mini-gene-rich regions are further separated by intergenic NTR sequences consisting of retrotransposons (Sandhu and Gill 2002).

The composition of plant NTR DNA seems to be a result of multiple invasions by different retrotransposons. Subsequent replication of the retrotransposons was followed by their inactivation by transpositioning and/or heterochromatisation. It has also been postulated that pseudogenes are an important part of NTRs and should be abundant in wheat and in other polyploid species. In wheat most genes follow single factor inheritance which suggests that only 1 of the 3 copies is functional, thus the other 2 copies are either non-functional, or have acquired different functions (Sandhu and Gill 2002).

Hart (1987) described paralogous sets of enzyme structural gene loci in the A, B and D genomes of wheat (Table 2). Paralogous refers to the homology resulting from gene duplication so that both copies have descended side by side during the history of an organism.

Table 2. Chromosome arm locations of paralogous sets of enzyme structural gene loci in genomes A, B and D of bread wheat cv. Chinese Spring (Hart 1987)

Chromosome arm group	Paralogous sets	Chromosome arm group	Paralogous sets
1p	Glucosephosphate isomerase-1 (<i>Gpi-1</i>), Hexokinase-1 (<i>Hk-1</i>) ^a , Peroxidase-1 (<i>Per-1</i>) ^a	1q	Malate dehydrogenase-1(<i>Mdh-1</i>)
2S	none	2L	Superoxide dismutase-1 (<i>Sod-1</i>)
3p	Esterase-1 (<i>Est-1</i>), Phosphodiesterase-1 (<i>Pde-1</i>), Triosephosphate-1 (<i>Tpi-1</i>)	3q	Esterase-2 (<i>Est-2</i>) [#] , Esterase-5 (<i>Est-5</i>), Glutamic oxaloacetic transaminase-3 (<i>Got-3</i>)
4p	Alcohol dehydrogenase-1 (<i>Adh-1</i>), Lipoxygenase-1 (<i>Lpx-1</i>), NADH hydrogenase-1 (<i>Ndh-1</i>), Phosphoglucomutase-1 (<i>Pgm-1</i>) ^a	4q	Acid phosphatase-1 (<i>Acph-1</i>), β -Amylase-1 (β - <i>Amyl-1</i>) ^b
5p	Shikimate dehydrogenase-1 (<i>Skdh-1</i>)	5q	Aromatic alcohol dehydrogenase-1 (<i>Aadh-1</i>), Aconitase-2 (<i>Aco-2</i>), Lipoxygenase-2 (<i>Lpx-2</i>), Triosephosphate-2 (<i>Tpi-2</i>)
6p	Aminopeptidase-1 (<i>Amp-1</i>), Glutamic oxaloacetic transaminase-1 (<i>Got-1</i>)	6q	Aromatic alcohol dehydrogenase-2 (<i>Aadh-2</i>), Aconitase-1 (<i>Aco-1</i>), α -Amylase-1 (α - <i>Amyl-1</i>), Esterase-4 (<i>Est-4</i>), Glutamic oxaloacetic transaminase-2 (<i>Got-2</i>)
7p	Esterase-3 (<i>Est-3</i>) ^a	7q	α -Amylase-2 (α - <i>Amyl-2</i>), Endopeptidase-1 (<i>Ep-1</i>)

5. DISEASES AND PESTS OF WHEAT

Apart from the three rust diseases, Stripe Rust, Stem Rust and Leaf Rust, there are several taxonomically diverse pathogens which can limit wheat production in Australia. Control measures are similar for many of these diseases. Table 5 summarises most of the diseases reported to date in Australia. Pests of wheat in Australia include insects and mammals. In contrast to the diseases, however, most pests are considered opportunistic, except for pests of stored grain.

5.1 Diseases of wheat in australia

Wheat is economically the most important crop in Australia and wheat diseases can reduce the quantity and quality of grain yield. The six major diseases of wheat in Australia in order of potential economic losses per year are common bunt (\$269 million), take-all (\$214 million), stripe rust (\$181 million), crown rot (\$160 million), *Septoria tritici* blotch (\$152 million) and *Septoria nodorum* blotch (\$147 million). When diseases of wheat are considered in order of average annual losses per year they are *Septoria nodorum* blotch (\$58 million), crown rot (\$56 million), take all (\$52 million), yellow spot (\$49 million), cereal cyst nematode (\$37 million), and root lesion nematode (\$36 million) (Brennan & Murray 1998).

Present disease losses vary widely between regions. *Septoria* blotch causes an average annual production loss of 4.9% in Western Australia but only negligible losses in other regions. In contrast, root lesion nematode has an average loss of up to 8.0% in Queensland and northern New South Wales, and considerably lower losses elsewhere (Brennan & Murray 1998).

5.2 Pests of bread wheat

Pests of wheat may be divided into pests of stored grain (including mice and various weevil species) and pests of wheat plants and seed. The Western Australian Department of Agriculture (2004) has identified the following pests:

- birds (including emus) which feed on developing seeds and seedlings and also ripening grain;
- marsupials which graze on wheat plants;
- rabbits which also graze on wheat plants;
- rats and mice which eat seedlings and seed and ripening grain; and
- Arthropods, including insects and mites.

Arthropod pests of wheat plants include mites (Blue oat mites (*Penthaleus major*), Red Legged Earth Mite (*Halotydeus destructor*), Brown wheat mites (*Petrobia latens*)), and insects such as the Oat aphid (*Rhopalosiphum padi*), which can introduce viruses into wheat plants; cutworms (*Agrotis* spp.) and armyworms (*Persectania* spp.). The locust (*Chortoicetes terminifera*) has also been identified as an insect pest of wheat.

Table 5. Diseases of wheat reported in Australia (Brennan & Murray 1998).

Disease name	Causal organism	Area of occurrence on the plant
Viruses		
Barley yellow dwarf virus	Barley yellow dwarf luteoviruses	Foliage
Nematode diseases		
Cereal cyst nematode	<i>Heterodera avenae</i>	
Root lesion nematode	<i>Pratylenchus</i>	
Stubby-root nematode	<i>Paratrichodorus cristiei</i>	
Bacterial diseases		
Bacterial leaf streak or Black Chaff	<i>Xanthomonas campestris</i>	Foliage and heads of wheat
Bacterial leaf blight	<i>Pseudomonas syringae</i> pv. <i>syringae</i>	As above
Spike blight or Tundu	<i>Corynebacterium tritici</i>	As above
Basal glume rot	<i>Pseudomonas syringae</i> pv. <i>atropaciens</i>	As above
Minor bacterial blight	<i>Corynebacterium michiganense</i> ssp. <i>tessellarius</i> , <i>Bacillus megaterium</i> , <i>Erwinia rhapontici</i>	As above
Fungal + Oomycete diseases		
Common root and crown rot	<i>Bipolaris sorokiniana</i> ; <i>Fusarium roseum</i>	Roots, lower stems and crowns
root rot	<i>Pythium</i> spp.	Roots
Take-all	<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	As above
Root rot and sharp eyespot symptom	<i>Rhizoctonia solani</i> and <i>R. cerealis</i>	As above
Stripe	<i>Cephalosporium gramineum</i>	As above
Strawbreaker foot rot	<i>Pseudocercospora herpotrichoides</i>	As above
Leaf and head blight	<i>Septoria nodorum avenae</i> and <i>Leptosphaeria nodorum</i>	Foliage and heads of wheat
Tan spot or yellow leaf spot	<i>Pyrenophora tritici-repentis</i>	As above
Helminthosporium leaf blight	<i>Cochliobolus sativus</i> ; <i>Bipolaris sorokiniana</i>	As above
Alternaria leaf blight	<i>Alternaria triticina</i>	As above
Downy mildew (minor)	<i>Sclerophthora macrospora</i>	As above
Scab or head blight	<i>Gibberella zeae</i>	heads of wheat
Black point	<i>Alternaria alternata</i>	As above
Ergot	<i>Claviceps purpurea</i>	As above
Stem Rusts	<i>Puccinia graminis</i>	Foliage and heads of wheat
Leaf rusts	<i>Puccinia recondite</i>	As above
Stripe rusts	<i>Puccinia striiformis</i>	As above
Wheat smuts	<i>Ustilago tritici</i> (Loose smut) <i>urocystis</i>	As above

6. TOXICITY AND ALLERGENICITY OF BREAD WHEAT

6.1 *Anti-nutritional factors and toxicity*

A number of anti-nutritional factors occur in wheat and in extreme cases may have a toxic effect. These are described below.

6.1.1 Enzyme inhibitors

There are two main types of enzyme inhibitors present in wheat, inhibitors of proteases and amylases. Protease inhibitors, especially trypsin inhibitors, may decrease the digestibility of dietary proteins while amylase inhibitors may affect the digestibility of dietary starch. However these inhibitors do not appear to pose a serious risk to human health as they tend to be heat labile (OECD 2003).

6.1.2 Lectins

Lectins were first described in 1888 by Stillmark who was working on castor bean extracts. They are glycoproteins that bind to specific carbohydrate groups on cell surfaces, causing lesions to form (OECD 2003). In the intestinal tract, these lesions can seriously impair the absorption of nutrients.

Lectins are usually inactivated by heat and are therefore of greater importance where wheat is consumed raw. For example, muesli contains an unprocessed form of the lectins, whereas bread contains an inactivated form in which the biorecognitive properties of lectin are significantly reduced (Gabor et al. 2003). Lectins may also be present in animal feeds containing wheat.

Singh et al. (1999) reported that physiological stresses to the wheat plant produced increased levels of WGA in germinating wheat embryo and the highest accumulation of WGA occurred when the germinating wheat embryos were exposed to salt stress (other stresses were temperature and osmotic stress). The authors concluded that WGA enhancement in germinating embryos appears to be a general stress response.

6.1.3 Phytic acid

Phytic acid may reduce the bioavailability of trace elements in animal diets through chelation of minerals such as iron, zinc, phosphate, calcium, potassium and magnesium (OECD 2003). This anti-nutrient is of particular importance to monogastric animals, while ruminants possess digestive enzymes which degrade phytate, releasing the chelated minerals. The level of phytic acid is highest in wheat germ and lowest in wheat flour (OECD 2003).

Colnar (2004) discussed wheat bran in diets for horses. The most common problem with daily wheat bran use is a chronic dietary calcium-phosphorus imbalance, presumably as a result of phytic acid toxicity. If this imbalance is not corrected, horses develop Nutritional Secondary Hyperparathyroidism (Big Head Disease) where facial bones are enlarged and all bones in the body are weakened.

6.1.4 Nitrate poisoning

Nitrogenous products can accumulate in plants and ruminants have the ability to convert nitrates to toxic nitrites. In monogastric animals the risk of nitrate poisoning is much less because conversion to nitrites occurs closer to the end of the digestive tract (Yaremicio 1991). Hartwig and Barnhart (2004) claimed 'a useful rule of thumb is that cattle and sheep can tolerate up to 0.5% nitrate on a dry matter basis' and identified wheat, rye and rape as crop plants which can accumulate nitrate. Yaremicio (1991) identified wheat, barley, oat and rye greenfeeds as nitrate accumulators.

There are two forms of nitrate toxicity. Chronic nitrate toxicity and is commonly associated with reduced rate of weight gain, depressed milk production, reduced appetite and greater susceptibility to infection. This form of poisoning can occur when nitrate levels are 0.5 to 1.0 % of feed consumed (dry matter basis) (Yaremicio 1991).

In the case of the second type of nitrate toxicity, acute poisoning occurs when nitrate is rapidly converted to nitrite in the rumen and is immediately absorbed in large amounts into the bloodstream. Signs of acute poisoning in cattle, prior to death, include increased heart rate, muscle tremors, vomiting, weakness, blue-grey mucus membranes, excess saliva and tear production, staggered gait, frequent urination, low body temperature, disorientation and an inability to get up.

6.2. Allergenicity of wheat

Wheat is one of the most common allergenic foods in the human diet and is mainly associated with asthma and atopic dermatitis. Anaphylaxis has been reported to occur rarely in children (OECD 2003). Severe bronchial irritation is frequently caused by the inhalation of wheat dust. Simmonds (1989) reported that several types of allergic responses to wheat have been reported. Wheat grain, dust and the milled products can cause a range of allergic reactions. The symptoms range from mild rhinitis to asthma, and are responses to the inhalation of flour or dust. The allergenic proteins of wheat have not been identified, although some candidates exist (OECD 2003).

6.2.1 Coeliac Disease

Coeliac Disease (Gluten-sensitive enteropathy) is a disorder caused by intolerance to cereal storage proteins found in wheat, barley, rye and triticale (Fraser & Ciclitira 2001).

Inheritance of Coeliacs Disease is multigenic and is strongly associated with European populations (Kasarda 2004). However, the disease does affect people from all ethnic groups. Fraser and Ciclitira (2001) noted that the prevalence of Coeliac Disease was thought to be 1 in 1500 in western countries and reported that recent screenings of blood donors has shown a higher prevalence of 1 in 250 in Sweden and the USA. Screenings of schoolchildren in Italy revealed a rate of 1 in 184. Simmonds (1989) had previously reported that 1 in 2000-3000 individuals in the US suffer from the coeliac condition.

For sufferers of Coeliac Disease, the consumption of gluten results in diarrhoea, malabsorption, fat in the stool, and nutritional and vitamin deficiencies. Some sufferers may have only minimal changes in the epithelium and no obvious symptoms, yet others may have

severe damage to the lining of the intestine. The lesions may also affect the ileum and even stomach and rectum, and villi may be absent.

Some people manifest evidence of the disease in the first year of life, shortly after the introduction of gluten into the diet and others can experience the disease later. It has been hypothesised that environmental factors may trigger the disease. Candidates include viral infection, parasitic infection (*Giardia*) and surgery (Kasarda 2004).

7. WEEDINESS

Wheat is not considered to possess the characteristics commonly associated with successful weeds, such as prolonged seed dormancy, long persistence in the soil, germination under a broad range of environmental conditions, rapid vegetative growth, short lifecycle, very high seed output, high seed dispersal and long-distance seed dispersal (Keeler 1989; Keeler et al. 1996). Wheat has poor competitive ability and does not have the potential to develop into an invasive weed (Keeler 1989; Keeler et al. 1996).

During domestication of the modern wheat plant, characteristics that benefited farmers were modified. This process also eliminated the ability of cultivated wheat to survive without the intervention of farmers (Eastham & Sweet 2002). Non-shattering heads were favoured because of ease of harvest and this trait placed wheat plants at a competitive disadvantage to other species which could more efficiently distribute seed. The earlier forms of *Triticum aestivum* were of the spelta type and husked. Husk-less seeds were easier to thresh, but husk-less seeds emerging in the soil were more susceptible to environmental stresses. As a result of many years of cultivation, commercial cultivars of bread wheat have lost any capacity to spread in uncultivated habitats.

In Australia, post-harvest treatments include stubble burning to minimise disease outbreaks and livestock grazing. These practices have minimised the risk of weediness and high summer temperatures coinciding with moisture stress also reduce opportunities for bread wheat to behave as a weed. Wheat is not considered a problematic weed in Australia (Groves et al. 2003) or elsewhere. Nevertheless *T. aestivum* is considered to be naturalised and a minor weed of agricultural systems in all Australian states in which wheat is grown (Groves et al. 2003). Glover (2002) reported that wheat is a minor problem weed in some natural environments in Tasmania. In the USA, bread wheat is regarded as a common weed in some situations and has been reported to be weedy in Nepal (Holm et al. 1979; Bridges 1992).

7.1 Factors affecting weediness of wheat

7.1.1 Taxonomy

An important element in predicting weediness is taxonomic relationships, considering weediness within a taxon, including its history of weediness in any part of the world (Bergelson et al. 1998; Panetta 1993; Pheloung 1995). Wheat has been grown for centuries throughout the world without any reports that it is a serious weed pest. Only bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* ssp. *durum* L.) are cultivated in Australia and neither are considered to be a problematic weed in Australia (Groves et al. 2000; Groves et al. 2002). However, other species of *Triticum* and the closely related genus *Aegilops* are recognised as quarantine weeds in Australia.

7.1.2 Dormancy

Pickett (1993) provided the following definitions of various forms of dormancy:

INNATE DORMANCY: seeds will not germinate when all environmental factors favour germination;

ENFORCED DORMANCY: when seed fails to germinate because environmental conditions are unfavourable; seed in dry storage or deep in soil;

INDUCED DORMANCY: seed once able to germinate can no longer do so, although conditions for plant development are correct.

Pickett (1989) reported that coat-imposed dormancy in wheat may last 3 – 7 months in dry storage, depending on the variety, and dormancy is expressed more strongly if seed is not dried after harvest. This report was based on European wheat varieties, which have red coloured seed coats. The critical growth stage for seed dormancy is doughy ripeness. Environmental conditions during seed ripening influence the degree of dormancy that develops with cooler weather resulting in increased dormancy (Pickett 1989).

Seed dormancy restricts the timely elimination of volunteer cereals. Under European conditions, seed buried too deeply in soil for germination is usually imbibed, but is in a state of enforced dormancy and is not metabolically active during this period. Pickett (1993) claimed that the seed coat is responsible for an inhibitory effect in developing and harvest-ripe grain. This inhibition of germination can be caused by the inner layer of the green pericarp of wheat. In latter stages of maturation the outer pericarp layer exercises similar control.

Ploughing can bury a high proportion of seeds to a depth where dormancy will be enforced and at which germinating seeds will be unable to reach the surface and develop into plants (Pickett 1993). Komatsuzaki and Endo (1996) found that longevity of seed from wheat cultivars resistant to pre-harvest sprouting was greater than in cultivars which were susceptible to sprouting. The longevity of seeds in unthreshed ears was longer than of loose seeds in the soil at depths of 3, 6, 9, 12, 15, 18 and 21 cm. The incorporation of unthreshed ears in the soil tends to preserve seeds for emergence in the following autumn.

Wicks et al. (2000) sampled weeds in various weed management systems in northern NSW in the period 1981 - 1990. Self-sown wheat was a greater problem early in fallow periods rather than at mid-fallow or late fallow. The authors also suspected that self-sown wheat would be a greater problem under experimental conditions because small-plot harvesters were less efficient than commercial harvesters. Where the harvest of buffer, or border plots was delayed, volunteer wheat was always increased in the early fallow period. Treatment with the herbicide glyphosate in January or February reduced the density of these volunteers. Viable seeds persisted later in dry seasons in no tillage plots. At Winton (1983) viable seeds persisted until June and at Warialda (1986) viable seeds persisted until May.

Red wheats are widely grown in Europe and North America and have higher levels of sprouting tolerance and typically are dormant for longer periods after harvest than the white wheats grown in Australia. Anderson and Soper (2003) reported that classical burial studies suggested that wheat seeds were short-lived in soil, persisting less than 1 year. In field studies however, volunteer wheat seedlings were still emerging 16 months after harvest and

seedlings were observed 2 years after harvest. Pickett (1993) claimed that unproven reports suggested that wheat could survive in the soil for 5 years. Pickett (1989) also noted earlier reports of germination inhibitors found in the seed coat of 18 red grained varieties of wheat.

White wheats lack the anthocyanins that colour the seed coat in red wheats. Pre-harvest sprouting tolerance is an important selection criterion in Australian wheat breeding programs as rainfall coincident with harvest can initiate germination processes and reduce bread making quality characteristics.

There are no indications that wheat can become established as a self-sustaining population on a long-term basis (Sukopp and Sukopp 1993; Newman 1990). There have been no reports of bread wheat becoming an invasive weed in Australia or elsewhere. Wheat is reported as naturalised in some agricultural environments, but is not considered a problem weed in most states, although it is considered a minor problem in a few natural environments in Tasmania (Glover 2002).

8. GENE TRANSFER

Potentially, wheat genes can be transferred to:

- (1) other *Triticum* species, including *T. aestivum*;
- (2) other sexually compatible species;
- (3) other plant genera; and
- (4) other organisms.

Bread wheat belongs to the tribe *Triticeae* (Subfamily Pooideae, Family Poaceae). The members of the *Triticeae* are listed in Table 2 with their chromosome formulae. Gene transfer from bread wheat to other members of the *Triticeae* is dependent upon pollen transfer, compatibility of the parent genomes and formation of viable embryos. Hybridisation between wheat and *Hordeum* spp., *Elytrigia* spp. and *Leymus* spp. has been achieved, but embryo rescue was required to produce viable plants (Eastham & Sweet 2002).

8.1 Gene transfer to other TRITICUM species, including TRITICUM AESTIVUM

Gene transfer through cross pollination or outcrossing can only occur to other wheat plants that are in very close proximity and that flower synchronously. Intergeneric hybrids involving *Triticum* spp., but many of the hybrids only occurred under artificial conditions (see reviewed by Maan 1987). Both bread wheat and durum wheat (*Triticum turgidum* ssp. *durum*) are grown in Australia, while other species of *Triticum* are not known to be present in Australia.

Wheat stigmas are receptive for 2 - 13 days after anthesis, although they are most receptive in the first 2 - 5 days after anthesis (Waines & Hedge 2003). A wheat stigma intercepts an area of 10mm² on average (Bitzer and Patterson, 1967, cited by Waines & Hedge 2003). Increased gene flow may be achieved through larger stigmas although pollen availability and movement are the most important limiting factors over large areas. Hybrid wheat seed production

strategies have attempted to improve pollen flow while minimising the male parent to female parent ratio.

Bread wheat is predominantly self pollinating. Outcrossing can occur at frequencies of up to ~5 % between adjacent rows (Waines and Hedge 2003). Pollen dispersal in wheat plants is wind mediated. However, wheat pollen is heavy in comparison to other grass pollen and falls rapidly, 60 cm/second from a plant height of 1 m (Lelley 1966). Field conditions including temperature, relative humidity and wind intensity have a great influence upon pollen viability. Under field conditions, wheat pollen is viable for only a limited period of time (up to 30 minutes) (OECD 1999).

Allan (1987) reported outcrossing of 3 % at 40 m and 7 % at 20 m on male sterile wheat plants. When male sterile plants were used to measure pollen movement, Waines and Hedge (2003) reported that seedset was 71 % on male sterile spikes between 0.75 m and 2.25 m from the pollinator. Glover (2002) also noted that earlier reports measured gene flow on male sterile plants to be on average less than 10 % at 1 m and detected none at 20 m from the pollen source plant. Glover also noted that outcrossing frequencies would be lower in male fertile wheat populations.

The NSW certified seed specifications require no separation distance between wheat crops grown for certified seed, but simply that a physical barrier (eg. fence) be in place to prevent seed mixing during harvest (Glover 2002). Similarly the international body that issues seed certification guidelines, AOSCA, requires only that foundation crops of wheat be isolated from other wheat crops so as to prevent mechanical mixing during harvest (Association of Official Seed Certifying Agencies 2001). The USDA has similar guidelines for various pedigree seed classes (summarised in Waines and Hedge 2003; Hucl and Matus-Cadiz 2001).

Hucl and Matus-Cadiz (2001) studied outcrossing in Canadian spring wheats and noted that the single sowing time reduced synchrony of flowering in different varieties. In this study, the highest outcrossing rate was 3.8 % at 0.5 m from the pollen source. Outcrossing decreased with distance from the pollen source and in some Canadian wheat varieties outcrossing was restricted to a distance of 3 m from the pollen source. Outcrossing varied among the 4 varieties studied, with 95% of the outcrossing occurring within 1 to 12 m of the pollen source, depending on variety, wind direction and other environmental conditions. In two varieties, 'Robin' and 'Oslo', some outcrossing was observed at 27 m. The authors suggested that 30 m separation is required during the production of certified seed and registered seed of these 2 varieties, to avoid contamination through outcrossing. The study indicated that a 30 m separation zone would be expected to eliminate outcrossing problems in wheat

A similar study by Hanson et al. (2005) conducted at five locations in the Pacific Northwest (USA) examined cross-pollination among blue-alurone wheats and soft-white winter wheats commonly grown in the area. The study was conducted from 2000 to 2003 and showed that about 98% of the samples contained no blue seed (indicating that cross-pollination had not taken place). At four locations, there was no detectable cross-pollination beyond 30 m from the pollen source, while at the fifth location, cross-pollination occurred as far as 42 m from the pollen source. The study suggested a 45 m separation zone may be appropriate to eliminate outcrossing in winter wheat grown in the Pacific Northwest.

Gene flow studies on wheat under Australian conditions indicated out-crossing frequency was very low, 0.012% at the outer edge of a 2 m wide buffer. These studies were conducted

by CSIRO during releases under the former voluntary Genetic Manipulation Advisory Committee (GMAC) (final report on PR65 and PR66). Wheat generally was rated as having low potential for outcrossing and consequently, low potential for causing impacts upon farming and other environments (Glover 2002).

Gene flow experiments were conducted in the field by Matus-Cadiz et al. (2004) at Saskatoon, Canada in 2000 and 2001. In 2000, mean gene flow (over 8 directions) at 0.2 m was 0.20 % and at 1 m gene flow was 0.17 %. In 2001, average gene flow was 0.08 % and 0.06 % respectively. Matus-Cadiz et al. (2004) attributed variability in pollen movement and gene flow to environmental factors including prevailing winds and wind speed, temperature and humidity.

Long distance intraspecific gene flow was not detected in the field beyond 300 m. In 2000, trace gene flow (0.005 %) was detected at 300 m and was associated with prevailing winds. In 2001, the pollination period was hotter and less humid than in the previous season and long distance gene flow was not observed.

Matus-Cadiz et al. (2004) evaluated interspecific gene flow at Saskatoon, Canada in the two years, 2000 and 2001. Interspecific hybrids between durum wheat (*Triticum turgidum* ssp. *durum*) and a bread wheat pollinator were detected by shrivelled grain and confirmed by subsequent 'grow outs' of these suspected hybrids. Interspecific gene flow greater than 40 m from bread wheat pollen source to durum was not observed in either. In 2000, at 0.2 m from the pollen source (bread wheat), average gene flow over 8 directions was 0.08 % and at 1 m this was 0.04 %. In 2001, gene flow at 0.2 m averaged 0.05 % and had decreased to 0.002 % by 20 m.

In 2000, approximately 71 % and 94 % of cumulative gene flow occurred within 1 m and 10 m of the pollinator respectively. In 2001, 54 % and 98 % of cumulative gene flow occurred within 0.2 m and 0.5 m of the pollinator. Matus-Cadiz et al. (2004) suggested that the shrunken endosperm, indicating successful hybridisation between bread and durum wheat, would inhibit germination and seedling vigour and therefore reduce the possibility of gene introgression. In 2000, only 21 % of identified inter-specific hybrid seed, germinated and produced plants, and in 2001, 41 % produced plants.

In contrast to earlier results (see Hucl and Matus-Cadiz 2001, above), Matus-Cadiz et al. (2004) found that intraspecific cross pollination could occur at very low frequency of 0.005% at 300 m from the pollen source in the prevailing wind direction.

Jacot et al. (2004) also described earlier experiments which measured seed set on emasculated wheat spikes over several distances. At distances less than 4 m, hybridisation occurs at low rates and hybrids were found at 14 m from the pollen source. When pollen flow was measured in fertile spikes, after 1 m 'the likelihood of pollination decreases distinctly and is nearly nil beyond 20 m'. In both instances, wind direction and temperature influenced pollen movement and viability.

Wheat is primarily self-pollinating and pollen movement is mediated by wind. Nearly all (95 to 98%) of reported inter- and intraspecific outcrossing appears to occur within a distance of 0.5 to 12 m from the pollen source. Gene flow from bread wheat to other bread wheat or durum wheat has been observed at very low frequencies to a maximum of 300 m or 40 m, respectively (Hucl and Matus-Cadiz 2001, Matus-Cadiz, 2004).

8.2 Gene transfer to other Sexually compatible species

In general, bread wheat and some related genera are cross compatible and hybrids between the different genera can be produced under controlled or artificial conditions. These hybrids are highly male sterile and backcross progeny can be produced from pollination with parental lines or other related species (Knobloch 1968).

Intergeneric hybrids involving *Triticum* spp. and *Elytrigia*, *Elymus* (= *Elytrigia*), *Haynaldia*, *Secale*, or *Hordeum* species are possible, but most hybrids between bread wheat and other genera were grown in embryo culture and were self sterile (reviewed by Maan 1987). Ellstrand et al. (1999) also observed that natural hybrids, between wheat and its wild relatives are highly sterile, ‘although seeds may occasionally be found’. Hybrid sterility may explain why hybridisation appears to be restricted to the F₁ generation with little evidence of subsequent introgression. The probability of gene flow from wheat crops to wild species, including *Hordeum* spp., *Elytrigia* spp. and *Leymus* spp., was considered to be minimal in Europe because embryo rescue was required to produce plants (Eastham and Sweet 2002).

In a review of cross-pollination and introgression between bread wheat and wild relatives in North America, Hedge and Waines (2004), indicated that a number of natural barriers exist that preclude hybrid formation between wheat and wild relatives. These natural barriers include: asynchronous flowering, gametic or zygotic incompatibility, and reduced hybrid fitness or hybrid sterility. The barriers arise mainly from the fact that wheat and its wild relatives have distinctly different sets of genomes (see Section 2). The chromosomes of these different genomes do not pair during gamete formation in the F₁ hybrids or may result in developmental instability, which reduces the hybrid’s ability to survive in parental habitats.

8.2.1 Interspecific hybridisation requiring artificial conditions

Elytrigia species have been cross-pollinated with wheat, but only under controlled glasshouse conditions. The very common couch grass, *Elytrigia repens* (= *Agropyron repens* or *Elymus repens*), which is widespread in Australia, has no reliable reports of hybridization with wheat (Eastham and Sweet 2002). In a review article on hybridization between wheat and wild relatives, Jacot et al. (2004) indicated that no hybrids were obtained from artificial crosses between bread wheat and *E. repens* under controlled conditions or under field conditions. *Elytrigia elongata* (= *Agropyron elongatum*) was crossed with bread wheat under artificial conditions and hybrids obtained with the use of embryo rescue (Jacot et al. 2004). *A. elongatum* appears to be a rare plant in Australia, with only 2 reports of in NSW (Australia’s Virtual Herbarium, AVH 2006, www.cpbr.gov.au/cgi-bin/avh.cgi) There are no reports of hybrids forming between bread wheat and *E. elongata* under natural or field conditions.

Cross-pollination between *Elymus giganteus* and bread wheat also produced hybrid plants (Maan 1987). *E. giganteus* is synonymous with *Elymus racemosus*, *Leymus giganteus*, *Leymus racemosus* and *Elymus arenarius* var. *giganteus*. A closely related species (or possibly synonymous species) *Leymus arenarius* has been cross-pollinated with bread wheat using artificial conditions, but required embryo rescue to obtain hybrids (Eastham and Sweet 2002). This species is synonymous with *Elymus arenarius*. None of the above species have been reported as present in WA (FloraBase 2006), while in the rest of Australia, there is only a single report each of *L. arenarius* in Victoria and *L. racemosus* in the ACT (AVH 2003). There are no reports of hybrids between bread wheat and these species occurring naturally.

Haynaldia villosa has been crossed with bread wheat, but the F₁ hybrids were completely male sterile and partially female fertile (see review in Maan 1987). This species is not known to be present in Australia (AVH 2006). There are no reports of bread wheat and *Haynaldia* forming hybrids under natural conditions.

Zemetra et al. (1998) demonstrated that transfer of genetic material from bread wheat to *Ae. cylindrica* is possible under glasshouse conditions and claimed that genes could be transferred between bread wheat and jointed goatgrass after only two backcrosses. However, because the hybrid is pentaploid and lacks pairing during meiosis (except for the D genome), most of the F₁ hybrids were completely sterile. Mallory-Smith et al. (1996) had reported that 2 % of interspecific hybrids were female fertile in glasshouse conditions and this allowed for backcrossing to occur between the interspecific hybrid and either parent.

Jacot et al. (2004) also reported the formation of hybrids between bread wheat and *T. turgidum* ssp. *durum*, *Aegilops biuncialis*, *A. ovata* and *A. cylindrica*; embryo rescue was required to produce plants from the cross between bread wheat and *A. cylindrica*. Jacot et al. (2004) reported that artificial hybridisation between wheat and wild relatives (using wheat as the pollen donor) is likely to occur at low rates; after hand pollination, hybrids were recovered in 12 of 17 crosses between wheat and 17 related taxa. Hand pollination of three *Aegilops* spp. by *T. turgidum* ssp. *durum* resulted in viable seeds. This procedure required hand emasculation of female spikes, to prevent self pollination and application of pollen by hand 1-3 days later.

Wheat has been artificially crossed with rye (*Secale cereale* L.) resulting in the cereal triticales (*Triticale hexaploide*). The first deliberate wheat-rye hybrid was observed in Scotland in 1875. However, fertile hybrids were not produced until 1888 by Rimpau. Bread wheat (2n=42, AABBDD) crossed with rye (2n=14,RR) results in a sterile hybrid (2n=28, ABDR), which can be treated with colchicine to artificially double the chromosome number and create a fertile hybrid (2n=56, AABBDDRR). Most recently developed triticales are the secondary amphiploids of durum wheat and rye (2n = 42, AABBRR). Primary triticales are the 21 chromosome hybrid, containing the A, B, and R genomes of durum wheat and cereal rye. Colchicine treatment of the primary triticales can produce 42 chromosome progenies (Varughese et al. 1997). Wheat x rye crossing is affected by the genotype of wheat varieties, most of the 1400 wheat varieties tested for crossing with rye exhibited greatly reduced seed set (Hedge and Waines 2004).

In artificial crosses, wheat x rye hybrids are easier to obtain than rye x wheat hybrids. Most wheat x rye hybrids are completely male sterile and highly female fertile (Hedge and Waines 2004).

The genomes of wheat and barley are considered incompatible. Hybrid plants derived from crossing wheat and barley have been achieved, but these have required extensive human intervention such as manual pollination, chemical treatment and embryo rescue and resultant plants are self-sterile (Islam et al. 1978; Koba et al. 1991; Molnar-Lang et al. 2005). The only successful artificial crosses have involved barley as the male parent (ie pollen donor) (Koba et al. 1991). There are no reports that cultivated wheat x barley hybrids exist naturally (Eastham and Sweet 2002).

There are several reports of haploid wheat plant production by pollination of wheat plants with maize pollen and subsequent embryo rescue. Colchicine treatment of the haploid plants,

grown from the rescued embryos, produces doubled haploid seeds. Li et al.(1996) described high yields of embryos in wheat pollinated with gamma grass (*Tripsacum dactyloides*).

The genotype of the male parent influences the production of haploid wheat plants (Garcia-Llamas et al. 2004). Laurie and Bennett(1988) tested *Sorghum bicolor* L. as a pollinator and Laurie (1988) tested *Pennisetum glaucum* L. as pollinators. Gene transfer, between wheat and maize chromosomes, in these instances has not been reported.

Sea barley (*Hordeum marinum*) has been artificially crossed with bread wheat (Munns 2004), see section on field studies below for further discussion.

8.2.2 Interspecific hybridisation under natural conditions

In field experiments with mixed plantings, hybrids were obtained between bread wheat and *T. durum*, *A. biuncialis*, *A. cylindrica*, *A. ovata*, embryo rescue was also required for the cross between bread wheat and *A. cylindrica* (Jacot et al., 2004).

In field studies of spontaneous hybridisation, Jacot et al. (2004) reported that the *A. ovata* x *T. aestivum* and *A. ovata* x *T. durum* hybrids were recovered. The morphology of the *A. ovata* x *T. durum* hybrid was intermediate between the two parental species and corresponded to the description of *Triticum triticoides*. Only one hybrid produced viable seed demonstrating that the production of non-reduced gametes is rare (Jacot et al., 2004).

Jacot et al. (2004) also analysed hybridisation records from Switzerland, southern France and northern Spain. Biogeographical studies and morphological character analyses were performed on herbarium specimens of wheat and related wild species (*A. squarrosa*, *A. cylindrica*, *A. ovata*). Scatter diagrams of 45 selected parameters distinguished bread wheat from its wild relatives and hybrid forms and separated bread wheat and *Aegilops* for all species studied. Hybrid F₁ plants (*A. triticoides*), F₂ and backcross (BC) plants of *A. triticoides* x bread wheat were found between *A. ovata* and bread wheat.

The herbarium survey conducted by Jacot et al. (2004) demonstrated that *A. ovata* can hybridise with bread wheat in the field. However, backcrosses of the F₁ progeny with the wheat parent and the F₂ progeny are only known from botanical gardens or private gardens, thus there is no clear evidence for the introgression of genes from bread wheat into *A. ovata* occurring naturally. Jacot et al. (2004) also noted that the distribution of several *Aegilops* /wheat hybrids is concentrated in southern France. There are no records of the presence of *Ae. ovata* in Australia (AVH 2006).

In the western USA, jointed goatgrass (*Aegilops cylindrica*) is recognised as a major weed of winter wheat (Zemetra et al. 1998). Eastham and Sweet (2002) reported that *Ae. cylindrica* has the genome configuration CCDD (2n =28) and the D genome is shared with bread wheat. This common genome enables the production of hybrids in the field. Natural hybridization between *Ae. cylindrica* and bread wheat has been documented in the USA (see review by Hedge and Waines, 2004). These natural hybrids had a 2.2% frequency of seed set. Morrison et al. (2002) found that bread wheat x *Ae. cylindrica* hybrids could backcross to either parent under field conditions. Although jointed goatgrass is recognised as a major weed of winter wheat in western USA, it is not known to exist in Australia except for 1 report in Tasmania (AVH 2006).

There is one report of possible hybridisation in nature between bread wheat and *H. marinum*. Guadagnuolo et al. (2001) used RAPD (random amplified polymorphic DNAs) markers to search for evidence of introgression from cultivated bread wheat to adjacent naturalised populations of sea barley. Seed was harvested from the sea barley population, but no F₁ hybrids were found among germinated seedlings, suggesting there had been no hybridisation during the growing season. However, one of the *H. marinum* plants in the naturalised population (from which seed was collected) generated a few RAPD markers which were specific to bread wheat. This particular plant had 9 of the possible 40 RAPD markers specific to bread wheat and was morphologically indistinguishable from all the other *H. marinum* plants in the area. All other *H. marinum* plants analysed had RAPD markers specific to sea barley.

The authors suggested that hybridization between the two species had occurred at some previous time and that subsequent back crossing between the hybrid and pure *H. marinum* could lead to the introgression of wheat DNA into sea barley (Guadagnuolo et al. (2001). However, bread wheat (*T. aestivum*) is a hexaploid (AABBDD) containing the A, B, and D genomes and these genomes are shared with many other *Triticum* or related species. It is probable that a portion of the RAPD markers are specific to the each of the three different genomes of bread wheat. Thus, for example, hybridisation between *H. marinum* and *T. boeoticum* (AA), *T. turgidum* (AABB), *Aegilops tauschii* (DD), *Ae. cylindrica* (CCDD), or others, may account for the results obtained by Guadagnuolo et al. (2001). The authors could find no evidence for further introgression of the wheat DNA into the *H. marinum* population, suggesting that differences in ploidy levels likely rendered the putative hybrid sterile.

H. marinum is present in the wheat growing areas of Australia (AVH 2006) and the applicant has indicated it is likely to be present at the release site. *H. marinum* is an annual weed. It is salt tolerant to levels approaching seawater (Munns 2004).

Although successful artificial hybrids between wheat and rye (*Secale cereale* L.) have been reported, there have been no natural hybrids between these species reported in Europe (Eastham and Sweet 2002) or the USA, while there are non-peer reviewed reports of naturally formed hybrids from Canada (Hedge and Waines 2004). Artificial crosses between rye and wheat gave rise to triticale (see section 8.2.1), but there are no reports of hybridisation between bread wheat and triticale occurring in nature.

8.3 Gene transfer to other plants

Bread wheat is genetically incompatible with all other grass species in Australia. There are no reports of gene transfer from wheat to species other than those mentioned in the above sections. Recombination of wheat chromosomes and chromosomes of other *Triticum* species is induced through the presence of homoeologous pairing mutant genes.

8.4 Gene transfer to other organisms

There is negligible risk of transferring bread wheat genes to other sexually incompatible organisms such as humans, other animals, fungi, bacteria, other microorganisms and viruses. A complex series of events would be necessary for successful horizontal gene transfer to occur. In general, gene transfers are detected over evolutionary time scales (Lawrence & Ochman 1998). Phylogenetic comparison of the sequences of plant and bacterial genes

suggests that horizontal gene transfer from plants to bacteria during evolutionary history has been extremely rare, if occurring at all (Nielsen 1998).

Most gene transfers have been from virus to virus (Lai 1992), or between bacteria (Ochman et al. 2000). Viruses have transferred genes to their hosts (Harper et al. 1999) and these gene transfers have been identified through analyses of gene sequences (Ochman et al. 2000; Worobey & Holmes 1999).

Evidence from gene sequences indicates that transfers of genes between plants and other organisms such as animals, bacteria, fungi or viruses is exceedingly rare (Mayo & Jolly 1991; Aoki & Syono 1999). The transfer of plant genes to bacteria and viruses has been observed in laboratory and glasshouse experiments (Nielsen et al. 2000; Schoelz & Wintermantel 1993; Greene & Allison 1994). However, in all cases this was achieved only with related gene sequences (homologous recombination), using highly sensitive or powerful selection methods to detect rare gene transfer events. Horizontal gene transfer from plants to bacteria has not been demonstrated under natural conditions (Syvanen 1999; Nielsen et al. 1997; Nielsen 1998) and deliberate attempts to induce such transfers have so far failed (Schlüter et al. 1995; Coghlan 2000).

9. PREVIOUS RELEASES OF GM WHEAT

9.1 GM Wheat releases in Australia

Two applications involving genetically modified (GM) wheat lines have been approved for limited and controlled release under current legislation. These are field trials testing salt tolerance (DIR053/2004) and altered starch (DIR054/2004) of GM wheat. DIR053/2004 is being conducted by Grain Biotech in the Shire of Corrigin, Western Australia. The scale of this trial is 0.45 hectares and involves some of the same wheat lines as in the proposed application. DIR054/2004 is being conducted by CSIRO in the Australian Capital Territory and the scale of the trial is 500 m².

The Canadian Food Inspection Agency (CFIA) website lists numerous field trials of plants with novel traits in recent years, www.inspection.gc.ca/english/plaveg/bio/triesse.shtml. Included in this list are 13 field trials for 2005 and 38 trials for 2004 testing herbicide, fungal or other disease resistance genes in GM bread or durum wheat.

There have been five field trials of GM wheat under the former voluntary system that was overseen by the Genetic Manipulation Advisory Committee (GMAC). These releases are listed in Table 6. NLRDs involving wheat have been listed in Table 7.

Table 6. Field releases of GM wheat under the GMAC system

GMAC Identification	Period of release	Title	Applicant	Area of release	Parent organism	Genetic modification
PR65	June 1996-Jan 1997	Evaluation of the potential for gene flow from transgenic wheat, using a herbicide-resistance marker	CSIRO	325 wheat plants	<i>Triticum aestivum</i> L.	Field performance of wheat genetically modified to contain the Basta-resistance gene
PR66		Evaluation of the performance of transgenic wheat with altered starch composition under field conditions	CSIRO	325 plants	<i>Triticum aestivum</i> L.	Test wheat that is genetically modified for altered starch composition
PR102	August 1998-Jan 1999	Transgenic wheats with modified grain qualities	CSIRO	400m ² (1500 plants)	<i>Triticum aestivum</i> L.	Field performance of wheat modified to overproduce glutenin in the grain
PR102X	August 2000-June 2001	Transgenic wheats with modified grain qualities	CSIRO	400m ² (1500 plants)	<i>Triticum aestivum</i> L.	Field performance of wheat modified to overproduce glutenin in the grain
PR107	Autumn 1999	Evaluation of the performance of transgenic wheat under field conditions	University of Adelaide	400m ² (600 plants)	<i>Triticum aestivum</i> L.	2 markers to identify GM wheat

Table 7. Notifiable Low Risk Dealings (NLRDs) of GM wheat

Notification number	Applicant	Title of NLRD
NLRD 1253/2004	The University of Sydney	Use of GFP-constructs to assay targeted mutagenesis in wheat
NLRD 989/2003	The University of Melbourne	Expression of value added products in wheat
NLRD 951/2003	University of Southern Queensland	Genetic engineering to increase frost tolerance in wheat III
NLRD 907/2003	CSIRO Plant Industry	Genetic Improvement of crops (barley, wheat and soybean) for yield under stress
NLRD 844/2003	La Trobe University	Genetic manipulation of wheat for tolerance to abiotic stresses
NLRD 842/2003	La Trobe University	Genetic manipulation of wheat and barley for tolerance to abiotic stresses
NLRD 585/2003	The University of Adelaide	Genome structure manipulation for improving wheat and canola transformation
NLRD 584/2003	The University of Adelaide	Embryo and endosperm development in wheat and barley
NLRD 383/2002	The University of Adelaide	Meiosis, recombination and pollen development in wheat
NLRD 239/2002	Grain Biotech Australia Pty Ltd	Transgenic approaches to drought and salt tolerance in wheat
NLRD 238/2002	Grain Biotech Australia Pty Ltd	Colour modification in wheat
NLRD 237/2002	Grain Biotech Australia Pty Ltd	Production of <i>Barley yellow dwarf virus</i> resistant wheat plants by transgenic methods
NLRD 236/2002	Grain Biotech Australia Pty Ltd	Production of therapeutic peptides in wheat
NLRD 071/2001	CSIRO (Livestock Industries)	Molecular genetics of <i>Fusarium spp</i> infecting wheat and cotton
NLRD 039/2001	Grain Biotech Australia Pty Ltd	Production of <i>Barley Yellow Dwarf Virus</i> (BYDV) resistant transgenic wheat
NLRD 026/2001	The University of Queensland	Molecular genetics of <i>Fusarium spp.</i> infecting wheat and cotton

9.2 International releases of gm wheat

Monsanto submitted a petition to Animal and Plant Health Inspection Service in the USA in early 2004 to trial genetically modified glyphosate-tolerant wheat. In June 2004, Monsanto announced that this petition would be withdrawn.

Table 8 lists the recent applications for field releases of GM wheat in Europe.

Table 8. Applications for field release of GM wheat in Europe (Joint Research Centre, 2004).

Date of acknowledgment	Notification	Title	Breeding line	Introduced trait	Proponent
4/10/2002	B/DE/02/143	Fungal resistant wheat in Germany	UC703	FRG; PMI	Syngenta GmbH
2/12/2002	B/GB/02/R34/4	To compare the pathogen infestation level and mycotoxin level of wheat modified to express an enhanced resistance to Fusarium pathogens with existing non-modified varieties, grown under standard agronomic conditions	UC703	FRG: gene of fungal origin conferring tolerance to Fusarium pathogens; PMI: Phosphomannose Isomerase gene isolated from E.coli, conferring tolerance to mannose	Syngenta Seeds Ltd
10/10/2003	B/DE/03/151	Fungal resistant wheat Germany 2004 (I)	UC703	FRG: gene of fungal origin conferring tolerance to Fusarium pathogens; PMI: Phosphomannose Isomerase gene isolated from E.coli, conferring tolerance to mannose	Syngenta GmbH
14/10/2003	B/DE/03/152	Fungal resistant wheat Germany 2004 (II)		FRG: gene of fungal origin conferring tolerance to Fusarium pathogens; PMI: Phosphomannose Isomerase gene isolated from E.coli, conferring tolerance to mannose	Syngenta GmbH
09/01/2004	B/ES/04/08-CON	Evaluation in field conditions of fungal resistant wheat		<i>frg</i> gene: codes for a protein capable of conferring a Fusarium fungal resistance characteristic; <i>pmi</i> gene: marker gene used for selection during transformation, which gives the plant the option to use mannose as a carbon source	Instituto de Agricultura Sostenible Consejo Superior de Investigaciones Cientificas

03/05/2004

B/IT/04/02

Study of the stability of the transgene and *his* heritability of genetically modified wheat under open field conditions

Bob white

Gene for the sub-unit Dx5B: fragment EcoRI of 8.7 Kb that contain the gene Glu-D1-1b under transcriptional control of the endogenous promoter for tissue-specific expression in wheat endosperm;
- Gene for the sub-unity Dy10A: EcoRI fragment of 6.4 Kb that contain the gene Glu-D1-2b under transcriptional control of the endogenous promoter for tissue-specific expression in wheat endosperm;
- Gene for the sub-unity Ax2: contain the gene Glu-A1-1c under transcriptional control of the endogenous promoter for tissue-specific expression in wheat endosperm

Metapontum
Agrobios s.c.a.r.l.

10. REFERENCES

- ABARE (2003). Australian Crop Report. 128, Australian Bureau of Agricultural and Resource Economics
Commonwealth of Australia, Canberra 2601. pp 1-20.
- Acevedo, E., Silva, P., Silva, H. (2002). Wheat growth and physiology. *In* "Bread wheat. Improvement and Production", BC Curtis, S Rajaram, H Gomez Macpherson, eds. Food and Agriculture Organisation, Rome.
- Allan, R.E. (1987). Wheat. *In* "Principles of cultivar development", WR Fehr, ed. Macmillan Publishing Company, New York. pp 699-749.
- Allard, R.W. (1999). Principles of plant breeding. 2 edition. John Wiley & Sons, Inc., New York, USA.
- Anderson, R.L., Soper, G. (2003). Review of volunteer wheat (*Triticum aestivum*) seedling emergence and seed longevity in soil. *Weed Technology* **17**: 620-626.
- Aoki, S., Syono, K. (1999). Horizontal gene transfer and mutation: *Ngrol* genes in the genome of *Nicotiana glauca*. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 13229-13234.
- Austin, R.B., Jones, H.G. (1975). The Physiology of wheat: In Plant Breeding Institute Annual Report-1974. Cambridge UK, Cambridge. pp 20-73.
- Australian Wheat Board (2004). Wheat statistics.
<http://www.awb.com.au/AWBL/launch/Site/AboutAWB/Content/CommunityEducation/HistoricalGrainStatistics/> .
- AVH (2006) Australia Virtual Herbarium database, www.cpbr.gov.au/cgi-bin/avh.cgi, accessed January 2006.
- Bergelson, J., Purrington, C.B., Wichmann, G. (1998). Promiscuity in transgenic plants. *Nature* **395**: 25.
- Brennan, J.P., Murray, G.M. (1998). Economic Importance of Wheat diseases in Australia. NSW Agriculture GRDC,
- Bridges, D.C. (1992). Crop Losses due to weeds in the United States. Weed Science Society, Champaign, IL. US, IL, U.S.
- Briggle, L.W., Curtis, B.C. (1987). Wheat Worldwide. *In* "Wheat and Wheat Improvement", EG Heyne, ed Ed. 2nd. American Society of Agronomy Inc. Publishers (2 more societies), Madison, Wisconsin USA. pp 4-31.
- Brocklehurst, P.A., Moss, J.P., Williams, W. (1978). Effects of irradiance and water supply on grain development in wheat. *Ann Appl Biol* **90**: 265-276.

- CFIA (1999). Regulatory Directive Dir1999-01: The Biology of *Triticum aestivum* L. (Wheat). <http://www.inspection.gc.ca/english/plaveg/bio/dir/dir9901e.shtml>
- Cholick, F.A., Welsh, J.R., Cole, C.V. (1977). Rooting patterns of semi-dwarf and tall winter wheat cultivars under dryland field conditions. *Crop Science* **17**: 637-639.
- Coghlan, A. (2000). So far so good: for the moment, the gene genie is staying in its bottle. *New Scientist* **2231**: 4.
- Colnar, R. (2004). Against the grain? A look at wheat bran.
- D'Souza, L. (1970). Investigations concerning the suitability of wheat as pollen-donor for cross-pollination by wind as compared to rye, Triticale and Secalotricum. *Zeitschrift fur Pflanzenzuchtung* **63**: 246-269.
- de Vries, A.P.H. (1971). Flowering Biology of Wheat, particularly in view of hybrid seed production - A review. *Euphytica* **20**: 152-170.
- Dewey, D. R. (1984). The Genomic Classification as a Guide to Intergeneric Hybridisation with the Perennial Triticeae., Univ of Missouri- Columbia. pp. 209-280.
- Eastham, K., Sweet, J. (2002). Genetically modified organisms (GMOs): The significance of gene flow through pollen transfer. Environmental issue report No. 28, European Environment Agency (EEA), Copenhagen, Denmark, http://reports.eea.eu.int/environmental_issue_report_2002_28/en. pp 1-75.
- Ellstrand, N.C., Prentice, H.C., Hancock, J.F. (1999). Gene flow and introgression from domesticated plants into their wild relatives. *Annual Review of Ecology and Systematics* **30**: 539-563.
- Erayman, M., Sandhu, D., Sidhu, D., Dilbirligi, M., Baenziger, P.S., Gill, K.S. (2004). Demarcating the gene-rich regions of the wheat genome. *Nucleic Acids Research* **32**: 3546-3565.
- Evans, L.T., Bingham, J., Fischer, R.A. (1975). Wheat. In "Crop Physiology" Ed. Evans, L. T. Cambridge Univ Press, Cambridge, pp 101-149.
- Feldman, M. (1979). New evidence on the origin of the B genome of wheat. Ramanujam, S. eds, New Delhi, India. pp. 120-132.
- Feldman, M., Kislev, M. (1977). *Aegilops searsii*, a new species of section Sitopsis (Platystachys). *Israel Journal of Botany* **26**: 190-201.
- FloraBase (2006) Western Australian Herbarium database, <http://florabase.calm.wa.gov.au>, accessed January 2006.
- Fraser, J.S., Ciclitira, P.J. (2001). Pathogenesis of coeliac disease: implications for treatment. *World J Gastroenterol* **7**: 772-776.

- Friebe, B., Kim, N.S., Kuspira, J., Gill, B.S. (1990). Genetic and cytogenetic analysis of the A genome of *Triticum monococcum*. VI production and identification of primary trisomics using the C-banding technique. *Genome* **33**: 542-555.
- Gabor, F., Bogner, E., Weissenboeck, A. Wirth, M. (2003) The lectin-cell interaction and its implications to intestinal lectin-mediated drug delivery. *Advanced Drug Delivery Reviews* **56**:459-480.
- Gale, M.D., King, R.W. (1988). Semi-dwarf genes in Australian wheats. *Agricultural Science* **1**: 18-20.
- Garcia-Llamas, C., Ramirez, M.C., Ballesteros, J. (2004). Effect of pollinator on haploid production in durum wheat crossed with maize and pearl millet. *Plant Breeding* **123**: 201-203.
- Garcke, A. (1972). *Illustrierte flora*. Paul Parey Verlag, Berlin,
- Glover, J. (2002). Canberra, Australia, Gene flow study: Implications for the release of genetically modified crops in Australia. 1-71. Bureau of Rural Sciences.
- Gonzalez, J.M., Bernard, S., Bernard, M. (1993). Metaphase I analysis of *Triticum aestivum* x *T. monococcum* hybrid by the C-banding technique. *Euphytica* **68**: 187-192.
- Greene, A.E., Allison, R.F. (1994). Recombination between viral RNA and transgenic plant transcripts. *Science* **263**: 1423-1425.
- Groves, R.H., Hosking, J.R., Batianoff, D.A., Cooke, D.A., Cowie, I.D., Keighery, B.J., Rozefelds, A.C., Walsh, N.G. (2000). The naturalised non-native flora of Australia: its categorisation and threat to native plant biodiversity. Unpublished report to Environment Australia by the CRC for Weed Management Systems.
- Groves, R.H., Hosking, J.R., Cooke, D.A., Johnson, R.W., Lepschi, B.J., Mitchell, A.A., Moerkerk, M., Randall, R.P., Rozefelds, A.C., Waterhouse, B.M. (2002). The naturalised non-native flora of Australia: its categorisation and threat to agricultural ecosystems. Unpublished report to Agriculture, Fisheries and Forestry Australia by the CRC for Weed Management Systems.
- Guadagnuolo R., Savovabianchi D, Kellersenften J. and Felber (2001) Search for evidence of introgression of wheat (*Triticum aestivum* L.) traits into sea barley (*Hordeum marinum* s. str. Huds.) and bearded wheatgrass (*Elymus caninus* L.) in central and northern Europe, using isozymes, RAPD and microsatellite markers. *Theor Appl Genet* **103**: 191-196.
- Hadjichristodoulou, A., Della, A., Photiades, J. (1977). Effect of sowing depth on plant establishment, tillering capacity and other agronomic characters of cereals. *J Agric Sci* **89**: 161-167.
- Hanson, B.D., Mallory-Smith, C.A., Shafii, B., Thill, D.C., Semetra, R.S. (2005) Pollen-mediated gene flow from blue aleurone wheat to other wheat cultivars. *Crop Science* **45**:1610-1617.

- Harper, B.K., Mabon, S.A., Leffel, S.M., Halfhill, M.D., Richards, H.A., Stewart, C.N.Jr. (1999). Green fluorescent protein as a marker for expression of a second gene in transgenic plants. *Nature Biotechnology* **17**: 1125-1129.
- Hart, A.L. (1987) Physiology. In "White Clover" Baker, M.J. and Williams W.M. eds. CAB International, Wallingford.
- Hartwig, N.R., Barnhart, S.K. (2004). Nitrate Toxicity. <http://www.westwayfeed.com/documents/TechUpdates> .
- Health Canada (2004). Novel food information-food technology. Imidazolinone tolerant wheat. http://www.hc-sc.gc.ca/food-aliment/mh-dm/ofb-bba/nfi-ani/e_imidazolinone_tolerant.
- Hedge, S.G., Waines, J.G. (2004) Hybridization and introgression between bread wheat and wild weedy relatives in North America. *Crop Science* **44**:1145-1155
- Heslop-Harrison, J. (1979). An Interpretation of the hydrodynamics of Pollen. *Am J Botany* **66**: 737-743.
- Holm, L., Pancho, J., V, Herberger, J.P., Plucknett, D.L. (1979). A geographical atlas of world weeds. John Wiley and Sons, Brisbane, Australia.
- Hucl, P. (1996). Out-crossing rates for ten canadian spring wheat cultivars. *Canadian Journal of Plant Science* **76**: 423-427.
- Hucl, P., Matus-Cadiz, M. (2001). Isolation distances for minimizing out-crossing in spring wheat. *Crop Science* **41**: 1348-1351.
- Jacot, Y., Ammann, K., Rufener, P., Mazyad, A., Chueca, C., David, J., Gressel, J., Loureiro, I., Wang, H., Benavente, E. (2004). Hybridization Between Wheat and Wild Relatives, a European Union Research Programme. In "Introgression from Genetically Modified Plants into Wild Relatives", HCM den Nijs, D Bartsch, J Sweet, eds. CAB International, UK. pp 63-73.
- Jain, S.K. (1975). Population structure and the effects of breeding system. In *Crop Genetic Resources for Today and Tomorrow*. In , OH Frankel, JG Hawkes, eds. Cambridge University Press., pp 15-36.
- Johnson, J., Haley, S., Westra, P. (2004). Clearfield* wheat. Colorado State University Cooperative Extension Fact Sheet 3116.
- Kasarda, D.D. (2004). Grains in Relation to Celiac (Coeliac) Disease.
- Keeler, K.H. (1989). Can genetically engineered crops become weeds? *Bio/Technology* **7**: 1134-1139.
- Keeler, K.H., Turner, C.E., Bolick, M.R. (1996). Movement of crop transgenes into wild plants. In "Herbicide resistant plants", SO Duke, ed. CRC Press Inc., pp 303-330.

- Kimber, G.K., Sears, E.R. (1987). Evolution of the genus *Triticeae* and origin of cultivated wheat. In "Wheat and wheat improvement", EG Heyne, ed. second. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc., Madison, Wisconsin, USA. pp 154-164.
- Kirby, E.J.M. (1974). Ear development in spring wheat. *J Agric Sci* **82**: 437-447.
- Kirby, E.J.M. (1983). Development of the cereal plant. In "The yield of cereals", WW D, ed. Royal Agriculture society of England, London. pp 1-3.
- Kirby, E.J.M., Appleyard, M., Fellows, G. (1983) Leaf emergence and tillering in wheat. Report, 1982 Plant Breeding Institute, Cambridge. pp. 114-116.
- Kirby, E.J.M., Appleyard, M. (1981). Cereal development guide. National Agricultural center Cereal Unit, Stoneleigh, UK,
- Kirby, E.J.M. (2002). Botany of the wheat plant. In "Bread wheat. Improvement and Production", BC Curtis, S Rajaram, H Gomez Macpherson, eds. Food and Agriculture Organisation, Rome.
- Klepper, B., Belford, R.K., Rickman, R.W. (1984). Root and shoot development in winter wheat. *Crop Science* **76**: 117-122.
- Knobloch, I.W. (1968). A checklist of crosses in the Gramineae. New York.
- Komatsuzaki, M., Endo, O. (1996). Seed longevity and emergence of volunteer wheat in upland fields. *Weed Research, Japan* **41**: 197-204.
- Korber-Grohne, U. (1988). Nutzpflanzen in Deutschland-Kulturgeschichte und Biologie. Theiss Verlag, Stuttgart, Germany.,
- Lai, M.M.C. (1992). RNA recombination in animal and plant viruses. *Microbiological Reviews* **56** (1): 61-79.
- Laurie, D.A., Bennett, M.D. (1988). Cytological evidence for fertilisation in hexaploid wheat x sorghum crosses. *Plant Breeding* **100**: 1063-1067.
- Lawrence, J.G., Ochman, H. (1998). Molecular archaeology of the *Escherichia coli* genome. *Proceedings of the National Academy of Sciences of the United States of America* **95**: 9413-9417.
- Lelley, J. (1966). Observations on the biology of fertilisation with regard to seed production in hybrid wheat. *Die Zuchter* **36**: 314-316.
- Lersten, N.R. (1987). Morphology and Anatomy of the Wheat Plant. In "Wheat and Wheat Improvement", EG Heyne, ed. 2nd. American Society of Agronomy, Inc. Crop Science Society of America Inc. Soil Science Society of America, Inc. Publishers., Madison, Wisconsin, USA. pp 33-71.

- Li, D., Qio, P., Ouyang, Q., Yao, Q.X., Dawei, L.D., Jiwen, Q., Ping, O., Qingxiao, Y. (1996). High frequencies of fertilisation and embryo formation in hexaploid wheat X *Tripsacum dactyloides* crosses. *Theor Appl Genet* **92**: 1103-1107.
- Li, W., P.Zhang, Fellers, J.P., Friebe, B., Gill, B.S. (2004). Sequence composition, organization, and evolution of the core Triticeae genome. *The Plant Journal* **40**: 500-511.
- Lupton, F.G.H., Oliver, F.B., Ellis, B.T., Barnes, K.R., Howsw, P.J., Wellbank, P.J., Taylor, P.J. (1974). Root and shoot growth of semi-dwarf and taller winter wheats. *Ann Appl Biol* **77**: 129-144.
- Maan, S.S. (1987). Interspecific and Intergeneric Hybridisation in Wheat. In "Wheat and Wheat Improvement", EG Heyne, ed. American Society of Agronomy, Madison. pp 453-461.
- Mackay, M.C. (1983). 'Torres'. *Jnl Aust Inst Ag Sci* **49**: 47.
- Mackay, M.C. (1984a). 'Skua'. *Jnl Aust Inst Ag Sci* **50**: 252.
- Mackay, M.C. (1984b). 'Sundor'. *Jnl Aust Inst Ag Sci* **50**: 253.
- Mackay, M.C. (1987). 'Vasco'. *Jnl Aust Inst Ag Sci* **53**: 54.
- Mackey, J (1973). The wheat root. Sears, E. R and Sears, L. M. S eds, Columbia. 4th Int. Wheat Genet. Symp., columbia MO, University of Missouri. pp. 827-842.
- Mallory-Smith, C.A., Hansen J., Zemetra, R.S. (1996) Gene transfer between wheat and *Aegilops cylindrica* p.441-445. In Proc. 2nd Int. Weed Control Congress, Copenhagen, Denmark. Published by Dept. Weed control and Pesticide Ecology, Copenhagen.
- Mandy, G. (1970). Pflanzenzuchtung-kurz und bundig. VEB deutscher Landwirtschaftsverlag, Berlin,
- Martin, T.J. (1990). Out-crossing in twelve hard red winter wheat cultivars. *Crop Science* **30**: 59-62.
- Matus-Cadiz, M.A., Hucl, P., Horak, M.J., Blomquist, L.K. (2004). Gene flow in wheat at the field scale. *Crop Science* **44**: 718-727.
- Mayo, M.A., Jolly, C.A. (1991). The 5'-terminal sequence of potato leafroll virus RNA: evidence of recombination between virus and host RNA. *Journal of General Virology* **72**: 2591-2595.
- McFadden, E.S., Sears, E.R. (1946). The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *Journal of Heredity* **37**: 81 and 107-89 and 116.
- Munns, R. (2004) Wild grass helping salinity. Farming Ahead, CSIRO Publishing, No.153, http://www.clw.csiro.au/publications/farming_ ahead/2004/38%20FA%20OCTOBER%202004_153.pdf
- Nath, J., McNay, J.W., Paroda, C.M., Gulati, S.C. (1983). Implication of *Triticum searsii* as the B-benome donor to wheat using DNA hybridisations. *Biochemical Genetics* **21**: 745-760.

Newman (1990). Pollen transfer from transgenic plants: Concept for risk assessment and data requirements.

Nielsen, K.M. (1998). Barriers to horizontal gene transfer by natural transformation in soil bacteria. *APMIS* **106**: 77-84.

Nielsen, K.M., Gebhard, F., Smalla, K., Bones, A.M., van Elsas, J.D. (1997). Evaluation of possible horizontal gene transfer from transgenic plants to the soil bacterium *Acinetobacter calcoaceticus* BD 413. *Theoretical and Applied Genetics* **95**: 815-821.

Nielsen, K.M., van Elsas, J.D., Smalla, K. (2000). Transformation of *Acinetobacter* sp strain BD413(pFG4 Delta nptII) with transgenic plant DNA in soil microcosms and effects of kanamycin on selection of transformants. *Applied and Environmental Microbiology* **66**: 1237-1242.

Ochman, H., Lawrence, J.G., Grolsman, E. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature* **405**: 299-304.

OECD (1999). Consensus Document on the Biology of *Triticum aestivum* (Bread Wheat). ENV/JM/MONO(99)8, Environment Directorate; Organisation for Economic Co-operation and Development, Paris, France. [http://www.olis.oecd.org/olis/1999doc.nsf/LinkTo/env-jm-mono\(99\)8](http://www.olis.oecd.org/olis/1999doc.nsf/LinkTo/env-jm-mono(99)8)

OECD (2003). Consensus Document on Compositional Consideration for New Varieties of Bread Wheat (*Triticum aestivum*): Key Food and Feed Nutrients, Anti-nutrients and toxicants. ENV/JM/MONO(2003)7, Environment Directorate; Organisation for Economic Co-operation and Development, Paris, France.

Panetta, F.D. (1993). A system of assessing proposed plant introductions for weed potential. *Plant Protection Quarterly* **8**: 10-14.

Patrick, J.W. (1972). distribution of assimilate during stem elongation in wheat. *Australian Journal of Biological Sciences* **25**: 455-467.

Pheloung, P.C. (1995). Determining the weed potential of new plant introductions in Australia. Department of Agriculture, Perth, Australia.

Pickett, A.A. (1989). A review of seed dormancy in self-sown wheat and barley. *Plant Varieties and Seeds* **2**: 131-146.

Pickett, A.A. (1993). Cereals: seed shedding, dormancy and longevity. *Aspects of Applied Biology* **35**: 17-28.

Poehlmann, M. (1959). Breeding of field crops. Henry Holt and Company, New York,

Pomeranz, Y. (1987). Modern Cereal Science and Technology. VCH Publishers Inc.,

Sandhu, D., Gill, K.S. (2004). Gene-Containing Regions of Wheat and Other Grass Genomes. *Plant Physiology* **128**: 803-811.

- Sarkar, P., Stebbins, G.L. (1956). Morphological evidence concerning the B genome of wheat. *American Journal of Botany* **43**: 297-304.
- Schlüter, K., Fütterer, J., Potrykus, I. (1995). Horizontal gene transfer from a transgenic potato line to a bacterial pathogen (*Erwinia chrysanthemi*) occurs - if at all - at an extremely low frequency. *Bio/Technology* **13**: 1094-1098.
- Schoelz, J.E., Wintermantel, W.M. (1993). Expansion of viral host range through complementation and recombination in transgenic plants. *The Plant Cell* **5**: 1669-1679.
- Sears, E.R. (1954). The aneuploids of common wheat. *Missouri Agricultural Experimental Research Station Bulletin* **572**:
- Sears, E.R. (1966). Nullisomic-tetrasomic combinations in wheat. In "Chromosome Manipulation and Plant Genetics", R Riley, KR Lewis, eds. Oliver and Boyd, Edinburgh. pp 29-45.
- Simmonds, D.H. (1989). Wheat and wheat quality in Australia. CSIRO Australia, Queensland.
- Simmonds, N.W. (1986). Principles of crop improvement. second edition. Longman Science and Technology, New York.
- Simmons, S.R. (1987). Growth, development, and Physiology. In "Wheat and Wheat Improvement", EG Heyne, ed Ed. 2. ASA Inc, CSSA, Inc and SSS of America Inc., Madison Wisconsin, USA. pp 77-104.
- Sims, H.J. (1990). Grain crops. In "The manual of Australian Agriculture", RL Reid, ed. Butterworths Pty Ltd, pp 1-894.
- Singh, P., Chatterjee, S., Pathania, R., Bhullar, S.S. (1999). Enhanced wheat germ agglutinin accumulation in the germinating embryos of wheat (*Triticum aestivum* L.) appears to be a general stress response. *Current Science (Indian Academy of Science)* **76**: 1140-1142.
- Smith, E.L., Schlehuber, A.M., Young Jnr, H.C., Edwards, L.H. (1968). Registration of 'Agent' wheat. *Crop Science* **8**: 511-512.
- Sukopp, U., Sukopp, H. (1993). Das Modell der Einführung und Einbürgerung nicht einheimischer Arten. *Arten GAIA* **5**: 268-288.
- Syvanen, M. (1999). In search of horizontal gene transfer. *Nature Biotechnology* **17**: 833.
- Tsunewaki, K (1988). Cytoplasmic variation in *Triticum* and *Aegilops*. In "Proceedings of the Seventh International Wheat genetics Symposium", Miller, T. E. and Koebner R. M. D. eds, Institute of Plant Science Research, Cambridge, U.K. pp. 53-62.
- Tsunewaki, K (1991). A historical review of cytoplasmic studies in wheat. In "Nuclear and organellar genomes of wheat species.", pp. 16-30.
- Varughese, G., Pfeiffer, W.H., and Pena, R.J. (1997). Triticale: A Reappraisal.

- Waines, J.G., Hedge, S.G. (2003). Intraspecific gene flow in bread wheat as affected by reproductive biology and pollination ecology of wheat flowers. *Crop Science* **43**: 451-463.
- Wardlaw, I.F., Moncur, L. (1995). The response of wheat to high temperature following anthesis: I The rate and duration of kernel filling. *Aust J Plant Physiol* **22**: 391-397.
- Wardlaw, I.R. (1970). The early stages of grain development in wheat: Responses to light and temperature in a single variety. *Aust J Biol Sci* **23**: 765-774.
- Western Australian Department of Agriculture (2004). Endemic wheat threats of economic importance Vertebrates.
- Wicks, C.L., Felton, W.L., Murison, R.D., Martin, R.J. (2000). Changes in fallow weed species in continuous wheat in northern New South Wales, 1981-90. *Aust J Exp Agric* **40**: 831-842.
- Wilson, J.A. (1968). Problems in hybrid wheat breeding. *Euphytica* **17**: 13-34.
- Wilson, J.A., Ross, W.M. (1962). male sterility interaction of *Triticum aestivum* and *Triticum timopheevii* cytoplasm. *Wheat Information Service* **14**: 29-31.
- Worobey, M., Holmes, E.C. (1999). Evolutionary aspects of recombination in RNA viruses. *Journal of General Virology* **80**: 2535-2543.
- Yaremcio, B. (1991). Nitrate poisoning and feeding nitrate feeds to livestock. Alberta Agriculture Food and Rural Development.
- Zemtra, R.S., hansen, J., Mallory-Smith, C.A. (1998). Potential for gene transfer between wheat (*Triticum aestivum*) and jointed goatgrass (*Aegilops cylindrica*). *Weed Science* **46**: 313-317.