Australian Government

Department of Health and Ageing
Office of the Gene Technology Regulator

The Biology of
Triticum aestivum L. em Thell. (Bread Wheat)

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This document provides an overview of baseline biological information relevant to risk assessment of genetically modified forms of the species that may be released into the Australian environment.

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PREAMBLE

This document describes the biology of *Triticum aestivum* L. em Thell. (bread wheat), with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *T. aestivum*, general descriptions of its morphology, reproductive biology, development, biochemistry, biotic and abiotic interactions. This document also addresses the potential for gene transfer to occur to closely related species. The purpose of this document is to provide baseline information about the parent organism in risk assessments of genetically modified *T. aestivum* that may be released into the Australian environment.

In Australia, the majority of wheat grown is *T. aestivum* and its cultivars. The other wheat species grown in Australia is *Triticum turgidum* ssp. *durum* L, also know as durum or pasta wheat. The terms 'wheat' and 'bread wheat' will be used as general terms to refer to *T. aestivum*.

Bread wheat is an annual grass generally grown in Australia as a rotation crop. The varieties grown in Australia are spring wheat varieties although they are grown during the winter growing season and harvested in early summer. Bread wheat is the most widely grown food crop in the world and Australia is one of the four major exporters of wheat in the world.

SECTION 1   TAXONOMY

Triticum aestivum L. em Thell. is recorded in the National Center for Biotechnology Information Taxonomy Browser as belonging to the family Poaceae (BEP clade), subfamily Pooideae and tribe Triticeae. It has the recorded synonyms *Triticum aestivum* L., *Triticum vulgare, Triticum aestivum* subsp. *aestivum* and the common names, wheat, bread wheat and common wheat (NCBI Taxonomy Browser). The scientific and common names which will be used throughout this document are defined in the Preamble.

Bread wheat is an allohexaploid (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 homologue in each of the other 2 genomes.

This homology 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.). 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 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 *Aegilops tauschii* (Coss.) Schmal. (formerly *Triticum tauschii or Aegilops squarossa*). 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 1.

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

The specific identity of the B genome donor remains unclear. It was originally proposed that the B genome donor was based upon *Aegilops speltoides* (Tausch) (Sarkar & Stebbins 1956). Feldman (1979) concluded that *Triticum 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 *Triticum searsii* was the possible source of the B genome after studying several likely progenitors with DNA hybridisations. It now seems probable that the original B genome donor of wheat no longer survives in the wild but was probably a member of the Sitopsis section of the triticeae most closely related to *Aegilops speltoides*. The origin and taxonomy of cultivated wheat have be recently reviewed by Feuillet et al. (2007).

Worldwide, two 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. The second, *T. turgidum* ssp. *durum*, includes the durum and red durum wheat classes (macaroni or pasta 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.

SECTION 2   ORIGIN AND CULTIVATION

2.1   Centre of diversity and domestication

The domestication of diploid and tetraploid wheat is thought to have occurred in the fertile crescent of the Middle East. Domestication of the diploid and tetraploid wheat is thought to have occurred at least nine thousand years ago with the hybridisation event producing hexaploid wheat occurring more than six thousand years ago (Simmons 1987; Feuillet et al. 2007).

Table 1. 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
Triticum boeoticum L.		14	A	*T. zhukovskyi* Men & Er.		42	A.A.G
Aegilops speltoides	*T. speltoides*	14	S	*T. timopheevii* (Zhuk.) Zhuk.	*T. araraticum*	28	A.G
Aegilops tauschii	*T. tauschii,* *Ae. squarrosa*	14	D	*T. crassum* (4x) (Boiss.) Aitch. & Hensl.	*Aegilops crassa*	28	D.M
T. bicorne Forsk.	*Ae. bicornis*	14	S^b	*T. ventricosum* Ces.	*Ae. ventricosa*	28	D.Un
T. longissimum (Schweinf. & Muschli in Muschli) Bowden	*Ae. longissima*		S^l	*T. crassum* (6x) (Boiss.) Aitch. & Hensl.	*Ae. crassa*	42	D.D.M
T. searsii (Feldman & Kislev) Feldman, comb. nov.		14	S^s	*T. syriacum* Bowden	*Ae. crassa* ssp. *vavilovii*	42	D.M.S
T. tripsacoides (Jaub & Spach) Bowden	*Ag. mutica*	14	Mt	*T. juvenile* Thell.	*Ae. juvenalis*	42	D.M.U
T. comosum (Sibth. & Sm.) Richter	*Ae. comosa*	14	M	*T. kotschyi* (Boiss.) Bowden	*Ae. kotschyi*	28	U.S
T. uniaristatum (Vis.) Richter	*Ae. uniaristata*	14	Un	*T. ovatum* (L.) Raspail	*Ae. ovata*	28	U.M
T. dichasians (Zhuk.) Bowden	*Ae. caudata*	14	C	*T. triaristatum* (4x) (Willd.) Godr. &Gren.	*Ae. triaristata*	28	U.M

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

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2.2 Commercial uses

Bread wheat is the most widely grown food crop in the world. In 2003/04 the total world production of wheat was 553.92 million tonnes compared to 391.19 million tonnes of milled rice (Food and Agriculture Service (FAS) of the USDA 2005). In the same time period Australia produced 24.9 million tonnes of wheat and exported 15.2 million tonnes (Australian Wheat Board 2007a). World wheat production doubled during the 25 year period to 1984-85 (Briggle & Curtis 1987) and in absolute terms, more than half of this increase occurred in the developed world.

Australia is considered one of the four leading exporters of wheat with exports averaging 17 million tonnes per annum over the five years from 2001-06 (Australian Wheat Board 2007b). This level of export can be achieved due to the relatively low demand of the domestic market.

The consumption of wheat products is long-standing in developed countries while in developing countries wheat consumption is increasing. The consumption of wheat in developing countries increased by 73% in the 10 year period 1972-82 (Briggle & Curtis 1987). In the period 1996/97 developing countries utilized (for food, feed and other uses) 330 million tonnes of wheat while developed countries used 248 million tonnes in the same period (Food and Agriculture Organization of the United Nations 1998).

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 or seitan (used as an alternative to soy based products in vegetarian cooking).

Other than its primary use as a human food source wheat has a number of alternative uses in Australia and around the world. These include, but are not limited to, use in animal feed, conversion of wheat starch to ethanol, brewing of wheat beer, the production of wheat based cat and pet litter, wheat based raw materials for cosmetics, wheat protein in meat substitutes and to make wheat straw composites.

The feed wheat class in Australia has in the past been classified as sprouted wheat suitable for feed (Simmonds, 1989). However, wheat use in the domestic animal feed market increased between 1995 and 2000 and the increase was forecasted to continue. The increase in demand of feed wheat has lead to the introduction of specialty feed wheat lines in Australia. The main consumers of feed wheat in Australia are the pig and poultry industries, the beef feedlot industry and the dairy industry. Wheat stubble is also used as feed for sheep and fodder wheats are grown in Australia for hay and chaff production and for livestock grazing (Rowland & Perry 2000; Impiglia et al. 2000). In the USA, only 10% of wheat produced goes to livestock feed (Kansas Wheat 2007) due to competition from corn prices. As well as livestock feed, wheat is also used to a limited degree by the US poultry and fish industries which use grain and middlings (the leftovers from flour milling) as feed (Sparks, 2002).

Conversion of wheat to ethanol is currently undertaken by extracting the starch from grains which is then hydrolysed to glucose or sucrose. The sugar is then fermented to

produce ethanol and carbon dioxide (Sparks, 2002). Ethanol production from wheat occurs to a limited but increasing degree in Australia. One main producer was providing ethanol blended fuel to service stations in 2005 (Thyer 2005). Plans for five bio-fuel plants across Australia have been announced by one enterprise with their first ethanol plant due to be operational in Victoria in 2009. Grain crops will be used as a feedstock for the plant (Media-Newswire.com 2007). In the USA, ethanol is also produced from wheat although this production is limited as corn is the preferred source of plant material (Sparks, 2002). Wheat is also used in the production of biofuels in Europe. France is considered the largest producer of biofuels in Europe and converted 13,885 ha of wheat to ethanol and ethyl tertio butyl ester (ETBE; added to high octane petrol) in 2001 (Kotati & Henard 2001). In Canada, research is currently under way into alternative methods for producing bio-ethanol from the cell walls of wheat stalks (Thyer 2005).

2.3   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.

2.3.1   Commercial propagation

In Australia, wheat planted for commercial seed production may have restrictions on how it is grown in the field depending on its classification. Classification classes include certified, basic and pre-basic. Restrictions may include what was previously grown in the field and separation of the crop from other cereal crops (Smith & Baxter 2002). These standards are designed to reduce contamination with seed from other sources in the final certified seed. Standards also set out the allowed contaminant levels in the seed after harvest.

The standards in use by the Australian Seeds Authority Ltd were designed to comply with the OECD Seed Certification Guidelines (Australian Seeds Authority Ltd. 2006). For wheat seed to be classified as either basic or certified seed the wheat plants must be separated from other cereal plants by at least a 2 m strip in which no cereal plants are grown or a physical barrier to stop seed mixture at harvest. Controls on previous uses of the field also exist and include, the field must not have been used to grow the same species for the two previous years and no cereal species is allowed to be grown on the field in the year proceeding certified or basic seed production (Smith & Baxter 2002).

2.3.2   Scale of cultivation

Yields in Australia have improved substantially, through the introduction of semi-dwarf genes and improved resistance to diseases. However, drought conditions are a frequent impediment to maximised production. In Western Australia, the wheat belt underwent a significant expansion over the period 1961 to 1990 and has increased in area from 2.275 million ha (10 year average 1961-70) to 4.174 million ha (10 year average 1981-90) (Australian Wheat Board 2007a).

A substantial increase in wheat production started in the mid-1950s and continues (Table 2). The wheat growing areas of Australia (wheat belt) are shown in Figure 1. See Section 6.1 for a discussion of factors limiting the growth of wheat plants.

Table 2. Wheat production statistics for Australia, 1939-2005[1] (Australian Wheat Board 2007a).

Period	Average area (1000 ha)[2]	Average yield (tonnes/ha)	Average production (1000 tonnes)
1939-50	4596	0.86	3962
1951-60	3907	1.22	4754
1961-70	7681	1.23	9415
1971-80	8734	1.30	11361
1981-90	11174	1.30	15022
1991-2000	8688	1.76	17254
2001-05	11980	1.71	20609

[1]For 10 year periods data averages determined in reference, for the period 2001-05 averages calculated from available data in reference.
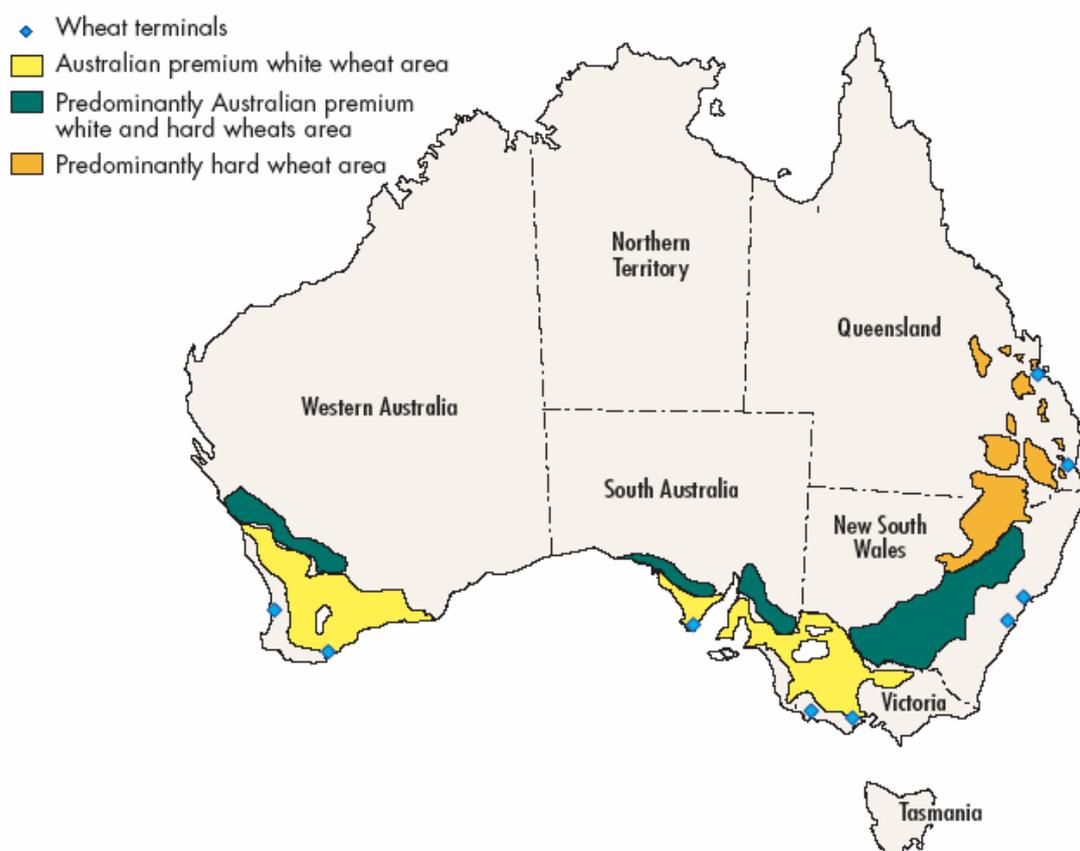[2]All data refer to Australia wide averages.

Figure 1. The wheat growing areas of Australia which make up the Australian wheat belt (ABARE 2007).

2.3.3   *Cultivation practices*

In Australia, spring wheat varieties of bread wheat are grown as a winter crop. True winter wheats require a period of cold stimulus (vernalisation) to initiate floral development. However, 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.

Soil types in the Australian wheat growing areas vary from heavy, deep clays in northern New South Wales (NSW) and southern Queensland, to very light and sandy soils in Western Australia (WA; Simmonds 1989). This results in different wheat varieties being grown in different areas of the Australian wheat belt resulting in different grain protein contents and quality grades (Simmonds 1989). The different wheat classes grown in different areas of the Australian wheat belt can be seen in Figure 1.

Planting time is determined by soil moisture availability. Sowing depth depends on soil moisture, as seeds should be sown into moist soil. Typically wheat would be sown to a depth of about 3 to 5 cm. Deeper sowing delays emergence and can result in weaker seedlings which are poorly tillered (Jarvis et al. 2000). 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).

It was once common to cultivate the field prior to seeding, but more farmers are opting for no-till or low-till practices which can help to conserve moisture and improve soil structure, reduce erosion, increase yields and in some cases decrease disease. There are a number of tillage systems in use and no one system is ideal for all soils and situations (Jarvis et al. 2000).

There are a number of pests and diseases of wheat, which may require management (eg application of herbicide or pesticide) during the growing season. Weed control using specific classes of herbicides usually involves both a pre- or post-emergence application (Jarvis et al. 2000). Weed control or the losses from weed contamination in the harvested crop can be the most significant cost in wheat production (Bowran 2000). The aim of weed control in the field before wheat is sown is to control winter active weeds while the weeds are small. Glyphosate is recommended as it is a broad knock down herbicide as are paraquat and diquat. The differences between the recommended pre-emergence, early post-emergence and late post-emergence herbicides reflect the differing developmental stages of the crop. For an overview of recommended herbicides and application times (see Bowran 2000).

The recommended method of control for annual grass weeds in wheat crops in northern NSW and southern Queensland is the use of rotation cropping. Sowing of a summer crop such as sorghum or a winter grain legume is recommended (Laffan 1999). It was also suggested by the author that shallow cultivation to stimulate seed germination and then use of a knockdown herbicide is a useful method of weed control. Rowland and Perry (2000) suggest a legume rotation system would improve the control of grass weeds.

The application of glyphosate based herbicides is considered a cost effective method of controlling small weeds, prior to seeding of the crop. Animal grazing or the use of

a 'hot burn' are also considered valuable control measures for weed reduction (Bowran 2000).

Time of harvest depends on grain moisture content. In the northern parts of the wheat belt harvest occurs in October-November and in December in the southern regions. Sims (1990) noted that in the cooler regions of the wheat belt harvest can continue into February. Wheat can be harvested when the moisture content is between 10 and 20% (Jarvis et al. 2000).

Rotation cropping in wheat farming systems is not only used as a weed control strategy but also has a number of other benefits. These benefits include increased pest and disease control improved soil structure and nutrient availability (Rowland & Perry 2000). The use of a legume rotation crop improves soil fertility through nitrogen fixation and improved nutrient availability in the soil. The use of pasture rotations with wheat crops has declined however they are still useful in areas where the yield of an alternative rotation crop may be poor (Rowland & Perry 2000). Canola is also considered a beneficial rotation crop in the Australian wheat belt as its inclusion in the farming system provides an opportunity to reduce disease occurrence in the field and to adopt the use of alternative weed control measures (Rowland & Perry 2000).

2.4   Crop Improvement

2.4.1   *Breeding*

A number of methods are used to generate new wheat lines through breeding. These include mutation breeding, hybrid wheat production using chemicals to induce male sterility or mechanical methods to remove anthers. The single seed descent method is also used for the rapid production of inbred lines (Lucken 1987; Konzak 1987; Knott 1987; Simmonds 1989).

The production of hybrid wheats using manual male sterilisation usually occurs in the controlled environment of a glasshouse. The first step involves the removal of the awns from the developing wheat head followed by the removal of the anthers from the female parent plants. The anthers from the male parent plants can then be manually brushed against the stigmas of the receptive female parent plants producing the controlled generation of hybrid seed (Simmonds 1989).

Hybrid wheat seed can also be produced using wheat plants that have been treated with a chemical hybridizing agent before anthesis to generate male sterile plants. The male and female (chemically treated) parent plants can then be planted in alternating rows in the field and the female parents wind pollinated. The disadvantage of this method over using a genetic system to control male fertility is the need to apply a chemical agent in the field (Lucken 1987).

Mutation breeding is a complementary method to traditional wheat breeding techniques and utilises methods to induce mutations, usually in the seed. These include exposure of seeds to chemical mutagens or ionizing radiation and treatment of pollen with ultraviolet radiation (Konzak 1987).

Single seed descent is a method used to rapidly select inbred lines with desirable characteristics. A single seed is taken from each plant, usually starting at the F_2

generation, and used to produce the next generation. It is reported that, while the distribution of traits across the lines varies greatly in the F_2 generation, the lines become more similar by the F_6 generation (Knott 1987). This method can be used by breeders to reduce the number of plants propagated in the early generations before testing of the lines begins.

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. Quality characteristics of different Australian wheat classes are described in Table 3. Other characteristics selected for in wheat breeding include reduced height of plants, nuclear male sterility and other advantageous alterations to plant physiology (Konzak 1987).

Table 3. Australian wheat classes[1].

Wheat class	Protein (%)	Dough strength	Grain quality	End use
Australian prime hard	>13	High	Hard, excellent milling qualities	Bread, high protein flour
Australian hard	>11.5	Good	Good milling and good dough qualities	Bread
Australian standard white (ASW)	10-12	Varies because of range of collection sites	Varies because of range of collection sites	Bread, chinese noodles
Australian soft	8.4	Weak	Low protein, weak extensible doughs	Biscuit wheat
Australian general purpose	N/A[2]	N/A	Grain that has failed standards tests for milling quality, due to foreign material, weed seed content, etc.	N/D[3]
Australian feed	N/A	N/A	Usually severely sprouted grain.	Animal feed

[1]Information tabulated from (Simmonds 1989). [2]N/A, not applicable. [3]N/D, not defined.

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 *Rht*1. Cultivars 'Hartog' (Pavon 76), 'Suneca' and 'Kite' selections carried the semi-dwarfing *Rht*2 gene.

Wheat-alien translocations involve the transfer of chromosomal material between wheat chromosomes and their wild wheat or alien homologues. Wild wheats have provided an important source of new disease resistance in wheat breeding. The 'Agent' source of resistance has provided both leaf rust (*Lr*24) and stem rust resistance (*Sr*24) genes to bread wheat. This was a spontaneous translocation between chromosome 3D of hexaploid wheat and the alien homologue derived from *Thinopyrum ponticum*

(Smith et al. 1968). The modified translocation, 3*Ag*#3, providing resistance to rust in wheat is present in cultivar (cv.) 'Torres' (Mackay 1983). Another modified translocation, 3*Ag*#14, also providing rust resistance is present in cultivars 'Skua', 'Sundor' and 'Vasco' (Mackay 1984a; Mackay 1984b; Mackay 1987).

Wheat carrying a mutation to the acetohydroxyacid synthase (*AHAS*) gene, which confers tolerance to imidazolinone herbicides, has been developed using chemical mutagenesis (Canadian Food Inspection Agency 1999). This spring wheat variety was developed using the chemical mutagen sodium azide against the cultivar 'Fidel' followed by crossing and back crossing of the selected line to the cultivar 'Grandin'. The resulting spring wheat line is not affected by treatment with an imidazolinone herbicide at normal field application rates (Canadian Food Inspection Agency 1999).

Another imidazolinone tolerant line of wheat was developed using the chemical mutagens ethylmethane sulfonate and diethyl sulfate on the seeds of the American variety 'Gunner'. The tolerance to imidazolinone herbicides in this line was again the result of a mutation to AHAS, in this case a single amino acid substitution (Canadia Food Inspection Agency 2004).

Comprehensive reviews of plant breeding methodologies, including for wheat, 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.

2.4.2   Genetic modification

There has been recent progress on genetic modification techniques for use with wheat. These include particle bombardment and *Agrobacterium* mediated transformation (Bhalla et al. 2006). Particle bombardment has been used to develop successful transformants of both *T. aestivum* and *T. durum*, although this technique can result in several undesirable events including the insertion of multiple copies of the transgene (Bhalla et al. 2006). The authors suggest that *Agrobacterium* mediated transformation is now a viable alternative to particle bombardment, the technology having overcome the initial problems encountered when it was applied to wheat and other cereals (see also Shrawat & Lorz 2006). *Agrobacterium* transformation methods have the benefit of introducing a single or a low copy number of genes into the genetically modified (GM) plant.

Both *Agrobacterium* mediated transformation and particle bombardment in cereals is limited by a number of factors (Bhalla et al. 2006). The authors suggest that the choice of cultivar and explant type are two of the main factors affecting successful generation of GM wheat. Cultivar choice can affect the success of callus induction and plant regeneration while the use of explants derived from mature embryos can help reduce the time needed to generate explant material (Bhalla et al. 2006). The ability of *Agrobacterium* strains to infect wheat is a problem with this technique (Shrawat & Lorz, 2006).

To date three applications involving GM wheat lines have been approved for limited and controlled release in Australia under the Gene Technology Act 2000. These are GM wheat field trials testing salt tolerance (DIR 053/2004), altered starch

(DIR 054/2004) and drought tolerance (DIR 071/2006) (http://www.ogtr.gov.au/gmorec/ir.htm#table). Additionally, there have been five field trials of GM wheat in Australia under the former voluntary system that was overseen by the Genetic Manipulation Advisory Committee (GMAC; http://www.ogtr.gov.au/volsys/infosheets.htm).

The Canadian Food Inspection Agency (CFIA) website lists field trials of plants with novel traits including 13 field trials for 2005 and 38 trials for 2004 testing herbicide, fungal or other disease resistance genes in GM bread or durum wheat (http://www.inspection.gc.ca/english/plaveg/bio/confine.shtml). There have also been releases of GM wheat in Europe and the USA with traits such as fungal resistance and novel protein production being trialled (http://gmoinfo.jrc.it/gmp_browse.aspx; http://www.aphis.usda.gov/biotechnology/status.shtml.)

SECTION 3   MORPHOLOGY

3.1   Plant morphology

3.1.1   The Stem

The mature wheat plant consists of a central stem from which leaves emerge at opposite sides (Figure 2). It is made up of repeating segments, called phytomers, which contain a node, a hollow internode, a leaf and a tiller bud found in the axil of the leaf (Kirby 2002). The leaf sheath wraps around the stem providing support to the shoot (Setter & Carlton 2000). The stem terminates in the ear of the wheat plant.
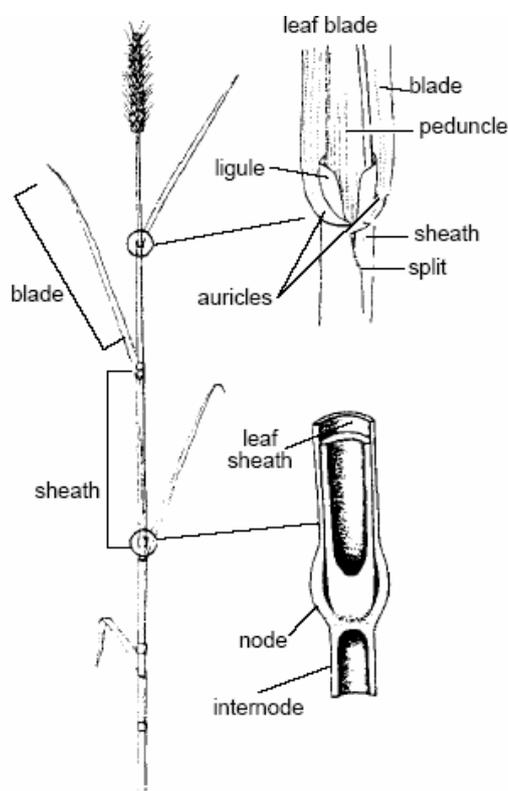

Figure 2: The stem and leaf structure of a mature wheat plant. Reproduced in original form with permission from (Setter & Carlton 2000).

3.1.2   The Leaf

The leaf structure consists of the sheath and the leaf blade which form from separate meristems (Figure 2). At the base of the leaf blade, where it joins the sheath, are a set of structures called the ligule and auricles (Kirby 2002). Leaves are produced on alternative sides of the stem and are numbered so that all even numbered leaves are on one side of the plant (Setter & Carlton 2000). The length of leaves increases from the base until one or two leaves before the flag leaf, in spring wheat varieties (Kirby 2002).

The leaf tissue is made up of three tissue types. The cell types making up the epidermis differ on either side of the leaf with the epidermis on the underside of the leaf having fewer cell types. Both epidermal layers are covered with an epicuticular wax. The mesopyll is enclosed by the epidermal layers and transected by the vascular tissue (Kirby 2002).

3.1.3   Tillers

Tillers are lateral branches which are produced off the main stem of the wheat plant (Kirby 2002). They produce leaves on opposite sides of their central stem in the same manner as the leaves of the main stem are produced and are also able to produce an ear at their terminal (Setter & Carlton 2000). Not all tillers will survive and produce an ear and this is thought to be due to competition for light and nutrients (Kirby 2002).

3.1.4   The Roots

A mature wheat plant has two distinct root types. The seminal roots develop from the root primordia contained within the grain and are the first root type to emerge (Perry & Belford 2000; Kirby 2002). The nodal roots emerge at the same time that tiller development starts (Kirby 2002).

3.2   Reproductive morphology

3.2.1   The Ear

The ear of a wheat plant is made up of two rows of spikelets (Figure 3). The spikelets contain the florets and are arranged on opposite sides of a central rachis (Setter & Carlton 2000) in a similar manner to the arrangement of the leaves on the central stem. The florets are enclosed by a lemma and a palea and are composed of the carpel (the ovary and the stigmas) and three stamen and anthers (Setter & Carlton 2000). Each anther consists of four loculi enclosing the pollen grains (Kirby 2002).

Each lobe of an anther contains a cylindrical column of microspore mother cells. These columns are each surrounded by a nutritive layer, the tapetum (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 isolates 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.
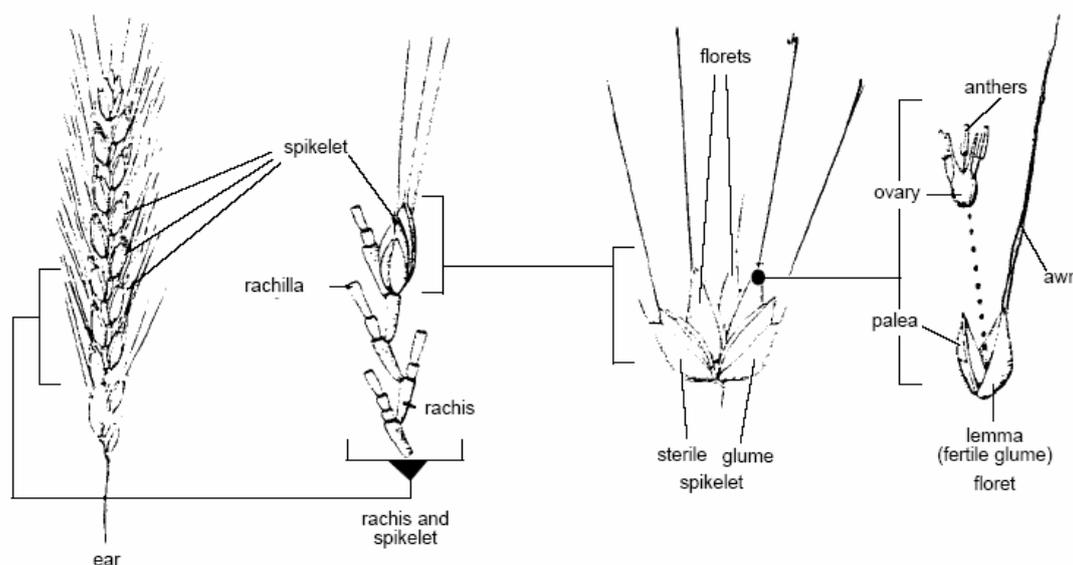
Figure 3: The structure of the wheat ear showing the structure of the spikelets and florets. Reproduced in original form with permission from (Setter & Carlton 2000).

3.2.1   *The Caryopsis*

The caryopsis or grain of the wheat plant is made up of the bran coat and the endosperm surrounding the embryo (Setter & Carlton 2000). The bran coat consists of three layers, the pericarp, testa and aleurone. The endosperm makes up 83% of the wheat grain (Setter & Carlton 2000). It stores the starch and protein important both for the developing plant and flour production (Setter & Carlton 2000). The embryo makes up only a small percentage of the grain but contains the root radicle and the shoot apex surrounded by the coleoptile. The scutellum separates the endosperm from the embryo (Setter & Carlton 2000).

SECTION 4   DEVELOPMENT

4.1   Reproduction

4.1.1   *Sexual reproduction*

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 (OECD 1999). 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. In a study of wheat sown in May in Narrabri (northern NSW) the time from sowing to flowering was approximately 105-120 days and the time from flowering to maturity was approximately 35-45 days (in the ten year period 1990-2000; Sadras & Monzon 2006).

4.2   Pollination and pollen dispersal

Wheat is largely cleistogamous, which means that pollen is shed before the flower opens (Frankl & Galun 1977) and thus wheat is primarily self-pollinating with low

rates of out-crossing. Any out-crossing that may occur is facilitated by wind dispersal. Generally, wheat flowers lack nectaries to attract insects (Eastham & Sweet 2002) and the role of insects in cross-pollination is considered to be minimal (Glover 2002).

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, through the swelling of part of the ovary.

In field conditions, the viability of pollen grains may be less than 30 minutes (D'Souza 1970). Field conditions including temperature, relative humidity and wind intensity have a great influence on pollen viability and pollen movement. 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 (CFIA, (1999). In wheat, the stamens are smaller and produce fewer pollen grains (1000-3800 pollen grains per anther; 450,000 pollen grains per plant) than other cereal grasses. This compares to approximately 4 million pollen grains per rye ear (*Secale cereale* L.) and 18 million pollen grains per maize tassel (*Zea mays* L.; de Vries, 1971).

In a three year field study of wheat varieties there was variation in the number of anthers emerging from flowers of 14 to 80% of anthers per ear (D'Souza 1970). Approximately 80% of the pollen from an anther protruding from the spikelet is dispersed into the air. Laboratory experiments have shown that pollen can travel a distance of about 60 m at a height of 1 m (D'Souza 1970). In field experiments, Wilson (1968) found 10% seedset on male sterile wheat plants 30 m from the pollen donor plants.

Outcrossing rates up to 10% or higher can occur depending on the population density, genotype and environmental conditions (Jain 1975). Wind-borne cross fertilisation of wheat depends on physical factors such as weather and 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). 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. 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.

A majority of studies suggest that more than 90% of wheat pollen falls within 3 m of the source (reviewed by Hedge & Waines 2004). Under Australian conditions, pollen-mediated gene flow from a small release of GM wheat was observed only at low frequencies (0.012% and 0.0037%) over short distances (the maximum distance over which gene flow was detected was no more than 8 m) (Gatford et al. 2006).

In northern America, levels of gene flow have been shown to be dependent on the size of the wheat field (Matus-Cadiz et al. 2004; Matus-Cadiz et al. 2007; Gaines et al. 2007b). Gaines et al. (2007b) compared commercial field scale and experimental field scale gene flow in wheat. A greater level of gene flow was measured from the commercial scale fields (0.25% at 61 m) than the experimental scale fields (0.02% at 31 m). In another study, gene flow from an experimental scale field has been detected up to 100 m at rates of 0.002% to 0.003% (Matus-Cadiz et al. 2004), although gene flow was also detected at a single distance of 300 m from the pollen source in one season. Another study on long distance gene flow with a commercial scale field planting of wheat detected very low levels of gene flow (≤0.01%) in rare incidences of up to 2.75 km from the pollen source (Matus-Cadiz et al. 2007).

There have been no reports of pollen-mediated gene flow between bread wheat and durum wheat at or beyond 40 m, with 0.01-0.02% gene flow detected at 20 m (Matus-Cadiz et al. 2004).

4.3   Fruit/seed development and seed dispersal

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, the kernels formed in central spikelets and proximal florets within an individual spikelet are usually largest (Kirby, 1974; Simmons, 1987). Each wheat ear can produce approximately 30 to 50 kernels while the number of ears a wheat plant produces depends on the number of tillers produced and the number of tillers that produce a mature ear (Tennant et al. 2000).

Wheat is generally considered to have lost its natural seed dispersal mechanisms with domestication. The genes that control seed dispersal have been characterised in domesticated wheat, with it having the *brbrtgtgQQ* genotype (Li & Gill 2006). The *br* allele encodes for a non-brittle spike which is present in the wild type ancestor as is the dominant *Br* allele which produces a brittle spike. The *tg* and *Q* alleles are involved in glume toughness and seed threshability, respectively (Li & Gill 2006).

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 & 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 in of temperature from 18/13°C (day/night) to 30/25°C (day/night).

Kangaroos, rabbits, mice and rats are known pests of wheat (Hill et al. 1988; AGRI-FACTS 2002) and therefore potential distributors of viable wheat seeds. The possession of small dormant seeds is vital for seeds to survive chewing and digestion

(Malo & Suárez 1995). White wheats have large seeds with low dormancy and a thin seed coat and are therefore likely to be easily broken down in the digestive system of mammals (Hansen 1994). However, 30% of wheat grain fed to cattle is excreted whole and undamaged (Kaiser 1999), suggesting there is the potential for livestock to disperse viable wheat seed after consumption.

Although rabbits are known pests of wheat plants, viable wheat seeds have not been found in rabbit dung (Malo & Suárez 1995). In a study that looked at the germination of seeds on dung from cattle, red deer, sheep, hare, rabbit and red grouse, the number of germinations was least on rabbit dung (Welch 1985). Similarly, a study that looked at viable grass seeds in dung from cattle, pronghorn and rabbit, found few seedling populations of any species emerged from rabbit dung (Wicklow & Zak 1983). Rodents may eat seeds, thus destroying them, at the seed source or they may hoard seed elsewhere thus acting to disperse the seed (AGRI-FACTS 2002).

Emus have been shown to disperse seeds (Calvino-Cancela et al. 2006), however germination rates are generally very low (Rogers et al. 1993; McGrath & Bass 1999). Viable seed from *Avena sativa*, a grass from the same subfamily as wheat (Pooideae), was detected in emu droppings (Calvino-Cancela et al. 2006). It has been stated that seeds of wheat will also germinate after passage through an emu's digestive system, although no experimental evidence was provided (Davies 1978).

An extensive search of the literature did not identify any reports of other birds transporting and dispersing wheat seed (eg through the digestive tract or taking panicles containing viable seed) or seedlings from wheat crops. The white wheat varieties have a thin seed coat (Hansen 1994) and are readily digested by birds (Yasar 2003).

A variety of insects are likely to feed on the wheat crop, however, it is unlikely that most of these would contribute to the dispersal of seeds beyond the field. It is possible that ants may remove seeds for underground storage, but to depths where germination is highly unlikely. Although there are differences in ant behaviour and territory size across species, seed dispersal occurs at a local scale, such that seeds are usually only moved a few metres (Cain et al. 1998; Peters et al. 2003). Maximum seed dispersal distances by ants in Australia and the rest of the world are typically less than 40 m, with a mean dispersal distance of 0.96 m (Berg 1975; Beattie 1982; Gómez & Espadaler 1998).

4.4   Seed dormancy and germination

Seed dormancy restricts the timely elimination of volunteer cereals. Pickett (1993) provided the following definitions of various forms of dormancy:

INNATE DORMANCY: environmental conditions favour germination however seeds do not germinate;

ENFORCED DORMANCY: present in seed in dry storage or deep in soil or where seed does not germinate as environmental conditions are not correct;

INDUCED DORMANCY: seed is no longer able to germinate even when conditions favour germination, the inability to germinate may be the result of environmental conditions.

Under Northern European conditions seed that is buried too deeply in soil for germination can be imbibed but remain metabolically inactive in a state of enforced dormancy. Pickett (1993) claimed that the seed coat is responsible for an inhibitory effect in developing a 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.

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 (seed coat colour not specified) were short-lived in soil, persisting less than 1 year. However, in field studies volunteer wheat seedlings were still emerging 16 months after harvest and seedlings were observed 2 years after harvest (Anderson & Soper 2003). 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.

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 that of loose seeds in the soil at depths of 3 to 21 cm. The incorporation of unthreshed ears in the soil tends to preserve seeds for the emergence in the following autumn.

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).

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. Viable seeds persisted later in dry seasons in no tillage plots; at Winton (northern NSW; 1983) viable seeds persisted until June and at Warialda (northern NSW; 1986) viable seeds persisted until May, after harvest in the preceding Australian summer.

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).

4.5   Vegetative growth

Bread wheat is a cereal of temperate climates. Its various growth stages and their durations are listed in Table 4. Spring wheat varieties, which are grown in Australia, do 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.

Table 4. 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)	4-15
Vegetative: winter		280-350
Vegetative: spring		120-145

4.5.1   *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 semi-dwarf cultivars of winter wheat than in taller cultivars. Cholick et al. (1977) compared tall and semi-dwarf winter wheat genotypes and concluded that no correlation existed between cultivar height and rooting depth.

4.5.2   *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 1983).

4.5.3   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 to 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).

4.5.4   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 1983). Later formed tillers usually senesce prematurely.

SECTION 5   BIOCHEMISTRY

5.1   Toxins

Wheat is generally not considered toxic. While wheat grain contains haemagglutinin, amylase and protease inhibitors these are not present in large enough amounts to have adverse effects on humans (Simmonds 1989). However, a number of anti-nutritional factors and allergen occur in wheat and in extreme cases may have a toxic effect. These are described in Sections 5.2 and 5.3.

5.2   Allergens

Wheat is one of the most common allergenic foods in the human diet and is mainly associated with asthma and atopic dermatitis. 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 serve bronchial irritation and are responses to the inhalation of flour or dust. Anaphylaxis has been reported to occur rarely in children (OECD 2003). The allergenic proteins of wheat have not been identified, although some candidates exist (OECD 2003).

5.2.1   *Coeliac Disease*

Coeliac Disease (Gluten-sensitive enteropathy) is a disorder caused by intolerance to the ingestion of 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 although 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 (Catassi et al. 1996). Simmonds (1989) had previously reported that 1 in 2000-3000 individuals in the US suffer from the coeliac condition. In Australia the prevalence of Coeliac Disease in children in thought to be approximately 1 in 2000 while in adults it is 1 in 3000 with female sufferers outnumbering male sufferers 2 to 1 (Australian Gastroenterology Institute 1993).

For sufferers of Coeliac Disease, the consumption of gluten can result 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 (Australian Gastroenterology Institute 1993).

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).

5.3   **Other undesirable phytochemicals**

5.3.1   *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). Wheat germ is reported to contain a haemaglutinin that together with a protease inhibitor can affect the ability of poultry to utilise wheat germ effectively as a food source (Simmonds 1989).

5.3.2   *Lectins*

Lectins 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 a lectin, WGA (wheat germ agglutinin), in the germinating wheat embryo. 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.

5.3.3   *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).

5.3.4   *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 (Yaremcio 1991). Cattle and sheep can generally tolerate up to 0.5% nitrate on a dry matter basis. Wheat, rye and rape have been identified as crop plants which can accumulate nitrate (Yaremcio 1991; Hartwig and Barnhart (2004).

There are two forms of nitrate toxicity. Chronic nitrate toxicity 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; Yaremcio 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/brown mucus membranes, excess saliva production and staggering (Robson 2007).

5.4   **Beneficial phytochemicals**

Wheat is considered a good source of protein, minerals, B-group vitamins and dietary fibre (Simmonds 1989) although environmental conditions can affect the nutritional composition of wheat grains. A limited nutritional content of some important wheat products is shown in Table 5.

Table 5. The composition of wheat products per 100g edible portion[a].

	Protein[1]	Fat[1]	Carbo-hydrate[1]	Starch[1]	Total Sugar[1]	Vita-min E[2]	Thia min[2]	Ribo-flavin[2]	Niacin[2]	Folate[3]
Wheat Germ	26.7	9.2	44.7[*]	28.7[*]	16.0[*]	22.0	2.01	0.72	4.5	[?]
Wheat Bran	14.1	5.5	26.8	23.0	3.8	2.6	0.89	0.36	29.6	260
Brown flour	12.6	2.0	68.5	66.8	1.7	0.6	0.30	0.07	1.7	51
Whole-meal Flour	12.7	2.2	63.9	61.8	2.1	1.4	[^]	0.09	[^]	57
White flour (plain)	9.4	1.3	77.7	76.2	1.5	0.3	0.10	0.03	0.7	22
White flour (self-raising)	8.9	1.2	75.6	74.3	1.3	0.3[*]	0.10	0.03	0.7	19
White flour (bread making)	11.5	1.4	75.3	73.9	1.4	0.3[*]	0.10	0.03	0.7	31

[a]Data is taken from (Foods Standards Agency 2002). See reference for a full summary. [1]units are g; [2]units are mg; [3]units are μg; [*]values are estimates; [^]unfortified values not given; [?]no data given for amount of nutrient present

Wheat germ and wheat bran can be a good source of dietary fibre helping in the prevention and treatment of some digestive disorders (Simmonds 1989). Adom et al. (2003) studied the antioxidant activity and phytochemical content in milled grain of eleven wheat varieties which included a range of red and white wheat and durum wheat.

Significant differences were found in the carotenoid content between varieties (Adom et al. 2003). Lutein is the predominant carotenoid present in wheat (Adom et al. 2003; Abdel-Aal et al. 2007) and the bran/germ fractions of wheat contained greater amounts of carotenoids and antioxidant activity than the endosperm fractions (Adom et al. 2005). Lutein, along with zeaxanthin, is important for the health of skin and eyes in humans (Abdel-Aal et al. 2007).

SECTION 6　　ABIOTIC INTERACTIONS

6.1　　Abiotic stress limiting growth

6.1.1　　*Nutrient stress*

The three main nutrients required for successful production of a wheat crop are nitrogen, phosphorus and potassium. Sulphur and zinc are needed to a lesser degree (Laffan 1999). Laffan (1999) estimated that every 2 tons per hectare of wheat grain takes 42 kg of nitrogen, 9 kg of phosphorus, 10 kg of potassium and 2.5 kg of sulphur out of the soil.

Protein production in the wheat grain is reliant on nitrogen levels in the soil. Nitrogen fertiliser is commonly added to a field before sowing of the crop but can be added to the field again prior to flowering to boost grain yield and the level of protein in the grains (Laffan 1999). Legumes can also be used to fix nitrogen in the soil for subsequent crop use.

Phosphorus is applied to the field at sowing. It is required for the proper growth and reproduction of the wheat plants; for example proper grain ripening (Laffan 1999).

6.1.2　　*Temperature stress*

Wheat is grown across a wide range of environments around the world with the broadest adaptation of all the cereal crop species. It is a cool season crop requiring a minimum temperature for growth of 3ºC to 4ºC, with optimal growth occurring around 25ºC and tolerance of temperatures to a maximum of about 32ºC. Wheat flourishes in many different agro-climatic zones with production concentrated between latitudes 30ºN and 60ºN and 27ºS and 40ºS, but there are examples of wheat production beyond these limits (Briggle & Curtis 1987).

6.1.3　　*Water stress*

Wheat grows best on well drained soils anywhere from sea level up to heights of about 4500 m above sea level. It will grow in areas receiving 250 to 1750 mm annual precipitation, but most wheat production occurs in areas receiving 375 to 875 mm annually (Briggle & Curtis 1987).

Most wheat in Australia is grown as a dryland crop, with irrigated wheat contributing only a very small proportion to total production (Turner 2004). The wheat growing areas in Australia generally have a climate that is considered Mediterranean, in that there is a concentration of rainfall during the winter months while summer months are drier. The summers tend to be warm to hot with high solar radiation and the winters mild. In Western Australia (WA), the climate tends to more extreme Mediterranean and crop growth is highly dependent upon winter rains (Simmonds 1989). The winter-dominant rainfall of WA differs from the generally higher and evenly distributed rainfall of Victoria and southern New South Wales (NSW), and the summer-dominant rainfall of the northern wheat growing areas (Cramb et al. 2000).

6.2   Abiotic tolerances

Other important tolerances and sensitivities that wheat varieties display include tolerance to aluminium toxicity, boron sensitivity and resistance to the fungal disease Black Point (Littlewood 2004).

SECTION 7   BIOTIC INTERACTIONS

7.1   Weeds

There are a number of grass weeds that can be a problem in wheat crops. They include annual ryegrass, wild oats, drake, and canary, barley, silver and brome grasses. Bowran (2000) indicate that capeweed, doublegee and wild radish are the most important broad-leaved weeds of wheat crops. Capeweed seeds are easily wind dispersed between fields and its occurrence is widespread in pastures. Seed dormancy and the staggered germination displayed by both doublegee and wild radish make these weeds hard to control. See Section 2.3.3 for information on weed management practices in Australia.

7.2   Pests and pathogens

Damage to wheat crops by birds has been noted in Australia and around the world (Temby & Marshall 2003; Davies 1978; Jarman & McKenzie 1983; Jones 1987; Massam 2000; Massam 2001; Coleman & Spurr 2001). In Australia, birds, such as the sulphur-crested cockatoo, ducks, tree sparrows, house sparrows, long-billed corellas, galahs and emus, are known to cause damage to cereal crops. Birds such as cockatoos damage the cereal crop most during germination in autumn, but may feed on the crop at different times including grain ripening (Temby & Marshall 2003). When feeding on seed, cockatiels appear to prefer softer, younger seed to harder, mature seed (Jones 1987). Emus feed on a great variety of plant material, but prefer succulent foods, such as fleshy fruits, rather than drier items (Davies 1978).

Kangaroos are reported to damage grain crops by feeding on seedlings or trampling mature plants. Eastern grey kangaroos, for example, may feed on young green cereal crops when native grasses are dry and producing no new growth (Hill et al. 1988). Like kangaroos, rabbits prefer soft, green, lush grass (Myers & Poole 1963) and select the most succulent and nutritious plants first (Croft et al. 2002).

The main rodent pest in Australian wheat crops is the house mouse (*Mus domesticus*), causing average annual losses to Australian agricultural crops of US$10 million (ACIAR 2003). Rodents are opportunistic feeders and their diet can include seeds, the pith of stems and other plant materials (Caughley et al. 1998). Rodents may eat seeds, thus destroying them, at the seed source or they may hoard seed (AGRI-FACTS 2002). Caughley et al. (1998) indicate that the average territory size of mice varies between breeding and non-breeding seasons, from 0.015 to 0.2 hectares respectively, whereas others have suggested a much smaller territory of 3 to 10 m in diameter (AGRI-FACTS 2002). Reduced plant cover has been reported to be a deterrent to the movement of mice (AGRI-FACTS 2002).

Insects reported to be associated with wheat crops in Australia include *Nysius vinitor* Bergr (Rutherglen bug), *Tetraneura nigriabdominalis* Sasaki (oriental grassroot

aphid) *Agrotis ipsilon* Hufnagel (blackcut worm) *Pseudaletia convecta, Pseudaletia unipuncta* Haworth and *Cerodontha australis* Malloch (wheat sheath miner) (Miller & Pike 2002).

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, take-all, stripe rust, *Septoria tritici* blotch, stem rust and cereal cyst nematode (Brennan & Murray 1988).

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). Diseases of wheat that have been reported in Australia are summarised in Table 6.

7.3   Other biotic interactions

Endophytic actinobacteria has been isolated from surface sterilized healthy wheat plants (Coombs & Franco 2003). *Streptomyces caviscabies/Streptomyces setonii*-like and *Streptomyces galilaeus* isolates have been identified as the major components of the actinobacteria cultures isolated from root tissues (Coombs & Franco 2003). It has been suggested that these endophytic actinobacteria have a role in disease resistance and maintaining the health of the plants (Conn & Franco 2004). Fungal endophytes have also been isolated from wheat cultivars (Coombs & Franco 2003).

SECTION 8   WEEDINESS

Wheat shares some characteristics with known weeds, such as wind-pollination (although it is predominantly self-pollinating) and the ability to germinate or to produce some seed in a range of environmental conditions. However, it lacks most characteristics that are common to many weeds, such as the ability to produce a persisting seed bank, rapid growth to flowering, continuous seed production as long as growing conditions permit, very high seed output, high seed dispersal and long-distance seed dispersal (Keeler 1989). 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 selected. 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 *T. aestivum* were of the spelta type and husked type. 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.

Table 6. 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	*Heterodera avenae*	
Root lesion nematode	*Pratylenchus*	
Stubby-root nematode	*Paratrichodorus cristiei*	
Bacterial diseases		
Bacterial leaf streak or Black Chaff	*Xanthomonas campestris*	Foliage and heads of wheat
Bacterial leaf blight	*Pseudomonas syringae pv. syringae*	As above
Spike blight or Tundu	*Corynebacterium tritici*	As above
Basal glume rot	*Pseudomonas syringae* pv. *atrofaciens*	As above
Minor bacterial blight	*Corynebacterium michiganense* ssp. *tessellarius, Bacillus megaterium,* *Erwinia rhapontici*	As above
Fungal + Oomycete diseases		
Common root and crown rot	*Bipolaris sorokiniana; Fusarium roseum*	Roots, lower stems and crowns
Root rot	*Pythium* spp.	Roots
Take-all	*Gaeumannomyces graminis* var. *tritici*	As above
Root rot and sharp eyespot symptom	*Rhizoctonia solani and R. cerealis*	As above
Stripe	*Cephalosporium gramineum*	As above
Strawbreaker foot rot	*Pseudocercosporella herpotrichoides*	As above
Leaf and head blight	*Septoria nodorum avenae* and *Leptosphaeria nodorum*	Foliage and heads of wheat
Tan spot or yellow leaf spot	*Pyrenophora tritici-repentis*	As above
Helminthosporium leaf blight	*Cochliobolus sativus; Bipolaris sorokiniana*	As above
Alternaria leaf blight	*Alternaria triticina*	As above
Downy mildew (minor)	*Sclerophthora macrospora*	As above
Scab or head blight	*Gibberella zeae*	heads of wheat
Black point	*Alternaria alternata*	As above
Ergot	*Claviceps purpurea*	As above
Stem Rusts	*Puccinia graminis*	Foliage and heads of wheat
Leaf rusts	*Puccinia recondite*	As above
Stripe rusts	*Puccinia striiformis*	As above
Wheat smuts	*Ustilago tritici* (Loose smut) *urocystis agropyri* (Flag smut)	As above

8.1   Weediness status on a global scale

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 (Panetta 1993; Pheloung 1995; Bergelson et al. 1998). Wheat has been grown for centuries throughout the world without any reports that it is a serious weed pest.

There are no indications that wheat can become established as a self-sustaining population on a long-term basis (Newman 1990; Sukopp & Sukopp 1993). There have been no reports of bread wheat becoming an invasive weed. However, in California it is considered a naturalised species (Calflora 2007) and volunteer wheat was also found to be present as a weed in the Canadian prairies (Leeson et al. 2005).

8.2   Weediness status in Australia

Wheat is not classified as an invasive weed in Australia. It 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).

Only bread wheat (*T. aestivum* L.) and durum wheat (*T. 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). Bread wheat is classified as a known naturalised plant in agricultural habitats in Australia of minor significance with control warranted at three or less locations within any one state or territory (Groves et al. 2003). It is common along roadsides, railway lines, trucking yards in wheat growing areas and around paddocks cultivated with wheat in Australia (Jacobs & McClay 1993). However bread wheat is not always considered to be truly naturalised in the wheat growing state of Victoria (Walsh & Entwisle 1994).

Other species of *Triticum* and the closely related genus *Aegilops* are recognised as quarantine weeds in Australia.

8.3   Weediness in agricultural ecosystems

Wheat is listed as a naturalised non-native species present in all Australian states and territories with the exception of the Northern Territory (Groves et al. 2002). In all states and territories where a rank is given wheat is not given an agricultural weed rank by the authors indicating it is either not a problem or does not occur in agricultural environments. The exception is Western Australia where wheat receives the '3c' rank. This rank indicates it is a naturalised species known to be a minor problem with control warranted at four or more locations and that it is currently under active control in part of the state (Groves et al. 2002).

Wheat is a recognised volunteer weed in agricultural fields in the Canadian prairies (Leeson et al. 2005). A three year study of volunteer spring wheat emergence across the prairies found volunteer wheat emergence in approximately half the sites. The overall volunteer wheat emergence rate in continuous cropping fields, in the first monitored post harvest period, was 3.3 plants m^2. At the end of the three year monitoring period none of the wheat dispersed at the start of the trial was detected in the soil seed bank. From these results the authors suggest that volunteer spring wheat

will not become a major agricultural problem (Harker et al. 2005). In a study of non GM imidazolinone resistant wheat in a commercial production system in the Great Plains of the USA imidazolinone resistant wheat was detected in two samples of wheat seed grown on the same fields after a two year break from imidazolinone resistant wheat (Gaines et al. 2007a).

8.4 Weediness in natural ecosystems

Wheat is not considered a problem weed of natural ecosystems (see Section 8.2).

8.5 Control measures

Post-harvest, the wheat stubble may be left standing to reduce erosion, incorporated in to the soil or even burnt prior to seeding, depending upon the management system in place (Jarvis et al. 2000). Straw burning is also used as volunteer control method (Pickett 1989).

In Australia, post-harvest treatments of wheat crops include stubble burning to minimise disease outbreaks and livestock grazing have also minimised the risk of weediness.

When a cotton/wheat double cropping system is in use wheat stubble can be left standing to help reduce soil erosion, increase water infiltration and be a source of organic matter. In this situation it is suggested to spray wheat prior to flowering with either a glyphosate based herbicide or a contact herbicide (Waters & Kelly 2001). Treatment with the herbicide glyphosate in January or February reduces the density of volunteers.

SECTION 9   POTENTIAL FOR VERTICAL GENE TRANSFER

Vertical gene transfer is the transfer of genetic information from an individual organism to its progeny by conventional heredity mechanisms, both asexual and sexual. In flowering plants, pollen dispersal is the main mode of gene flow (Waines & Hedge 2003). For cultivated crops, vertical gene transfer could therefore occur via successful cross-pollination between the crop and neighbouring crops, related weeds or native plants (Glover 2002). Cultivated wheat is predominantly self-pollinating although cross-fertilization can occur at rates as high as 10% if conditions are favourable (refer to Section 4.2 for detail)

9.1 Intraspecific crossing

As discussed in Section 4.2, wheat is largely cleistogamous, which means that pollen is shed before the flower opens (Frankl & Galun 1977) and thus wheat is primarily self-pollinating with low rates of out-crossing. Any out-crossing that may occur is facilitated by wind dispersal.

Gene transfer from one wheat line to another can only occur if they are in very close proximity and flower synchronously. Under field conditions, wheat pollen has a viable lifespan of less than 30 minutes (OECD 1999). Field conditions such as temperature, relative humidity and wind intensity have a great influence on pollen viability and pollen movement (see Section 4.2).

9.2   Natural interspecific and intergeneric crossing

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. However, these hybrids are highly male sterile and backcross progeny can be produced from pollination with parental lines or other related species (Knobloch 1968). There have been no reports of interspecific gene flow between bread wheat and other sexually compatible species beyond 40 m (Matus-Cadiz et al. 2004).

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. Inter- and intraspecific hybrids between durum wheat and bread wheat can occur naturally under field conditions (Matus-Cadiz et al. 2004).

Intergeneric hybrids involving *Triticum* spp. and *Elytrigia, Elymus (=Elytrigia), Haynaldia, Secale*, or *Hordeum* species are possible, however 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 F_1 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 & Sweet 2002).

In a review of cross-pollination and introgression between bread wheat and wild relatives in North America, (Hedge & Waines 2004), indicated that a number of natural barriers exist that preclude the formation of hybrids between these species. 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 1). The chromosomes of these different genomes do not pair during gamete formation in the F_1 hybrids or may result in developmental instability, which reduces the hybrid's ability to survive in parental habitats.

In field studies of spontaneous hybridisation, Jacot et al. (2004) reported that the *Ae. ovata* x *T. aestivum* and *Ae. ovata* x *T. durum* hybrids were recovered. The morphology of the *Ae. 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 (*Ae. squarrosa, Ae. cylindrica, Ae. 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 F_1 plants (*Ae. triticoides*), F_2 and backcross (BC) plants of *Ae. triticoides* x bread wheat were found between *Ae. ovata* and bread wheat.

The herbarium survey conducted by Jacot et al. (2004) demonstrated that *Ae. ovata* can hybridise with bread wheat in the field. However, backcrosses of the F_1 progeny with the wheat parent and the F_2 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 *Ae. ovata* occurring naturally. Jacot et al. (2004) also noted that the distribution of several *Aegilops* x 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 (*Ae. 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 CC DD (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 & 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. Jointed goatgrass 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*. From the experimental results the authors suggested that hybridization between *T. aestivum* and *H. marinum* had occurred at some previous time and that subsequent back crossing between the hybrid and pure *H. marinum* had lead to the introgression of wheat DNA into sea barley (Guadagnuolo et al. 2001). However, bread wheat 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 (random amplified polymorphic DNAs) markers used to detect the possible hybridisation event are specific to 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 an annual weed present in the wheat growing areas of Australia and is salt tolerant to levels approaching seawater (AVH 2006; 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 & Sweet 2002) or the USA. However, there are non-peer reviewed reports of naturally formed hybrids from Canada (Hedge & Waines 2004). Artificial crosses between rye and wheat gave rise to triticale. There are no reports of hybridisation between bread wheat and triticale occurring in nature or reports that cultivated wheat x barley hybrids exist naturally (Eastham & Sweet 2002).

9.3   Crossing under experimental conditions

A number of successful hybridisations of bread wheat with wild relatives have been obtained under experimental greenhouse conditions and several under experimental field conditions (Jacot et al. 2004).

Jacot et al. (2004) reported that artificial hybridisation, between wheat and wild relatives, is likely to occur at low rates. After hand pollination, hybrids were recovered in twelve of seventeen crosses between wheat and seventeen related taxa. Experimental hybrids, using wheat as the pollen donor, were formed between bread wheat and *T. turgidum* ssp. *dicoccoides*, *Aegilops biuncialis*, *Ae. ovata*, *Ae. cylindrica*, *T. durum, T. timopheevii* and *T. monococcum*. However, embryo rescue was required to produce plants from the crosses between bread wheat and *Ae. cylindrica, Ae. speltoides, Ae. tauschii, Elytrigia elongata* and *Roegneria ciliaris*. 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 (Jacot et al. 2004).

Wheat has been artificially crossed with rye (*Secale cereale* L.) resulting in the cereal triticale (*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 triticale is the 21 chromosome hybrid, containing the A, B, and R genomes of durum wheat and cereal rye. Colchicine treatment of the primary triticale plants 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 & 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 & 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. 2000). The only successful artificial crosses have involved barley as the male parent (ie pollen donor) (Koba et al. 1991).

The genotype of the male parent influences the production of haploid wheat plants (Garcia-Llamas et al. 2004). 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.

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 & 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 were obtained with the use of embryo rescue (Jacot et al. 2004). *Ae. elongatum* appears to be a rare plant in Australia, with only 2 reports of it in NSW

(AVH 2006). There are no reports of hybrids forming between bread wheat and *Ag. elongatum* 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 & Sweet 2002). This species is synonymous with *Elymus arenarius*. In 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 F_1 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 F_1 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.

Li et al. (1996) described high yields of embryos in wheat pollinated with gamma grass (*Tripsacum dactyloides*). Laurie and Bennett (1988) tested *Sorghum bicolour* L. and *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 above for further discussion.

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