



Australian Government

Department of Health

Office of the Gene Technology Regulator

The Biology of *Triticum aestivum* L. (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.

This document is a minor update of Version 3 (January 2016).

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ABBREVIATIONS USED IN THIS DOCUMENT

ABARE	Australian Bureau of Agriculture and Resource Economics
ABARES	Australian Bureau of Agriculture and Resource Economics and Sciences
ABS	Australian Bureau of Statistics
ACIAR	Australian Centre for International Agricultural Research
AEGIC	Australian Export Grains Innovation Centre
APVMA	Australian Pesticides and Veterinary Medicines Authority
ASA	Australian Seeds Authority
BAA	Biofuels Association of Australia
DNA	Deoxyribonucleic acid
DAFWA	Department of Agriculture and Fisheries Western Australia
FAO	Food and Agriculture Organization of the United Nations
FAOStat	Statistics Division Food and Agriculture Organization of the United Nations
GM	Genetically modified
GMO	Genetically modified organism
GRDC	Grains Research & Development Corporation
ha	Hectare
m	Metres
n	Haploid number of chromosomes
NLRD	Notifiable Low Risk Dealing
NSW	New South Wales
NSW DPI	New South Wales Department of Primary Industries
NVT	National Variety Trials
OECD	Organisation for Economic Co-operation and Development
OGTR	Office of the Gene Technology Regulator
QDAF	Queensland Department of Agriculture and Fisheries
Qld	Queensland
SA	South Australia
spp.	Species
Tas.	Tasmania
USA	United States of America
USDA	United States Department of Agriculture
Vic.	Victoria
WA	Western Australia
WQA	Wheat Quality Australia

PREAMBLE

This document describes the biology of *Triticum aestivum* L. (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* subsp. *durum* (Desf.) Husn., also known as durum or pasta wheat. The terms 'wheat' and 'bread wheat' will be used as general terms to refer to *T. aestivum* throughout this document.

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.

Worldwide, two species of wheat are commonly grown. The first, *T. aestivum*, or bread wheat, includes the classes hard 'red winter', 'hard red spring', 'soft red winter', 'hard white' and 'soft white'. The second, *T. turgidum* subsp. *durum*, includes the 'durum' and 'red durum' wheat classes (macaroni or pasta wheats). In Australia, production is limited to these two types. Bread wheat grown in Australia is exclusively white and does not have the red colour typical for most bread wheat grown in the northern hemisphere.

SECTION 1 TAXONOMY

Triticum aestivum L. belongs to the family Poaceae (BEP clade), subfamily Pooideae and tribe Triticeae (Clayton et al. 2015). Synonyms include *Triticum vulgare* and there are also many synonyms for subspecies and cultivars (Clayton et al. 2015). All names of the members of Poaceae used in this document are currently valid according to The World Checklist of Selected Plant Families (Clayton et al. 2015).

Bread wheat is an allohexaploid (6x) that regularly forms 21 pairs of chromosomes ($2n = 42$) during meiosis. Chromosomes are organised in the A, B and D genomes (AABBDD). Each genome normally contains seven pairs of chromosomes (Hegde & Waines 2004) and the chromosomes belong to seven homeologous groups of three (Sears 1954; Hegde & Waines 2004). Chromosomes may be numbered such that the chromosomes of the AB genome are I to XIV and those of the D genome are XV to XXI (Sears 1954), or as 1A, 1B, 1D to 7A, 7B, 7D (Hegde & Waines 2004). Each chromosome in hexaploid wheat has a homologue in each of the other two genomes, however pairing between homeologous chromosomes of the A, B and D genomes is prevented by a gene, now designated *Ph1* (Riley & Chapman 1958; Sears 1976) on chromosome 5B (Riley & Chapman 1958). This gene acts as a dominant gene suppressing pairing of homeologous chromosomes while allowing pairing between homologous chromosomes (from the same genome) (Hegde & Waines 2004). The *Ph1* locus has been shown to prevent homeologous pairing between wheat and several related genomes in hybrids (Riley et al. 1959; Jauhar & Chibbar 1999), but conversely, expression of *Ph1* is suppressed in hybrids between bread wheat and some diploid *Aegilops* species, thus allowing homeologous pairing of chromosomes (Hegde & Waines 2004). Practical consideration of the role of this gene is needed in both breeding of hybrids and in interpreting phylogenetic relationships (Riley & Chapman 1958; Riley et al. 1959).

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 nullisomics¹, monosomics², telocentrics³ and isochromosomes⁴. Examination of wheat aneuploids has been important in furthering understanding of the evolution of the genome of modern cultivated wheat.

Currently it is thought that hexaploid wheat is the product of two hybridisation events. In the first, the A genome progenitor combined with the B genome progenitor to form a primitive tetraploid wheat ($2n=28$, AABB) (Feuillet et al. 2007). Analysis of chloroplast and mitochondrial genomes showed that this hybridisation occurred with the B genome - from the maternal parent (Tsunewaki 1988). The second event involved hybridisation between the tetraploid (AABB) form and the D genome progenitor to form the basic hexaploid configuration, AABBDD (Kimber & Sears 1987; Feuillet et al. 2007), again in the B genome cytoplasm.

While there is still some debate about the origin of the three genomes of *T. aestivum* (in particular the B genome), there is a degree of consensus for the A and D genomes.

Triticum uratu Thumanjan ex Gandilyan, has been suggested as the progenitor of the A genome in cultivated tetraploid (Feuillet et al. 2007) and hexaploid wheat (Kimber & Sears 1987; May & Appels 1987; Feuillet et al. 2007), as has *T. monococcum* (Kimber & Sears 1987), a cultivated diploid wheat (Feuillet et al. 2007). Early work (McFadden & Sears 1946a; McFadden & Sears 1946b) identified the D genome progenitor as *Aegilops tauschii* Coss. Schmal. (formerly *Triticum tauschii* Coss. or *Aegilops triuncialis* L.), which is also supported by later authors (Kimber & Sears 1987; Feuillet et al. 2007). A later review summarised much of the earlier work, concluding that *T. aestivum* originated from a cross between *T. turgidum* and *Ae. tauschii* (Matsuoka 2011).

The identity of the B genome donor remains unclear. It was originally proposed that the B genome donor was *Aegilops speltoides* Tausch (see Sarkar & Stebbins 1956). Feldman (1978) concluded that although *Ae. longissima* Schweinf. and Muschl in Muschler (as *Triticum longissimum* (Schweinf. & Muschl.) Bowden) was a candidate for the B genome progenitor, based on genetic compatibility, the lack of geographical contact between this species and tetraploid wheat or wild tetraploid wheat and suggested, as did (Feldman & Kislev 1977), that this was unlikely. The 1977 work suggested that *Ae. searsii* Feldman and Kislev, formerly believed to be a variant of *Ae. longissimi*, was the B genome progenitor, as did Nath et al. (1983) (as *Triticum searsii*). It has more recently been suggested 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 *Ae. speltoides* (Feuillet et al. 2007). The processes of interspecific hybridisation and the ubiquitous nature of the B genome cytoplasm have been reviewed by Tsunewaki (1991). The origin and taxonomy of cultivated wheat have been reviewed by Feuillet et al. (2007).

The progenitors and selected wild species are listed in Table 1.

¹ Nullisomics: $2n-2$ chromosomes; lacking one of the chromosomes normally present in the species. In hexaploid wheat the four homologous chromosomes apparently compensate for the missing pair of homologs.

² Monosomics: $2n-1$ chromosomes. A chromosome present only in a single dose. Occurs when an 'n-1' gamete occurring as a result nondisjunction during meiosis is fertilised by an 'n' gamete.

³ Telocentrics: a chromosome in which the centromere is located at the terminal end and which only has one 'arm'.

⁴ Isochromosomes: a chromosome with identical arms. Present due to mis-division or strand exchange during meiosis or mitosis.

Table 1: Chromosome number and genome(s) of selected species of the tribe *Triticeae*.

Chromosome and genome information from Dewey (1984) and Kimber and Sears (1987); taxonomic information from the Kew Royal Botanic Gardens World Checklist of Selected Plant Families (Clayton et al. 2015).

Species	Synonyms	N chromosomes	Genome code ¹
<i>Aegilops bicornis</i> (Forssk.) Jaub.& Spach.	<i>Triticum bicornis</i>	14	S ^b
<i>Ae. caudata</i> L.	<i>T. dichasians</i>	14	C
<i>Ae. columnaris</i> Zhuk.	<i>T. columnare</i>	28	U.M
<i>Ae. comosa</i> Sm.	<i>T. comosum</i>	14	M
<i>Ae. crassa</i> Boiss. Ex Hohen (4x)	<i>T. crassum</i>	28	D.M
<i>Ae. crassa</i> (8x)		42	D.D.M
<i>Ae. cylindrica</i> Host.	<i>T. cylindricum</i>	28	C.D
<i>Ae. juvenalis</i> (Thell.)	<i>T. juvenale</i>	42	D.M.U
<i>Ae. kotschy</i> Boiss.	<i>T. kotschyi</i>	28	U.S
<i>Ae. longissima</i> Schweinf. & Muschl. in Muschler	<i>T. longissimum</i>	?	S ¹
<i>Ae. lorentii</i> Hochst.	<i>Ae. biuncialis</i> , <i>T. machrochaetum</i>	28	U.M
<i>Ae. mutica</i> Boiss.	<i>T. tripsacoides</i>	14	M
<i>Ae. neglecta</i> Req. ex Bertol. (4x)	<i>T. ovatum</i> , <i>T. triaristatum</i>	28	U.M
<i>Ae. neglecta</i> (6x)		42	U.M.Un
<i>Ae. searsii</i> Feldman & Kislev	<i>T. searsii</i>	14	S ^S
<i>Ae. speltooides</i> Tausch.	<i>T. speltooides</i>	14	S
<i>Ae. tauschii</i> Coss.	<i>T. tauschii</i> , <i>Ae. triuncialis</i>	14	D
<i>Ae. triuncialis</i> L.	<i>T. triunicale</i>	28	U.C
<i>Ae. umbellulata</i> Zhuk.	<i>T. umbellulatum</i>	14	U
<i>Ae. uniaristata</i> Steud.	<i>T. uniaristatum</i>	14	Un
<i>Ae. vavilovii</i> (Zhuk.) Chennav.	<i>T. syriacum</i>	42	D.M.S
<i>Ae. ventricosa</i> Tausch.	<i>T. ventricosum</i>	28	D.Un
<i>Hordeum</i> spp. (barleys)		14	H
<i>Thinopyrum elongatum</i> (Host) DR Dewey	<i>Th. ponticum</i>	70	J-E
<i>Th. intermedium</i> (Host) Barkworth & DR Dewey		42	E1.E2.S
<i>T. aestivum</i> L.		42	A.B.D
<i>T. monococcum</i> subsp. <i>aegilopoides</i> (Link) Thell.	<i>T. baeoticum</i>	14	A
<i>T. timopheevii</i> (Zhuk.) Zhuk.	<i>T. araraticum</i>	28	A.G
<i>T. turgidum</i> L.		28	A.B
<i>Triticum</i> x zhukovskyi		42	A.A.G
<i>Secale</i> spp. (ryes)		14	R

¹ S genomes are designated S^b for *Triticum bicornis*; S¹ for *T. longissimum* and S^S for *T. speltooides* (Kimber & Sears 1987).

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 9000 years ago, with the hybridisation event that produced hexaploid wheat occurring more

than 6000 years ago (Feuillet et al. 2007; Matsuoka 2011; Luo et al. 2007). For an extensive review of wheat domestication see (Nesbitt & Samuel 1996).

2.2 Commercial uses

Bread wheat is the most widely grown food crop in the world. The global production of wheat in 2015/16 is estimated at 734.5 million tonnes (FAO 2015a). In 2011-12, total wheat production in Australia was 29.9 million tonnes, which was the highest production year since the collection of data started in 1861, while in 2012-2013 and 2010-2011 it was 22.5 and 27.4 million tonnes, respectively (ABS 2013a; ABARES 2013a). The gross value of wheat produced in Australia in the year 2012-2013 was \$7,021 million (ABS 2013b).

The major exporters of wheat are Argentina, Australia, Canada, the European Union, Kazakhstan, Russian Federation, Ukraine, and the United States (FAO 2015a). In 2014, approximately 174 million tonnes of wheat were exported worldwide (UN Comtrade 2016). In 2013/14 Australia exported 18.6 million tonnes, approximately 74% of the total harvest (ABARES 2013a).

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 3 °C to 4 °C, with optimal growth occurring around 25 °C and tolerance of temperatures to a maximum of about 32 °C. Wheat flourishes in many different agro-climatic zones with production concentrated between latitudes 30 °N and 60 °N and 27 °S and 40 °S, but there are examples of wheat production beyond these limits (Briggle & Curtis 1987; Kimber & Sears 1987).

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; Kimber & Sears 1987).

The primary use of bread wheat is for bread manufacture. National average (*per capita per year*) bread consumption was estimated to range from about 40 to 300 kg (Pomeranz 1987). In Australia the national average per capita for 1998-99 was 53.4 kg (ABS 2000). Wheat flour is also used to produce biscuits, confectionery products, noodles and vital wheat gluten or seitan (a powdered form of purified wheat gluten, 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 forecast to continue. The increase in demand for feed wheat has led 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 (Impiglia et al. 2000). Wheat stubble is also used as feed for sheep (Edward & Haagensen 2000) and fodder wheats are grown for hay and chaff production and for livestock grazing (GRDC 2014). In the USA Wheat is also used to a limited degree by the poultry and fish industries which use grain and middlings (the leftovers from flour milling) as feed (Sparks Companies Inc 2002). Forage wheats in Australia are generally winter-type wheats which are adaptable to a wide range of sowing dates (GRDC 2014).

Production of ethanol from grain wheat involves hydrolysis of extracted starch to glucose or sucrose, which is then fermented to produce ethanol and carbon dioxide (Sparks Companies Inc 2002). In 2013, Australia had three facilities that produced ethanol from plant material, but only one

of these, in Nowra, NSW, used wheat (waste starch) as its starting material (BAA 2013). In the United Kingdom, there is a biofuel plant in the Humber estuary, using wheat and other plants as its source material. In this system, wheat starch is converted to bioethanol and the remaining protein is used as animal feed (see the [Vivergo Fuels](#) website for more information). In the USA, there has been interest in the biofuel industry on using wheat for the production of bioethanol, but there has been no shift away from the current reliance upon corn (maize). Fluctuations in the relative prices of corn and wheat, in particular an increase in the price of corn in comparison to wheat, has meant that some ethanol plants in the USA have considered switching to wheat, but this has not eventuated (Gillam 2011; Schill 2013) due to economic considerations associated with the lower yields of bioethanol from wheat (Sparks Companies Inc 2002).

2.3 Cultivation in Australia

Wheat was introduced into Australia in 1788 at the time of European settlement. Early breeding in South Australia focussed on early maturity and drought tolerance, as well as strong straw, rust resistance and improved milling qualities. In New South Wales William Farrer developed wheat varieties adapted for Australian conditions with high yields, rust resistance and good milling quality. This was largely driven by his use of imported wheats, combined with a South Australian wheat, 'Purple Straw' for its productivity. This combination resulted in perhaps the best known and widely planted variety for the early twentieth century - Federation (Simmonds 1989).

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 permitted 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 (ASA 2011b; ASA 2011a; OECD 2016). 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. For certified or basic seed production, controls on previous uses of the field also exist and include that the field must not have been used to grow the same species for the two previous years and that no cereal species is allowed to be grown on the field in the previous year (Smith & Baxter 2002).

2.3.2 Scale of cultivation

Wheat is grown in a wide range of areas in Australia, from Queensland through to Western Australia, with small areas in Tasmania (see Table 1, Figure 2). This includes areas extending from 23 °S to 38 °S, mainly as a rain-fed crop (Richards et al. 2014) with irrigated wheat contributing only a very small proportion of the 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).

Yields in Australia have improved substantially through the introduction of semi-dwarf genes and improved resistance to diseases. Complete adoption of semi-dwarf varieties since 1980 has been one of the factors in the genetic component of increased wheat yield (Fischer et al. 2014). However,

drought conditions are a frequent impediment to maximised production. Despite fluctuations due to weather conditions, yield was consistently higher than 1 t/ha from the late 1940s, remaining fairly constant until 1.7 t/ha was achieved in 1979, remaining generally above 1.5 t/ha since then (calculated from Australian Bureau of Statistics data) (ABS 2013a)

A substantial increase in wheat production started in the early 1960s, but in the last decade has largely stabilised, any large fluctuations mainly representing the influence of climatic variables such as an occurrence of an El Niño event (Figure 1; Table 2). See Section 6.1 for a discussion of factors limiting the growth of wheat plants.

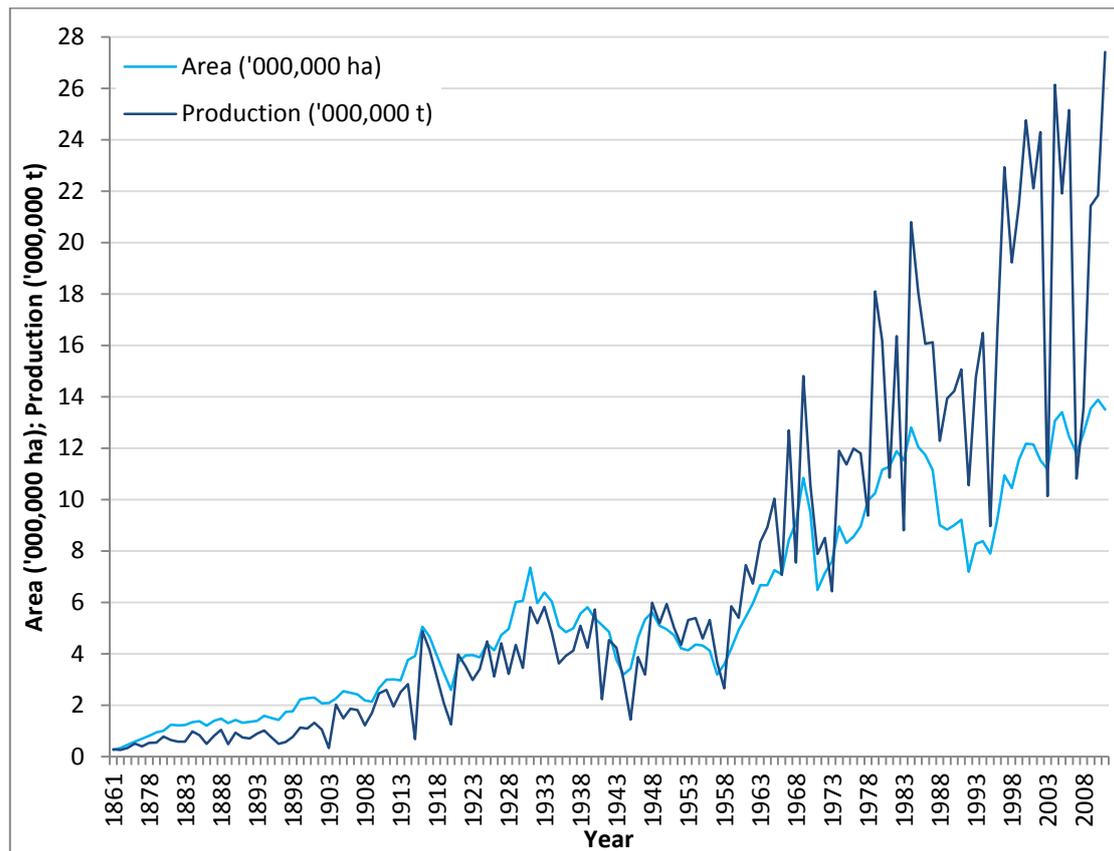


Figure 1. Production ('000,000 t) and area ('000,000 ha) of wheat grown in Australia from 1861 until 2011 (ABS 2013a).

Table 2. Wheat production statistics for Australia, 2005-2014 (ABARES 2013b; ABARES 2014; ABARES 2015)

Period	Area ('000 ha)	Yield (tonnes/ha)	Production ('000 tonnes)
2005-06	12443	2.02	25150
2006-07	11798	0.92	10822
2007-08	12578	1.08	13569
2008-09	13530	1.58	21420
2009-10	13881	1.57	21834
2010-11	13502	2.03	27410
2011-12	13902	2.15	29905
2012-13	12979	1.76	22856
2013-14 ^a	12613	2.01	25303

^a ABARES estimate

In Western Australia, the wheat belt underwent a significant expansion over the period 1961 to 1983 and increased in area from 1.63 million ha to 4.87 million ha, with recent years approximately 5 million hectares annually (ABARES 2013b; ABARES 2014; ABARES 2015). Increases in yield in Western Australia have been attributed to a number of factors including earlier seeding, improved water storage through crop residue retention, increased nitrogen fertiliser application, weed control and use of break crops in disease management (Fischer et al. 2014).

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, while 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 NSW and southern Queensland, to very light and sandy soils in Western Australia (WA) (Simmonds 1989). Differences in soil types and climates across these regions influence the different wheat varieties being grown across the Australian wheat belt resulting in different grain protein contents and quality grades (Simmonds 1989). The broad classes grown in different areas of the Australian wheat belt can be seen in Figure 2.

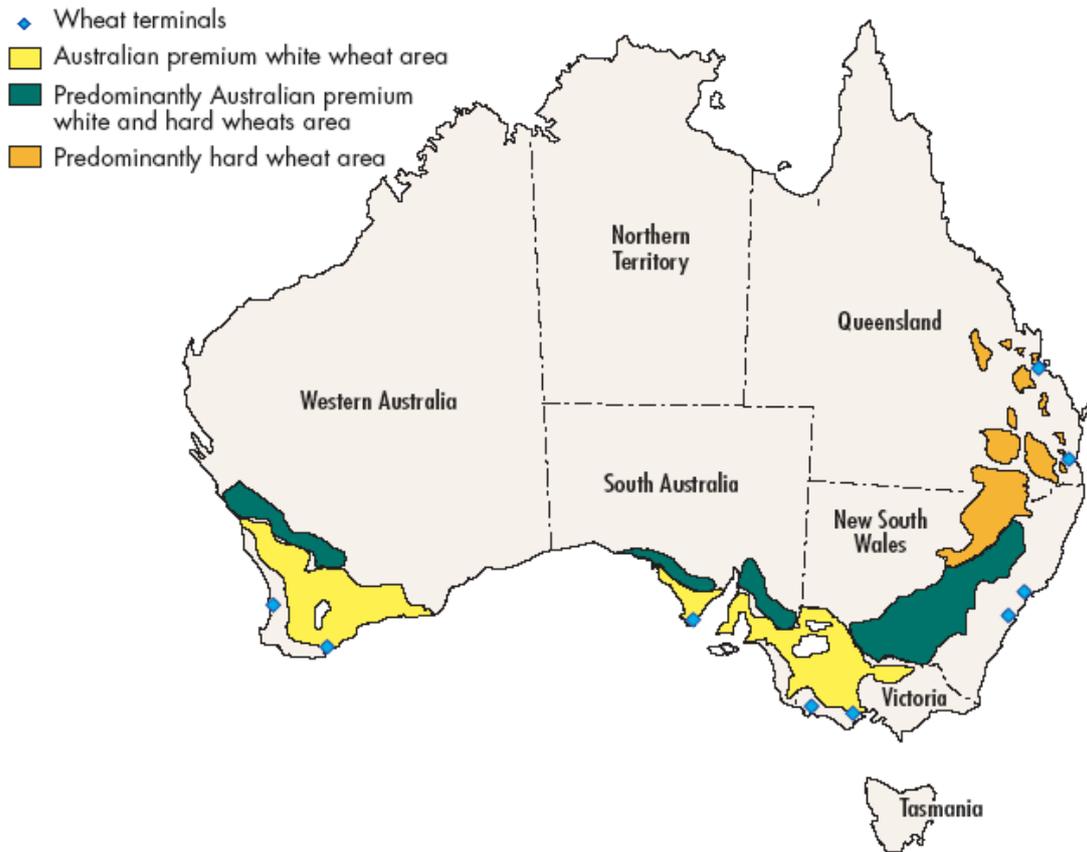


Figure 2. The Australian wheat belt, showing classes of wheat grown in specific areas (ABARE 2007).

Planting time is determined by a number of factors, including soil moisture and temperature, avoidance of sub-optimal conditions, particularly early and late in the growing season ensuring optimal flowering time (GRDC 2014; GRDC 2015c). Sowing depth depends on soil moisture, timing and seasonal outlook, the variety sown, seedbed temperature and moisture, as well as seed and soil applications such as fungicides and herbicides (GRDC 2014; GRDC 2015c). Deeper sowing can delay emergence and can result in weaker seedlings which are poorly tillered (Jarvis et al. 2000). Sowing rates vary from 20 – 150 kg/ha depending on the region, rainfall and use of dryland or irrigated conditions for cropping (Sims 1990; GRDC 2014).

It was 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. However, there are a number of tillage systems in use and no single system is ideal for all soils and situations (Jarvis et al. 2000).

The three main nutrients required for successful production of a wheat crop are nitrogen (N), phosphorus (P) and potassium (K). Arable soils in south-eastern Australia are usually low in nitrogen and phosphorus (Bowden et al. 2008). Sandy soils usually require more added nutrients than heavier clay soils (Laffan 1999). In the western wheat growing areas P, N and K may be deficient, depending on soil type and requirements for N are dependent on expected yield and protein levels (GRDC 2015c). Micronutrients (copper (Cu), manganese (Mn), molybdenum (Mo) and zinc (Zn)) may be of concern and sulphur deficiency is less common (GRDC 2015c). In the northern grain growing areas the most common deficiencies are N, P, K and Zn, with S, Cu and Mo of concern in some soils and B in some areas (Queensland Department of Agriculture and Fisheries) (QDAF 2010). In northern areas Mo and Mn toxicities can occur in acidic soils (QDAF 2010). It is estimated that every two 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 (Laffan 1999). Information on the nutrient removal from soils by a variety of crops is given in the QDAF summary of crop nutrition management (QDAF 2010).

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 different stages of wheat growth and reproduction, such as germination, root development or grain ripening (Laffan 1999).

Details of wheat cultivation practices are available in a number of publications, with information specific to different regions and cropping systems (GRDC 2014; GRDC 2015c).

There are a number of pests and diseases of wheat which may require management (*e.g.* application of herbicide or pesticide, cultural practices, integrated pest control strategies) during the growing season. A number of comprehensive documents give information regarding invertebrate pests and pathogens for different wheat growing regions, pest pressures and the need for control and discussion of control options, as well as links to a number of other sources of information (Bowran 2000; GRDC 2014; GRDC 2015c). There are a number of vertebrate pests of wheat including birds (Temby & Marshall 2003; Jones 1987; Coleman & Spurr 2001; Massam 2000; Massam 2001; Jarman & McKenzie 1983; Davies 1978), kangaroos (Hill et al. 1988), rabbits (Myers & Poole 1963) (Croft et al. 2002) and mice (ACIAR 2003). However, in general there are not easy solutions to protecting crops from such pests. Some strategies for protecting against cockatoo damage include use of scare guns, decoy feeding areas and feeding stock away from crop areas, as well as cooperative strategies across cropping districts to coordinate these controls (Temby & Marshall 2003). Monitoring of mouse populations and control within 24 hours of sowing is important as this is when wheat crops are most vulnerable to damage (GRDC 2015c). Clearing grain spills, removing rubbish and other cover around properties is key to reducing numbers in conjunction with baiting (GRDC 2015c).

A number of diseases caused by a range of pathogens may occur in Australian wheat crops including necrotrophic leaf fungi (leaf spot & blotch conditions), biotrophic leaf fungi (rusts and mildews), root and crown fungi ('rots'), inflorescence fungi (including ergot, smut, blight), nematodes, bacteria and viruses (Murray & Brennan 2009). In general, control measures include breeding of resistant lines, cultural practices such as stubble, tillage and crop rotations and pesticides in a variety of forms (Loughman et al. 2000; Murray & Brennan 2009). As with most crops, decisions regarding the application of these control measures will vary with severity, cost of control and cost of damage to the crop. A comprehensive review of wheat diseases and management costs associated with disease and control in Australia was published in 2009 (Murray & Brennan 2009). There are also a range of pests which can affect stored grains. Control of such pests relies on good storage conditions, including temperature and moisture, monitoring for pests and where necessary chemical control, although there are some issues with resistance to phosphine (GRDC 2013a; GRDC 2013b).

For more information on pests and pathogens see Section 7.2.

Effective weed control in wheat, as with most other crops, is dependent on a clear understanding of the types and densities of weeds, the control options available for specific weeds and threshold levels for weeds in a crop. Weed control, the losses from weed competition and from crop contamination and therefore lower returns for the harvested crop can be the most significant cost in wheat production (Bowran 2000), with the cost of weed control in winter cropping systems equivalent to up to 20% of the gross value of the Australian wheat crop (Storrie 2014). Integrated weed management strategies including agronomic (rotations, row spacing, seed densities, stubble management among others), biological (for example choice of resistant cultivars) and chemical to control weeds are likely to be the most effective (Bowran 2000; GRDC 2014; GRDC 2015c).

The aim of weed control in the field before wheat is sown is to control winter active weeds while they are small. The differences between the recommended pre-emergence, early post-emergence and late post-emergence herbicides reflect the differing developmental stages of the crop. However, many common weeds of wheat crops now exhibit herbicide resistance, including to glyphosate and paraquat. Worldwide, 24 weed species are resistant to glyphosate, of which six are found in Australia (Storrie 2014). Currently, there are 14 and ten species of weeds resistant to herbicides in the northern and western wheat-growing regions respectively (GRDC 2015c; GRDC 2014). These include the most important weed in wheat crops, wild radish (*Raphanus raphanistrum* L.), which is a major weed in western regions, and less of a problem in northern regions; wild oats (*Avena* spp.) and annual ryegrass (*Lolium rigidum* Gaudin) (Storrie 2014). More detailed information on weeds affecting wheat crops, herbicide regimes used for these weeds, and herbicide resistance in weeds of wheat crops is available (Bowran 2000; GRDC 2015c; GRDC 2014; Storrie 2014).

Integrated weed management is recommended by industry bodies to combat increasing resistance in crop weeds. For example, integrated management practices for control of annual ryegrass include a range of options, as opposed to restricting control to application of one herbicide alone (Storrie 2014):

- improving crop competition,
- burning residues,
- fallow and pre-sowing cultivation,
- double knockdown (two herbicides of differing modes of action used in quick succession),
- use of different pre- and post-emergence herbicides,
- manuring, mulching and hay-freezing,
- weed seed control at harvest.

Such strategies also consider individual weed control strategies within 'tactic' groups which target key parts of weed control strategies (Storrie 2014).

The use of rotation cropping has long been the recommended method of control for annual grass weeds in wheat crops, using a summer crop such as sorghum or a winter grain legume (Laffan 1999). Others suggest a legume rotation system would improve the control of grass weeds (Edward & Haagenzen 2000). In general, the benefits of specific crops in rotations will depend on the types of weeds in the system and the other benefits of using particular crops in the rotation.

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, improved use of capital and other production resources and providing alternative sources of income (Edward & Haagenzen 2000; GRDC 2014; GRDC 2015c). 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 and pasture rotations can be an effective means of providing organic matter and structural benefits for the soil (Edward & Haagenzen 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 (Edward & Haagenzen 2000; GRDC 2015c).

Wheat can be harvested when the moisture content is between 10 and 20% (Setter & Carlton 2000a), with harvest decisions based not only the moisture content but also on the ability to dry grain post-harvest (GRDC 2014). Western Australia grain receival standards require a moisture content of 12.5% on delivery (GRDC 2015c). Harvest generally occurs in late spring and early summer, roughly from September to December. For example in Queensland harvest may begin in September for Central Queensland and in December for the Darling Downs (QDAF 2012b).

More detailed information regarding wheat production, pests and disease management and links to other related information is available from a number of sources (Bowden et al. 2008; NSW DPI 2017; QDAF 2012b; QDAF 2012a; DAFWA 2016; Agriculture Victoria 2012).

Wheat sold in Australia is graded according to a number of specifications including protein content and other attributes which dictate its suitability for various end uses. The basic attributes and end uses for different wheat grades are shown in Table 3. Further information about the divisions within these broad classes can be found online (Graincorp 2015).

Table 3 Australian wheat grades (Blakeney et al. 2009).

Grade	Attributes	End-uses
Prime Hard	<ul style="list-style-type: none"> • Minimum protein content of 13% • Hard-grained varieties • Prime hard varieties • Excellent milling quality • High dough strength and functionality 	High volume pan bread and hearth bread High quality yellow alkaline and dry white salted noodles
Hard	<ul style="list-style-type: none"> • Minimum protein content of 11.5% • Hard-grained varieties • Superior milling quality • Good dough strength and functionality 	High volume pan bread, flatbreads and noodles
Premium White	<ul style="list-style-type: none"> • Minimum protein content of 10% • Hard-grained varieties • High milling performance 	Noodles, including instant noodles Middle Eastern and Indian-style flatbreads Pan bread Chinese steamed bread
Standard White	<ul style="list-style-type: none"> • Protein content less than 10% unless Australian Standard White classification 	Multipurpose (flatbread, steamed bread, noodles)
Noodle	<ul style="list-style-type: none"> • Protein content 9.6-11.5% • Soft grained varieties • Very good noodle quality 	Dry white salted noodles and Japanese udon noodles
Durum	<ul style="list-style-type: none"> • Very hard grained varieties • Good semolina yield • High yellow pigment levels 	Pasta and couscous
Soft	<ul style="list-style-type: none"> • Maximum protein content of 9.5% • Soft grained varieties • Weak doughs with low water absorption 	Biscuits, cakes and pastry
General Purpose	<ul style="list-style-type: none"> • Wheat that fails to meet higher milling grain receival standards, or with Australian General Purpose classification 	All purpose flours Blending applications
Feed	<ul style="list-style-type: none"> • Wheat suitable for animal feed, including all red grained varieties 	

Further information about these grades, testing of grain and products and the performance of Australian wheat in the 2014 season can be found in the Australian wheat quality report season 2014 (AEGIC 2015).

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 (Konzak 1987), hybrid wheat production using chemicals to induce male sterility

(Lucken 1987) or mechanical methods to remove anthers (Simmonds 1989). The single seed descent method is also used for the rapid production of inbred lines (Lucken 1987; Knott 1987; Konzak 1987; Simmonds 1989).

Traditional 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 where the female parent has 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 ionizing radiation, ultraviolet radiation or chemical mutagens (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.

Other characteristics selected for in wheat breeding include reduced height of plants, nuclear male sterility and other advantageous alterations to plant physiology (Konzak 1987). In Australia, wheat breeding has been focussed on the production of varieties which combine high yield, acceptable quality characteristics and resistance to diseases (Simmonds 1989). A 2006 report from the Australian Bureau of Statistics (ABS) has summarised wheat breeding in Australia (ABS 2006). Richards & colleagues also discuss the history of wheat breeding in Australia and some of the challenges and potential targets for wheat breeding to provide wheat cultivars adapted to Australian conditions into the future (Richards et al. 2014). Long-term agronomic challenges are key targets for Australian wheat breeding – yield, drought, frost, disease resistance and salinity (GRDC 2011).

Valuable genes for disease resistance have sometimes been derived from wild wheat species including rust resistance genes from wheatgrass (*Thinopyrum elongatum* (Host.) DR Dewey (=ponticum) (*Agropyron elongatum*)) for a rust resistant variety from the United States (Smith et al. 1968). The modified translocation, 3Ag#3, is present in Australian cultivar (cv.) 'Torres' (Mackay 1983), while another modified translocation, 3Ag#14, also providing rust resistance is present in the Australian cultivars 'Skua', 'Sundor' and 'Vasco' (Martin 1984; Ellison 1984; Brennan et al. 1987).

Comprehensive reviews of plant breeding methodologies, including for those used 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, which will be incorporated into the Australian Grains Genebank in Horsham (Stoutjesdijk 2013). This collection also includes wild relatives of wheat. Further information regarding the varieties available for planting in Australia is available online through a number of sources (GRDC 2015a; WQA 2015; Trainor et al. 2015).

2.4.2 Genetic modification

In Australia, limited and controlled releases of genetically modified wheat have been conducted since 2007. Modifications have included increased tolerance to abiotic stressors, altered composition, improved grain quality, yield stability, nutrient utilisation and disease resistance (see [OGTR website](#) for more information). Similarly, in Europe, Canada and the United States, wheat with modifications for increased herbicide tolerance, abiotic stressor tolerance, increased yields, pathogen resistance, and increased carbohydrate and protein content have been trialled (see the [Canadian Food Inspection Agency website](#), the [European Commission GMO Register](#) or the [United States Department of Agriculture Animal and Plant Health Inspection Service websites](#) for more information).

SECTION 3 MORPHOLOGY

3.1 Plant morphology

A brief description of the morphology of the wheat plant is provided below. More detailed descriptions and diagrams are available (Bowden et al. 2008; Kirby 2002; Setter & Carlton 2000b).

3.1.1 The stem

The mature wheat plant consists of a central stem from which leaves emerge at opposite sides (Figure 3). 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 2000b). The stem terminates in the ear of the wheat plant.

3.1.2 The leaf

The leaf structure consists of the sheath and the leaf blade which form from separate meristems (Figure 3). At the base of the leaf blade, where it joins the sheath, are a membranous ligule and a pair of small hairy projections known as auricles, which are characteristic of cereal species (Kirby 2002). Leaves are produced on alternate sides of the stem (Setter & Carlton 2000b). The final leaf before the ear is called the flag leaf. In spring wheat varieties the length of leaves increases from the base until one or two leaves before the flag leaf (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 cells. Both epidermal layers are covered with an epicuticular wax. The mesophyll is enclosed by the epidermal layers and transected by the vascular tissue (Kirby 2002).

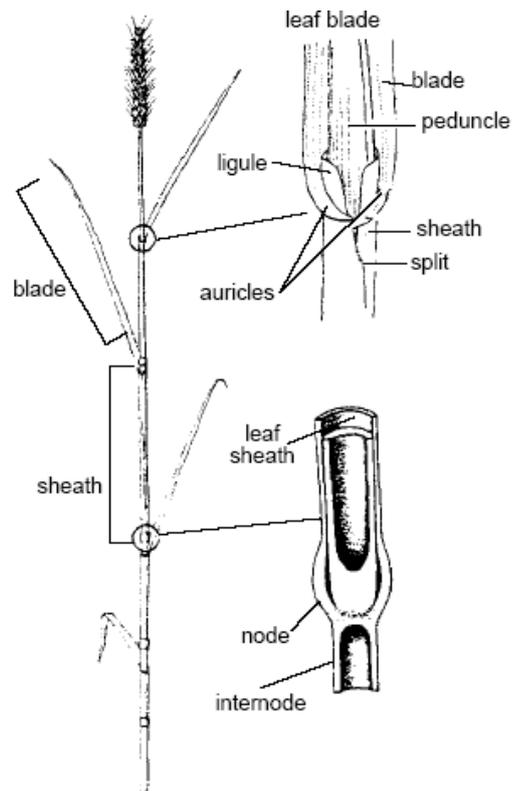


Figure 3: The stem and leaf structure of a mature wheat plant. Reproduced in original form with permission (Setter & Carlton 2000b).

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 2000b). 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 (Kirby 2002; Setter & Carlton 2000b). The nodal roots emerge at the same time that tiller development starts. The root system can grow 1-2 m deep, but most roots are concentrated in the top 30cm of soil (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 4). The spikelets contain the florets and are arranged on opposite sides of a central rachis (Setter & Carlton 2000b). The spikelet is surrounded by two sterile glumes which enclose up to 10 individual flowers (florets). The florets are enclosed by a lemma and a palea. The tip of the lemma may be extended to form an awn in some varieties. The florets are composed of the carpel (the ovary and the stigmas) and three stamen and anthers (Setter & Carlton 2000b). Each anther consists of four loculi enclosing the pollen grains (Kirby 2002).

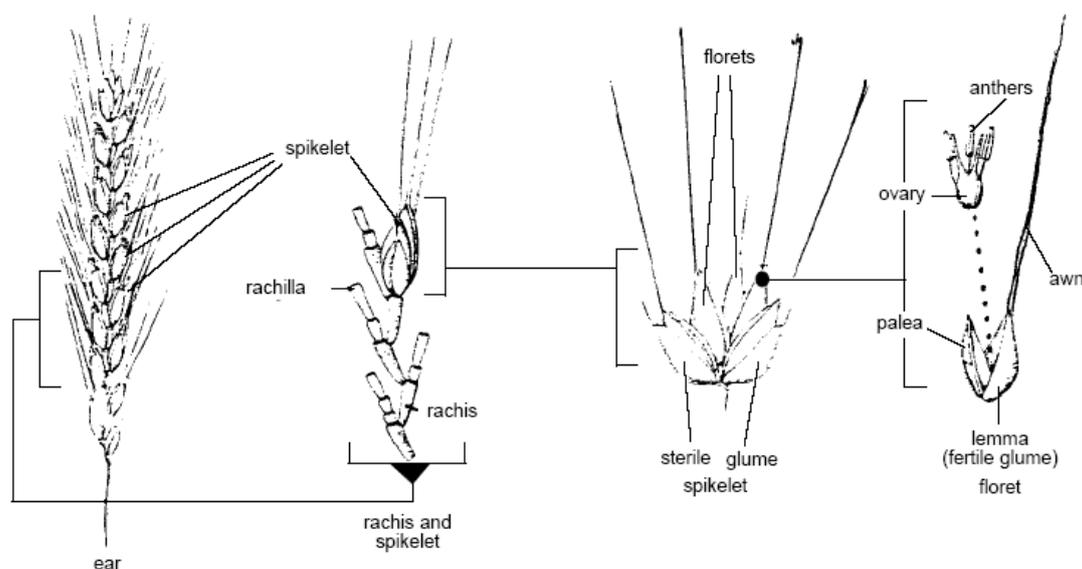


Figure 4: The structure of the wheat ear showing the structure of the spikelets and florets.

Reproduced in original form with permission (Setter & Carlton 2000b).

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 2000b). The bran coat consists of three layers, the pericarp, testa and aleurone. The endosperm makes up 83% of the wheat grain and stores the starch and protein important both for the developing plant and flour production (Setter & Carlton 2000b). 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 2000b).

SECTION 4 DEVELOPMENT

Wheat growth and development is often described in terms of the Zadoks decimal scale which helps to standardise the growth stages observed during wheat plant development (Zadoks et al. 1974). A number of publications discuss wheat development in Australia with reference to this scale (Bowden et al. 2008; GRDC 2013c; GRDC 2015c).

4.1 Reproduction

Wheat does not reproduce vegetatively, so all reproduction is sexual.

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, based on a ten year period from 1990 - 2000 (in the ten year period 1990-2000; Sadras & Monzon 2006).

4.2 Pollination and pollen dispersal

Flowers may be described as chasmogamic - opening to expose flowers and stamens to the air - or cleistogamic - remaining closed and thus necessarily self-fertilising (Sethi & Chhabra 1990). Considerable differences in flower opening occur amongst varieties and species of wheat, and De

Vries (1971) noted that 80-90% of bread wheats showed open flowers. The extent of flower opening is an important factor in influencing cross-pollination and potential gene flow during anthesis. Floral structure, anthesis and anther dehiscence patterns in wheat make it predominantly self-pollinating with low rates of out-crossing (Waines & Hegde 2003). 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). Any out-crossing that may occur is facilitated by wind dispersal.

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 four million pollen grains *per* ear for rye (*Secale cereale* L.) and 18 million pollen grains *per* maize tassel (*Zea mays* L., see de Vries 1971).

In general, approximately 80% of the pollen from an anther protruding from the spikelet is dispersed into the air, but pollen shedding capacity may depend on the cultivar. In a three year field study of wheat varieties, the number of anthers emerging from flowers was found to vary from 14 to 80% of anthers *per* ear (D'Souza 1970). In a study of 22 wheat cultivars, shedding ranged from 3 to 80% of the pollen produced was shed, with a strong influence of cultivar - tall varieties with more pollen grain/anther and longer filaments shed greater quantities of pollen outside the florets (Beri & Anand 1971).

The pollen load in the air at a given time is a function of the amount of pollen produced per anther, the amount of anther extrusion and the number of anthers per unit in a given area (discussed in (Virmani & Edwards 1983).

However, physical movement of pollen does not necessarily result in gene flow (Waines and Hegde 2003). Cross-pollination rates are usually less than 1% but rates up to 6% or higher can be observed, depending on cultivars and environmental conditions (Hucl 1996; Hucl & Matus-Cádiz 2001).

Wheat pollen grains are relatively heavy compared to other grasses, short-lived (up to 30 minutes under optimal field conditions (20 °C, 60 % relative humidity)) and typically travel very short distances in still air (Lelley 1966; de Vries 1971). A majority of studies suggest that more than 90 % of wheat pollen falls within three metres of the source (Hegde & Waines 2004). Cross-pollination due to insects is deemed unlikely as wheat flowers have no nectaries and produce relatively small quantities of pollen (de Vries 1971; Treu & Emberlin 2000). Any outcrossing occurring is facilitated by wind dispersal of pollen (Treu & Emberlin 2000). Studies in small pollinator blocks have shown that wheat pollen grains can travel up to 60 m from the pollen source (reviewed by (Waines & Hegde 2003). However, gene flow remains limited as less than 1 % average cross-pollination is observed beyond 6 m (D'Souza 1970; de Vries 1974). However, a number of researchers have also reported long distance pollen movement. At the field scale (Matus-Cádiz et al. 2004) and commercial scale (Matus-Cádiz et al. 2007) long distance pollen dispersal has been observed at trace levels (see section 9.1). Laboratory experiments have shown that pollen can travel a distance of about 60 m at a height of one metre (D'Souza 1970). In field experiments, Wilson (1968) found 10 % seed set on male sterile wheat plants 30 m from the pollen donor plants.

Physical movement of pollen does not necessarily result in gene flow (Waines & Hegde 2003) and long distance pollen movement does not necessarily result in a proportional increase in gene flow. Pollen grains quickly desiccate after release from the anthers (Heslop-Harrison 1979) and under field conditions, the viability of pollen grains may be less than 30 minutes (D'Souza 1970). Under optimal conditions of 5 °C and 60 % relative humidity, however, pollen can remain viable for over 90 minutes (D'Souza 1970). Field conditions including temperature, relative humidity and wind intensity have a great influence on pollen viability and pollen movement. Extreme cold or hot temperatures are unfavourable for pollination and fertilisation, and weather conditions also play an important role. Humid weather makes the pollen heavy, limiting dispersal distance from the plant, while dry weather causes desiccation and loss of viability (D'Souza 1970).

Heslop-Harrison (1979) reported that after release, wheat pollen attaches to the stigmatic branches and water is absorbed by the pollen grain through gaps in the stigma cuticle. This process enables the pollen tube to grow, which in turn facilitates fertilisation. Pollen tube growth is initiated 1-2 hours after pollination and fertilisation takes place after an additional 30 - 40 hours (de Vries 1971). The duration of stigma receptivity is an important consideration in understanding wheat reproductive biology. Estimates of the duration of receptivity vary from a few days to up to 13 days and estimates vary not only due to experimental and environmental conditions but also due to the methods used to determine receptivity (de Vries 1971). An extensive review of wheat flowering biology is available (de Vries 1971).

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 (Kirby 1974), the kernels formed in central spikelets and proximal florets within an individual spikelet are usually largest (Simmons & Crookston 1979). 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 (Setter & Carlton 2000a).

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 and both modern durum and bread wheats were found to have the genotype *brbrtgqQ* (Li & Gill 2006): *Br* controls rachis brittleness, *Tg* controls glume toughness, and *Q* controls seed threshability. In wild ancestral wheats, shattering is caused by a brittle rachis, which is conferred by a dominant *Br* allele. A recessive mutant allele *br* at this locus in modern wheats produces a non-brittle spike (Li & Gill 2006).

When rain coincides with harvest, pre-harvest sprouting can occur i.e. grains may germinate while still on the ear of the parent plant. Thus, in cereal crops some degree of dormancy during seed development can be advantageous. 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 (Wardlaw & Moncur 1995). However, wheat cultivars vary in their response to high temperature during kernel filling and the relationship may not be a simple temperature effect (Stapper & Fischer 1990; McDonald et al. 1983). 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 temperature from 18/13°C (day/night) to 30/25 °C (day/night).

Kangaroos (*Macropus* spp.), rabbits (*Oryctolagus cuniculus*), mice (*Mus musculus*) and rats (*Rattus* spp.) are known pests of wheat (Hill et al. 1988; AGRI-FACTS 2002) and therefore potential distributors of viable wheat seeds. Small dormant seeds are more likely to survive chewing and digestion (Malo & Suárez 1995). White wheats have large seeds with low dormancy and a thin seed coat and are therefore expected to be easily broken down in the digestive system of mammals (Hansen 1994). Intact seed may make up to 30 % (wheat) or 15 % (barley) of dry matter in the faeces of cattle fed grain (Beauchemin et al. 1994), however, the germination rates of this seed were not measured. In other studies wheat seeds have been shown to germinate in the dung of cattle and sheep (*Ovis aries*), but not donkeys (*Equus asinus*), after consumption (Semán 2007). This indicates the potential for livestock to disperse viable wheat seed after consumption. Wheat seeds can also be dispersed in the wool of sheep (Ryves 1988).

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 (*Cervus elephus*), sheep, hare (*Lepus capensis*), rabbit and red grouse (*Lagopus scotica*), the number of seeds germinating was least on rabbit dung (Welch 1985). Similarly, a study that looked at viable grass seeds in dung from cattle, pronghorn (*Antilocapra americana*) 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 and disperse the seed (AGRI-FACTS 2002).

Emus (*Dromaius novaehollandiae*) 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* L., 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).

The white wheat varieties have a thin seed coat (Hansen 1994) and are readily digested by birds (Yasar 2003). An unpublished study conducted under laboratory conditions showed that when wheat was fed to corellas and galahs (*Eolophus roseicapillus*), some wheat seeds remained intact following passage through the digestive tract, but at very low numbers (2.3 % and 0.7 %, respectively) (Woodgate et al. 2011). For that intact seed, the germination rate was 87.5 % from corellas and 100 % for galahs (Woodgate et al. 2011), such that overall germination rates under laboratory conditions were 2 % and 0.7 % respectively. In another study, seed of four crop species tested (maize, barley, safflower and rice) did not remain intact after passage through the digestive tract of birds (mallard duck, *Anas platyrhynchos*; ring-necked pheasant, *Phasianus colchicus*, red-winged blackbird, *Agelaius phoeniceus* and rock pigeon, *Columba livia*) (Cummings et al. 2008). However, the authors noted that seed remained intact within the oesophagus/crop and gizzard for several hours and this could be a mechanism for dispersal, *i.e.* if the birds were killed within hours of consuming the seed. Similarly, dispersal could occur via intact seed found on the muddy feet/legs (but not the feathers) of a few birds (Cummings et al. 2008). Ring-necked pheasants, mallard ducks, and rock pigeons have all been introduced into Australia ([Atlas of Living Australia](#), accessed 23 February 2015). An extensive search of the literature did not identify any reports of birds transporting and dispersing wheat seed by taking panicles containing viable seed or seedlings from wheat crops.

A variety of insects are likely to feed on the wheat crop, but 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).

It is important to remember that in Australia wheat is cultivated on about 14 million ha and produces as much as 26 million tonnes annually (Figure 1). Production on this scale involves considerable movement and loss of seed during transport, cultivation, harvest, storage, and processing; but also during distribution of animal feed stock, hay and straw. Wheat seeds have been dispersed on clothing (Ansong & Pickering 2014; Huiskes et al. 2014) and in the seed of other crop plants and grass seed (Conn 2012). Thus the greatest dispersal of wheat seed is likely through human intervention.

4.4 Seed dormancy, germination, seed banks and persistence

4.4.1 Dormancy and germination

Seed dormancy inhibits the germination of viable seeds under optimal conditions (Hilhorst & Toorop 1997). It is desirable for seeds of crop species to have a certain degree of dormancy to prevent sprouting if wet and moist conditions occur before harvest, but it can also restrict the timely elimination of volunteer cereals. Most of the commercial cultivars of wheat have been selected against dormancy to achieve quick and uniform germination, and thereby good stand establishment.

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.

Wheat may be capable of extended dormancy, but reported survival times vary widely depending on variety and environmental conditions. Australian wheats have a low level of dormancy that it is easily broken down, allowing germination to begin. By contrast, red wheats widely grown in Europe and North America have higher levels of sprouting tolerance and typically are dormant for longer periods after harvest than the white wheats. In dry regions, wheat seed can survive in the soil beyond two years (Anderson & Soper 2003; Beckie et al. 2001; De Corby et al. 2007; Harker et al. 2005; Nielson et al. 2009; Pickett 1989; Pickett 1993; Seerey et al. 2011; Willenborg & Van Acker 2008) and surveys from Western Canada indicated that, under certain conditions, there may be seed survival of up to five years (Beckie et al. 2001), but the mechanism of persistence is not known and may be due to reseedling (De Corby et al. 2007).

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.

Classical studies involving burial of wheat seed in retrievable containers have shown persistence of less than 1 year, but field data suggests survival and emergence of wheat seedlings up to 2 years post-harvest (Anderson & Soper 2003). One concern related to the classical studies was the high density of wheat seed which may provide conditions conducive to disease and thus reduce seed survival (see review by Anderson & Soper 2003). Pickett (1993) mention reports of wheat seeds surviving in the soil for five years, but note that these claims are unproven. Pickett (1989) also noted earlier reports of germination inhibitors found in the seed coat of 18 red-grained varieties of wheat. In Australia, under a 'no-till' system and dry conditions, some seed remained viable for 17-18 months post-harvest (Wicks et al. 2000).

Induction of secondary dormancy of buried hexaploid wheat has not been reported under field conditions (De Corby et al. 2007), although secondary dormancy has been induced in laboratory settings (King 1976). Komatsuzaki and Endo (1996) found that Japanese cultivars with greater primary dormancy remain dormant for longer and exhibit greater persistence in the soil. The longevity of seeds in unthreshed ears was longer than that of loose seeds in the soil at depths of 3 to 21 cm. Similarly, Seerey et al (2011) found that for wheat scattered at the soil surface, wheat spikes are less likely to emerge as a volunteer in the following growing season than their threshed counterparts.

Failure of seed due to unfavourable conditions is referred to as enforced dormancy (Pickett 1993). Ploughing can bury a high proportion of seeds to a depth where this occurs or at which germinating seeds will be unable to reach the surface and develop into plants, however, it may also affect the conditions which could release seed from enforced dormancy (Pickett 1993).

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).

4.4.2 Seed banks and persistence

Dormancy can affect the persistence of seeds in soil, but as discussed above, wheat seeds are generally short lived in the soil, with red wheats typically showing longer dormancy than white wheats, which should limit persistence in seed banks.

Seed lost at harvest could potentially persist and develop a seed bank which could lead to the dispersal of wheat from the field site (or other areas where it may grow as a volunteer) over many years. The amount of seed lost at harvest would depend heavily on the yield. Wheat yields can vary greatly between countries, ranging from 780 g/m² (United Kingdom, Denmark, Germany, France and Egypt) down to the low-yield range of 100 - 220 g/m² in countries such as Australia. The average worldwide yield is approximately 300 g/m² (FAO 2015b), or 7500 seed/m², assuming a weight of 0.04 g per seed. Seed loss during harvest is also variable; sometimes reaching more than 10 % (Clarke 1985), but 3 % loss is considered acceptable (Clarke 1985; Huitink 2014). In the United Kingdom, harvest losses of wheat averaged 2 % of yield, with 95 % of the surveyed farmers recording losses of less than 6 %. These results were probably for winter wheat, but this was not clearly stated. A 2 % loss from a yield of 3,000 kg/ha leaves about 240 seeds/m² whereas a 6% loss would leave more than 700 seeds/m² (Anderson & Soper 2003).

In Australia the average yield for 2012-13 was 1.76 tonnes/ha (see Table 2), which is 176 g/m² or about 4400 seeds/m². Assuming a 3 % loss, about 132 seeds/m² would have remained post-harvest. This amount is approximately the sowing rate for wheat (assuming anticipated yield of 2 tonne/ha and stand of 100 plants/m² (Anderson et al. 2000).

A three year study of volunteer hard red spring wheat emergence across the Canadian prairies found volunteer wheat emergence in approximately half the sites. Wheat seeds were dispersed in the autumn (post-harvest) at a density of 190 seeds/m². The overall volunteer wheat emergence rate in continuous cropping fields, in the spring following dispersal, was 3.3 plants m². 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 (Harker et al. 2005). Another Canadian study examined post-harvest emergence and persistence of hard red spring wheat varieties, which were broadcast in late autumn at a rate of 500 seeds/m² (to simulate post-harvest seed loss). Emergence of volunteer wheat ranged from 0.9 to 13 % (average 4.3 %) the following spring. Wheat that did not recruit (i.e. germinate and emerge) rapidly degraded in the soil and did not persist past 12 months (De Corby et al. 2007).

Based on the Canadian studies (above) volunteer densities in the spring following the autumn dispersal of seed were 3.3 and 21.5 plants/m², which represents average emergence rates of 1.7 and 4.3 %, respectively. There is little in the literature regarding emergence of volunteer wheat in Australia. An Australian study reported mid-fallow volunteers of wheat (i.e. about 10 weeks after harvest) of 0.7, 5.6 and 5.3 plants/m² for no-till, stubble-retained & cultivated and stubble-burned & cultivated treatments, respectively. From the data, it is unclear what these losses represent relative to the yield (Wicks et al. 2000). At early fallow (i.e. five weeks after harvest) the volunteer wheat was a greater problem than at mid-fallow (Wicks et al. 2000). 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. Although no densities were provided, it is reasonable to assume that the density of wheat volunteers was greater at early fallow compared to mid fallow.

The Canadian and Australian studies (above) examined persistence of volunteer wheat under a number of different farming systems (e.g. no-till, retained stubble & cultivation, chemical fallow etc.) and demonstrated that under normal farming practices, volunteer wheat would not persist beyond three years. Wheat seed dispersed along roadsides or other non-cultivated areas is unlikely to emerge and thrive (due to predation and germination at wrong time of year) and seed production per unit area is likely to be considerably less than that under crop conditions due to suboptimal germination and growth conditions (e.g. moisture and nutrients) and competition by other plants.

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. The relationship between root growth and plant height has been debated. Some have stated that root growth of a genotype is proportional to its top growth (MacKey 1973) and that more extensive root growth was seen in semi-dwarf cultivars of winter wheat than in taller cultivars (Lupton et al. 1974). Others compared tall and semi-dwarf winter wheat genotypes and concluded that no correlation existed between cultivar height and rooting depth (Cholick et al. 1977).

4.5.2 Leaf development

After germination the vegetative shoot apex initiates additional leaf primordia. The number of leaf primordia can vary from seven to 15 (Kirby & Appleyard 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 & Appleyard 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 1987).

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 those formed between the axils of the coleoptile and the first true leaf. In general, three phyllochrons (the interval between two successive leaves) separate the emergence of a leaf and its subtended tiller (phyllochron is the interval between two successive leaves; Kirby & Appleyard 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 & Appleyard 1983). Later formed tillers usually senesce prematurely.

SECTION 5 BIOCHEMISTRY

5.1 Toxins

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

5.2 Allergens

Wheat is one of the most commonly grown, processed and consumed human foods and is associated with intolerances and allergies (Tatham & Shewry 2008).

5.2.1 Dust and flour allergies

Wheat grain, dust and the milled products can cause physical irritation which may lead to a range of allergic reactions (Simmonds 1989). Allergy symptoms range from mild rhinitis to asthma and severe bronchial irritation in responses to the inhalation of flour or dust. Anaphylaxis has been reported to occur rarely in children (OECD 2003). Baker's asthma and rhinitis are well characterised allergic reactions to the inhalation of wheat and cereal flours (Tatham & Shewry 2008). There are a number of candidates for the allergenic proteins in wheat (OECD 2003). Baker's Asthma may be a response to a number of compounds in wheat flour including a number of α -amylase inhibitors, as well as cross-reactive carbohydrate determinants (Sander et al. 2011). In addition, wheat has been implicated in food-dependent exercise-induced anaphylaxis, where an allergic reaction is induced by intake of a causative food and subsequent exercise – the combination of both food and exercise are required (Tatham & Shewry 2008).

5.2.2 Coeliac disease

Coeliac disease is a condition in which the small intestine is damaged when exposed to gluten, which is found in wheat, barley, rye and triticale (Digestive Health Foundation 2012). This results in poor absorption of nutrients and a variety of related issues (Digestive Health Foundation 2012)

Inheritance of coeliac disease is multigenic and has been strongly associated with European populations (Kasarda 2004). It is more prevalent in females than in males (Hischenhuber et al. 2006). Estimates of the prevalence of coeliac disease vary widely across locations and times (Simmonds 1989; Fraser & Ciclitira 2001; Catassi et al. 1996). In Australia the prevalence of coeliac disease is estimated at approximately one in 100 (Digestive Health Foundation 2012), which is similar to recent rates estimated for Europe, North and South America, north Africa and the Indian subcontinent (Hischenhuber et al. 2006).

Symptoms of coeliac disease vary and sufferers may have many symptoms or none. They commonly include diarrhoea, weight loss, nausea, flatulence and abdominal discomfort, as well as tiredness and weakness often due to a degree of iron and/or folic acid deficiency and resultant anaemia (Catassi et al. 1996; Digestive Health Foundation 2012).

Onset of symptoms may occur very early in life or may be delayed even until very late in life, resulting in speculation about environmental triggers for the disease, potentially including 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) and references cited therein). Wheat germ is reported to contain a haemagglutinin 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) and references cited therein). 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, wheat germ muesli contains an unprocessed form of lectins, whereas wheat germ baked in bread contains an inactivated form which is not as easily recognised by the immune system (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.

The insecticidal properties of lectins and their role in crop protection has been reviewed, including their potential roles in wheat (Macedo et al. 2015). A transgenic wheat line which expresses a plant lectin was shown to affect the fecundity, but not survival of insects fed on wheat leaves. The authors of this study suggest that this indicates potential for use of such plants in integrated pest management systems (Stoger et al. 1999).

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. Wheat, rye and rape have been identified as crop plants which can accumulate nitrate (Stoltenow & Lardy 2008; Yaremci 1991), as can sorghum (Yaremci 1991). In monogastric animals the risk of nitrate poisoning is much less because conversion to nitrites occurs closer to the end of the digestive tract (Yaremci 1991). Cattle and sheep can generally tolerate up to 0.5% nitrate on a dry matter basis.

There are two forms of nitrate toxicity in stock. 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) (Yaremci 1991).

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 which can be fatal, 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. The nutritional content of a few important wheat products is shown in Table 5. More information is available (Simmonds 1989; Food Standards Agency 2002; OECD 2003) and references therein).

Table 5. The composition of wheat products per 100g edible portion (Food Standards Agency 2002).

Product	Protein ¹	Fat (g)	CHO (g)	Starch (g)	Total Sugar (g)	Vitamin E (mg)	Thiamin (mg)	Riboflavin (mg)	Niacin (mg)	Folate (µg)
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
Wholemeal 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

* values are estimates

^ unfortified values not given

? no data given

Wheat bran can be a good source of dietary fibre, helping in the prevention and treatment of some intestinal disorders, although care must be taken for older populations (Simmonds 1989). In a study comparing the phytochemical profiles, total phenolic and carotenoid content and antioxidant activity in milled grain of eleven wheat varieties including red and white wheat and durum wheat, significant differences were found between varieties for the carotenoid and total ferulic acid content (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). These authors also suggest the combination of both fractions exert greater overall physiological effects than each separately (Adom et al. 2005).

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic stress limiting growth

6.1.1 Nutrient stress

Common symptoms of nutrient deficiency include chlorosis, necrosis, reduced growth and reduced tillering/yield. Main symptoms are described in (Bowden et al. 2008). Nutrient deficiency is often linked to enzyme dysfunction or degradation. Rubisco (among other chloroplast proteins) is degraded during or after abiotic stresses, to allocate nitrogen to other compartments and organs (Feller et al. 2008). Nitrogen, phosphorus, potassium and sulphur deficiencies have been linked to a decrease in nitrate reductase activity (Harper & Paulsen 1969). Boron toxicity has also been observed in wheat (Bolland et al. 2000). Aluminium toxicity has also been noted in acidic soils in Western Australia (GRDC 2015c).

6.1.2 Temperature and water stress

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, with a concentration of rainfall during the winter months while summer months are drier. Wheat is subjected to drought and heat stress (as well as frost, to a lesser extent). Heat stress generally results in suppressed growth and lower yield but is rarely lethal. Heat stress can affect both vegetative and reproductive tissues, impacting on photosynthesis efficiency or male and female fertility (Gusta & Chen 1987). Under heat stress hormone homeostasis is altered, the rate of carbon assimilation decreases as Rubisco activity is impaired and oxidative damage is frequently observed (see (Barnabas et al. 2008) for review).

Freezing can impact grain yield and quality. Cold injuries increase with the length of exposure to low temperatures. Depending on the stage of development, yield can be reduced to zero. Frost during flower and seed development causes more damage than during vegetative growth (Gusta & Chen 1987).

Water deficit affects every aspect of wheat development, from germination to yield. Protein synthesis, photosynthesis, respiration and transpiration are most impacted by water stress (Gusta & Chen 1987; see also Barnabas et al. 2008 for review). Drought and heat stresses are often combined, and have a greater detrimental effect on growth compared to individual stress. Stomatal conductance is especially impaired (Barnabas et al. 2008).

6.1.3 Salt stress

Salinity is a significant issue in south-western Australia and in some parts of the Murray Darling Basin. In 2000, 5.7 million hectares of Australia were assessed as having a high potential to develop salinity. More than two million hectares of broadacre farmland were estimated to be affected by dryland salinity, with more than half in WA (ABS 2002). Predictions indicate that unless effective

solutions are implemented, the total area affected by soil salinity could increase to 17 million hectares by 2050, more than 11 million hectares of which is agricultural land (ABS 2013c).

Salt stress impairs wheat growth and development, reduces photosynthesis efficiency, decreases respiration and protein production. Salt can also trigger physiological responses seen in drought stress (see Sairam et al. 2002 for review).

6.2 Abiotic tolerances

Some wheat varieties display tolerance to aluminium toxicity (Trainor et al. 2015). Likewise some varieties show tolerance to boron toxicity (Bolland et al. 2000; GRDC 2014; GRDC 2015b).

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

A number of weeds occur in Australian wheat crops, however not all warrant control in wheat production or in all seasons. In the western growing region the most common weeds in wheat crops include wild radish (*Raphanus raphanistrum*), annual ryegrass (*Lolium rigidum* Gaudin), wild oats (*Avena fatua* L.) and brome grasses (*Bromus* spp.) (GRDC 2015c). In the northern wheat growing region, the main weeds are wild oats (*A. fatua*), paradoxa grass (*Phalaris paradoxa* L.), awnless barnyard grass (*Echinochloa colona* (L.) Link.), annual ryegrass (*L. rigidum*) and fleabane (*Conyza* spp.) (GRDC 2014). Herbicide tolerance has become an important problem in the management of weeds in wheat crops. Several of the most common weeds, namely wild radish, annual ryegrass (in both western and northern regions) and awnless barnyard grass, exhibit resistance to herbicides including glyphosate (GRDC 2015c; GRDC 2014). See Section 2.3.3 for information on weed management practices in Australia.

7.2 Pests and pathogens

7.2.1 Vertebrate pests

Damage to wheat crops by birds has been noted in Australia and around the world (Temby & Marshall 2003; Jones 1987; Massam 2001; Jarman & McKenzie 1983; Davies 1978; Coleman & Spurr 2001; Massam 2000). In Australia, birds such as the sulphur-crested cockatoos (Temby & Marshall 2003), cockatiels (*Nymphicus hollandicus*) (Jones 1987), long-billed corellas (*C. tenuirostris*), galahs (Temby & Marshall 2003), tree sparrows (*Passer montanus*) and house sparrows (*P. domesticus*) (Massam 2000) and emus (Davies 1978) are known to cause damage to cereal crops. Birds such as cockatoos damage the cereal crop most during germination in autumn (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). Birds and mice may also damage grain stored on farm (GRDC 2014; GRDC 2015c).

Kangaroos are reported to damage grain crops by feeding on seedlings or trampling mature plants. Eastern grey kangaroos (*Macropus giganteus*), for example, may feed on young green cereal crops when native grasses are dry and producing no new growth (Hill et al. 1988). Kangaroos are more commonly a problem in dry years (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 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). The average territory size of mice varies between breeding and non-breeding seasons, from 0.015 to 0.2 hectares respectively (Krebs et al. 1995). Mice have been noted as moving up to 300m in a day and numbers can build up and decline quickly (GRDC 2015c).

7.2.2 Invertebrate pests

The five most important invertebrate pests associated with wheat crops in Australia are redlegged earth mites (*Halotydeus destructor*), blue oat mites (*Penthaleus* spp.), locusts (various spp.), lucerne fleas (*Sminthurus viridis*) and slugs (various spp.) (Murray et al. 2013). These five pests cost the wheat industry over \$100 million annually in losses and controls costs (Murray et al. 2013). Other invertebrates, such as snails, brown wheat mites (*Petrobia latens*), wheat curl mites (*Aceria tosichella*, a vector of wheat streak mosaic virus), various armyworms, cutworms and budworms (*Lepidoptera: Noctuidae*), beetles, earwigs and slaters infest wheat, but cause less overall losses to crops, however this analysis does not include the impact of invertebrate pests on grain quality (Murray et al. 2013). Rutherglen bug (*Nysius vinitor* Bergr) is also noted as an insect pest of wheat in Australia (Miller & Pike 2002; ALA 2010). Invertebrate pests are also found in the post-harvest grain. Lesser grain borers (*Rhyzopertha dominica*), rust-red flour beetle (*Tribolium castaneum*), rice weevils (*Sitophilus oryzae*), saw-tooth grain beetles (*Oryzaephilus surinamensis*), flat grain beetles (*Cryptolestes ferrugineus*) and book lice (order Psocoptera) all cause substantial economic losses when they attack stored wheat (GRDC 2013a; GRDC 2013b).

7.2.3 Pathogens

Wheat is economically the most important crop in Australia and wheat diseases can reduce the quantity and quality of grain yield (Table 6).

Table 6. Diseases of wheat reported in Australia (Murray & Brennan 2009).

Causal organism	Disease name
Necrotrophic Leaf Fungi	
<i>Cochliobolus sativus</i>	Bipolaris leaf spot
<i>Drechslera wirreganensis</i>	Wirrega blotch rot
<i>Mycosphaerella graminicola</i>	Septoria tritici blotch
<i>Phaeosphaeria avenaria</i> f.sp. <i>triticea</i>	Septoria avenae blotch
<i>Phaeosphaeria nodorum</i>	Septoria nodorum blotch
<i>Pyrenophora semeniperda</i>	Ring spot
<i>Pyrenophora tritici-repentis</i>	Yellow spot
Biotrophic Leaf Fungi	
<i>Blumeria graminis</i> f.sp. <i>tritici</i>	Powdery mildew
<i>Puccinia graminis</i> f.sp. <i>tritici</i>	Stem rust
<i>Puccinia triticina</i>	Leaf rust
<i>Puccinia striiformis</i>	Stripe rust
<i>Sclerophthora macrospora</i>	Downy mildew
<i>Urocystis agropyri</i>	Flag smut
Root & Crown Fungi	
<i>Fusarium culmorum</i>	Foot rot
<i>Fusarium pseudograminearum</i>	Crown rot
<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	Take-all
<i>Pythium</i> spp.	Damping off/root rot
<i>Rhizoctonia solani</i>	Barepatch

Causal organism	Disease name
<i>Tapesia yallundae</i>	Eyespot
<i>Wojnowicia graminis</i>	Basal rot
<i>Cochliobolus sativus</i>	Common root rot
Inflorescence Fungi	
<i>Claviceps purpurea</i>	Ergot
<i>Fusarium graminearum</i>	Fusarium head blight (scab)
<i>Tilletia laevis</i> , <i>Tilletia caries</i>	Common bunt
<i>Ustilago tritici</i>	Loose smut
Nematodes	
<i>Anguina tritici</i>	Seed gall nematode
<i>Heterodera avenae</i>	Cereal cyst nematode
<i>Merlinius brevidens</i>	Stunt nematode
<i>Pratylenchus crenatus</i>	Root lesion nematode crenatus
<i>Pratylenchus neglectus</i>	Root lesion nematode neglectus
<i>Pratylenchus penetrans</i>	Root lesion nematode penetrans
<i>Pratylenchus teres</i>	Root lesion nematode teres
<i>Pratylenchus thornei</i>	Root lesion nematode thornei
<i>Radopholus nativus</i>	Burrowing nematode nativus
<i>Radopholus vangundyi</i>	Burrowing nematode vangundyi
Bacterial diseases	
<i>Pseudomonas syringae</i> pv. <i>atrofaciens</i>	Basal glume rot
<i>Pseudomonas syringae</i> pv. <i>syringae</i>	Bacterial leaf blight
<i>Xanthomonas campestris</i> pv.	Black chaff
Viruses	
Barley yellow dwarf luteoviruses	Barley yellow dwarf virus
High plains virus	High plains disease
Wheat streak mosaic virus	Wheat streak mosaic

Incidence and severity of disease varies across and within wheat growing regions in Australia. One example is *Septorium nodorum* blotch which cause major loss in the Western region, but has negligible effect in other regions, while cereal cyst nematode causes significant losses in the South Australian and Western Victorian zones, but effectively no loss in other zones of the Southern region (Murray & Brennan 2009). It should be noted that in comparing three studies published over a 21 year period, the diseases ranked highest in terms of their potential or present loss⁵ varied between studies (Table 7). This highlights the fact that disease and pathogen incidence, severity and/or costs can vary over time as new challenges arise or previous challenges are managed.

⁵ Potential costs (or severity or incidence) of damage are those which would occur in the absence of control measures. Present costs are the costs (or severity or incidence) which occurs with current control measures.

Table 7: Ranking of losses from major wheat pests and diseases in Australia.

Disease	1988 ¹		Rank 1998 ²		2009 ³	
	Potential ^a	Present ^b	Potential	Present	Potential	Present
Bunt	1		1			
Take all	2	1	2	3		
Stripe rust	3		3		1	2
<i>Septoria tritici</i> blotch	4	2	5			
Stem rust	5				4	
Cereal Cyst Nematode	6	3		5	3	
Black Point		4				
Yellow Spot		5		4	2	1
Crown Rot			4	2	5	4
<i>Septorium nodorum</i> blotch			6	1		3
Root Lesion Nematode				6		
<i>Pratylenchus neglectus</i>						5

Sources: ¹ (Brennan & Murray 1988); ² (Brennan & Murray 1998); ³ (Murray & Brennan 2009)

^a based on costs calculated which would occur in the absence of control measures

^b based on costs calculated which occur with current control measures

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). These isolates lacked pathogenicity gene and did not produce a toxin and the authors suggest that there is an important and possibly beneficial relationship between the plant and the microorganisms (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 self- or wind-pollination 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 and seeds adapted for short and long range dispersal (Keeler 1989).

During domestication of the modern wheat plant, characteristics that benefited farmers were selected. This process also greatly reduced the ability of cultivated wheat to survive without the intervention of farmers (Eastham & Sweet 2002). Loss of seed shattering in wheat was selected in order to increase the ease of harvest, but this trait reduces the capacity for natural seed dispersal. Increased grain size was selected to improve germination rates under tillage, but this trait correlates with lower total number of seeds produced. Grains without hulls were selected to improve ease of threshing, however, hulled varieties have more reliable germination under environmental stresses (Purugganan & Fuller 2009).

8.1 Weediness status on a global scale

An important element in predicting weediness is a plant's history of weediness in any part of the world (Panetta 1993; Pheloung 2001). Wheat has been grown for centuries throughout the world

without any reports that it is a serious weed pest. There are a number of reports of wheat becoming naturalised in areas where it is not a native species, including California (Calflora 2015) and the Canadian prairies and North American central Great Plains (Harker et al. 2005 and references therein).

8.2 Weediness status in Australia

Wheat is not classified as a weed of national interest in Australia ([Department of Environment National Weeds Lists](#); accessed 18 Jan 2016). In natural ecosystems, wheat is classified as a naturalised plant known to be a minor problem warranting control at three or fewer locations within a state or territory (Groves et al. 2003). It is considered a minor problem in a few natural environments in Tasmania (Glover 2002). In agricultural ecosystems, wheat is classified as a naturalised plant known to be a minor problem warranting control at four or more locations within a state or territory (Groves et al. 2003). Elsewhere, it is suggested that although volunteer wheat grows where cultivated seed is dropped, it is probably not truly naturalised in Victoria or South Australia (Walsh & Entwisle 1994; Jessop et al. 2006).

Some other species of *Triticum* and all species of the closely related genus *Aegilops* are prohibited for import into Australia as they have been assessed as posing a high risk of becoming weeds in Australia ([Australian Biosecurity Import Conditions website](#); accessed 18 Jan 2016).

8.3 Weediness in agricultural ecosystems

Wheat is a naturalised non-native species present in agricultural ecosystems in all Australian states and territories with the exception of the Northern Territory (Groves et al. 2003). There are a few reports of volunteer wheat in the Northern Territory found along roadsides and in home gardens ([Atlas of Living Australia](#), accessed 4 March 2015); these likely represent transient rather than naturalised populations. Wheat is known to be a minor problem with control warranted at four or more locations within a state or territory. Volunteers occur in follow-on crops and if not controlled can harbor disease (Groves et al. 2003).

Volunteer wheat is a recognised weed in agricultural fields in the Canadian prairies and North American central Great Plains (Harker et al. 2005 and references therein). A three year study of volunteer spring wheat emergence across the prairies found that most volunteer wheat emerged during the first year following dispersal. The overall volunteer wheat emergence rate in continuous cropping fields, in the first year of the study, was 3.3 plants m². At the end of the three year monitoring period no viable wheat seeds were detected in the soil seed bank. From these results the authors suggest that volunteer wheat will not become a major agricultural problem (Harker et al. 2005).

8.4 Weediness in natural ecosystems

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

8.5 Control measures

In Australia, volunteer wheat is often controlled to reduce the risk of pests and diseases surviving between seasons. The most effective control technique is herbicide spraying, though heavy grazing or tillage can also be effective (GRDC 2009). As of 18 Jan 2016, there were 266 herbicide products registered by the APVMA for use on volunteer wheat ([APVMA website](#)). These include herbicides from mode-of-action groups A, B, I, L, M and N. The [National Variety Trials](#) website has links to information on testing of wheat varieties for tolerance to commercially used herbicides, listing whether or not applications of herbicides at recommended or above recommended rates has an effect on wheat yield.

8.6 Weed risk assessment of wheat

The weed risk potential of wheat has been assessed (Appendix A) using methodology based on the Australia/New Zealand Standards HB 294:2006 National Post-Border Weed Risk Management Protocol. The National Post-Border Weed Risk Management Protocol evaluates weediness by relating the likelihood of risk to the feasibility of control methods for weeds (Auld 2012). The Protocol has been used as the basis for several weed management systems, for example, the South Australian weed risk management guide (Virtue 2004). These properties relate to invasiveness, impacts and potential distribution. The distribution of wheat is driven by economics, as well as factors such as climate and soil suitability.

In summary, as a volunteer (rather than a crop) wheat is considered to:

- have a low ability to establish amongst existing plants
- have a low tolerance to average weed management practices in cropping and intensive land uses
- have a short time to seeding (less than one year)
- have a low annual seed production and a low ability for volunteers to establish in any land use
- not reproduce by vegetative means
- be unlikely to undergo long distance spread by natural means
- be commonly spread long distance by people from dryland and irrigated cropping areas, as well as from intensive land uses
- have a limited ability to reduce the establishment or yield of desired plants
- have a low ability to reduce the quality of products or services obtained from all land use areas
- have a low potential to restrict the physical movement of people, animals, vehicles, machinery and/or water
- have a low potential to negatively affect the health of animals and/or people
- be able to act as a reservoir for a range of pests and pathogens
- have a low effect upon soil nutrients, salinity, stability and the water table.

This is consistent with previous assessments of wheat in Australia summarised in Section 8.2, and provides a baseline for the assessment of GM wheat.

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

Vertical gene transfer is the transfer of genetic material from parent to offspring by reproduction, either sexual or asexual. Gene transfer can be intraspecific, interspecific or intergeneric. This section deals with gene transfer by sexual reproduction only, as wheat does not reproduce by any asexual mechanism. Gene transfer requires sympatry of the cultivated and wild species, synchronous pollen emission of the donor and stigma receptivity of the recipient, as well as viability of the progeny (Zaharieva & Monneveux 2006).

The likelihood of wheat gene transfer and establishment of subsequent hybrids depends on a series of factors summarized by (Gustafson et al. 2005). Plant mating system and pollen characteristics are the two main factors influencing gene flow between populations (Waines & Hegde 2003). Details of pollen production and outcrossing are given in Section 4.2 including information about pollen shedding rates, pollen movement and outcrossing rates. Varying estimates are given for these parameters based on factors such as variety and environmental conditions.

The environmental conditions needed for maximising wheat pollen-mediated gene flow can be summarised as follows. A hot, dry period prior to flowering would have to be followed by cool temperatures, with high relative humidity and strong, prevalent winds at anthesis. This would allow

maximum flower opening, pollen dispersal, pollen viability and stigma receptivity (Gustafson et al. 2005). Wheat has been described as a low risk crop for both intra- and interspecific gene flow (Eastham & Sweet 2002).

9.1 Intraspecific crossing

T. aestivum is a cultivated species, with no known wild or weedy strains (see Section 8). Thus, the potential for gene transfer to wild *T. aestivum* populations is low. However, cultivated varieties within the genome lineage of *T. aestivum* can successfully be cross-bred, naturally or under controlled conditions. Gene transfer may occur more frequently, as the parent lines are sexually compatible and may be grown in proximity to one another (Waines & Hegde 2003). The progeny is fertile, with fully developed endosperm (OECD 1999; Matus-Cádiz et al. 2004).

Intraspecific pollen-mediated gene flow has been studied at the field and commercial scales in Canada (Matus-Cádiz et al. 2004; Matus-Cádiz et al. 2007). The impact of 16 to 30 ha pollen blocks on neighbouring fields was examined within a 2.7 km radius (for the 16 ha pollen block) and 10 km radius (for the 30 ha pollen block) from the central pollinator source. The authors showed that intraspecific gene flow could be detected at trace rates ($\leq 0.01\%$) up to 300 m (for a 16 ha pollinator block) or 2.75 km (for a 30-ha pollinator block) (Matus-Cádiz et al. 2004; Matus-Cádiz et al. 2007). Gene flow was dependent on environmental conditions, with higher gene flow observed in cooler, more humid and wetter conditions (Matus-Cádiz et al. 2004). The authors suggest that the 0.01 % trace rate observed can be considered a worst-case scenario and a minor contribution to gene flow between cultivars (Matus-Cádiz et al. 2007). However, they conclude that, based on these results, a tolerance level of 0 % GM wheat in non-GM grains is unrealistic (Matus-Cádiz et al. 2004; Matus-Cádiz et al. 2007). Other authors have also concluded that a guarantee of zero gene flow is not possible for any plant that sheds pollen (Waines & Hegde 2003). A 1 to 5 % tolerance level was considered more realistic (Matus-Cádiz et al. 2004; Matus-Cádiz et al. 2007). Isolation distances of up to 45 m were recommended for wheat to reduce pollen-mediated gene flow to predictable levels (Hucl & Matus-Cádiz 2001; Hanson et al. 2005).

The rate of intraspecific pollen-mediated gene flow in south-eastern Australia has been shown to be lower than that observed overseas (Gatford et al. 2006). Using a series of small pollinator blocks, which has been shown to underestimate pollen flow (see above) these authors measured intraspecific gene flows far lower than those observed in similar conditions overseas, with a maximum rate of 0.055 % at 8 m from the pollen source (Gatford et al. 2006). This low gene flow could be explained by environmental and morphological factors. Low relative humidity and warmer temperatures could have accelerated pollen desiccation. Hot, dry weather conditions have been shown to lower pollen viability to less than 15 minutes (D'Souza 1970). It has also been suggested that as most Australian elite cultivars have a closed flower structure, floral morphology of the recipient could play a role in the gene flow rates observed (Gatford et al. 2006). Based on these results, they recommend a 12 m separation between GM and non-GM crops (Gatford et al. 2006).

Another study in Switzerland examined outcrossing between GM and non-GM wheat of the same and different lines. This study found that outcrossing from non-GM and GM lines to GM and non-GM lines varied between parental lines, with distance and with the location of crops in relation to one another (direction). In one experiment outcrossing rates declined from 0.7 % at 0.5 m to 0.03 % at 2.5 m (Rieben et al. 2011). A case-by-case approach was recommended in determining the likelihood of outcrossing between GM and non-GM crops due to the range of factors which might influence outcrossing rates (Rieben et al. 2011).

9.2 Natural interspecific crossing

Interspecific hybridization is considered a ubiquitous process in flowering plants. However, viable natural hybrids are generally rare and highly sterile, with a shrunken endosperm (Matus-Cádiz et al.

2004; Raybould & Gray 1993). Populations rarely persist unless hybrids can backcross with one of the parental lines (Raybould & Gray 1993; Zemetra et al. 1998).

Some successful natural hybridization events have nonetheless been observed between *T. aestivum* and the other lineages from the *Triticeae* tribe, with gene flow occurring at low rate (see (Jacot et al. 2004) for review). Traditional mixed cultivation of diploid, tetraploid and hexaploid wheats in the Middle East and Transcaucasia has given rise to new subspecies (Matsuoka 2011). For example, morphological and genetic studies have shown that the endemic Georgian wheat and macha wheat (respectively tetraploid and hexaploid) are issued from a cross between the tetraploid *T. turgidum* and *T. aestivum* (Matsuoka 2011; Dvorak et al. 2012). F₁ hybrids from *T. aestivum* x *T. turgidum* are pentaploids (AABB₁D), and the segregating progeny is fertile (82.27 % fertility rate) (Wang et al. 2005). Interspecific pollen-mediated gene flow is low, with trace levels (≤ 0.05 %) observed past 20 m from the pollinator source. No gene flow was detected at or beyond 40 m from the source (Matus-Cádiz et al. 2004). *T. aestivum* and *T. turgidum* are grown in overlapping areas in south Qld, northern NSW, western Vic. and south-western SA (Figures 5a and 5b).

9.3 Natural intergeneric crossing

Intergeneric hybridization has been observed in natural conditions. The first report of natural cross between wheat and *Aegilops* was documented in Europe in 1825 (van Slageren 1994). It was later demonstrated that *T. aestivum* originated from a cross between *T. turgidum* and *Ae. tauschii* (reviewed in (Matsuoka 2011)). Because of their common ancestor, wheat and *Aegilops* species share the same D genome. Thus gene flow between these species is expected to be more likely if genes are located within the D genome (Schoenenberger et al. 2006; Zemetra et al. 1998; Jacot et al. 2004). Spontaneous hybridizations between *T. aestivum* and *Aegilops* sp. have been observed on field margins (≤ 1 m from the field) in Spain, with a spontaneous hybridisation rate of 0.19 % (Loureiro et al. 2006). Average self-fertility for the pentaploid hybrid has been observed ranging from 0 to 3.22 % (Loureiro et al. 2008; Wang et al. 2001). Further restoration of tetra- or hexaploidy is possible, following backcrosses with the parent lines (Zemetra et al. 1998; Schoenenberger et al. 2006).

Ae. cylindrica is the *Aegilops* species with the most pronounced tendency to weediness. It is considered a noxious weed in winter wheat cropping systems in the western United States, mainly due to its hardiness and its competitiveness (one plant can produce up to 135 tillers) (Wang et al. 2001; Schoenenberger et al. 2006). The introgression of imidazolinone resistance from wheat to *Ae. cylindrica* in field conditions has been observed as a hybridization rate of 0.1 % and a maximum distance of 16 m (Gaines et al. 2008).

There are no *Aegilops* species native to Australia. The Australian government has declared *Aegilops* a pest. Its entry is prohibited, unless the seeds are to be grown under quarantine conditions for wheat breeding (Department of Agriculture and Water Resources). Although some specimens have been collected, presumably originating from seed accidentally introduced or straying from that brought in for breeding programs (ALA 2010), no *Aegilops* species is considered to be naturalised in Australia.

5a



5b

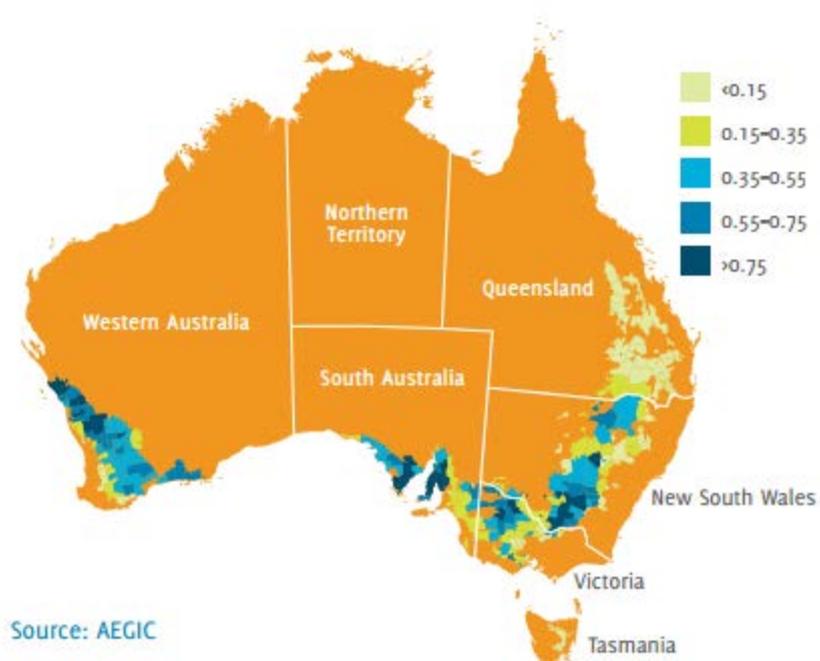


Figure 5: Wheat growing regions of Australia. 5a: *T. turgidum* cultivation areas in Australia (AEGIC 2014); 5b: Australian wheat growing areas with predicted yields for 2015 (AEGIC 2015).

Hybridisation between wheat and barley (*H. vulgare*) has not been recorded under natural conditions. A maximum frequency of pollen-mediated gene flow of 0.005 % was observed between wheat and barley over a distance of 10 m under field conditions in South Australia (Gatford et al. 2006). Only one case of natural hybridisation between wheat and the weedy species *H. marinum* has been reported (see Guadagnuolo et al. 2001). The authors suggest that this is a rare event but nonetheless recommend a 20 to 30 m isolation distance between GM wheat field and *H. marinum*.

H. marinum has been observed in the Australian wheatbelt area, more specifically in NSW, Vic., SA and WA (Simon & Alfonso 2014).

Other members of the *Triticeae* tribe have been described in Australia. Their distribution, potential weediness and the existence of hybrids with wheat are detailed in Table 8.

Table 8: Non-cultivated *Triticeae* genera in Australia: distribution, weediness, and known hybrids with wheat.

Genus	Status	Presence in the wheatbelt	Weed status	Hybrids
<i>Aegilops</i> ^{a,b,c}	Introduced	✗	Pest	✓
<i>Anthosachne</i> ^{b,d,e}	Native	✓ (Qld, NSW, Vic., SA, WA)	/	✗
<i>Australopyrum</i> ^{b,d,e}	Native	✓ (south-eastern NSW)	/	✗
<i>Elymus</i> ^{b,e,f}	Introduced	✓ (Qld, NSW, Vic., SA, WA)	Weed	✓*
<i>Eremochloa</i> ^{b,d}	Native [?]	✗	(Endangered)	✗
<i>Hordeum</i> ^{a,c,e}	Introduced	✓ (NSW, Vic., SA, WA)	Weed	✓
<i>Ophiorus</i> ^{b,e}	Native	✗	/	✗
<i>Parapholis</i> ^{b,e,g}	Introduced	✓ (NSW, Vic., SA, WA)	Weed	✗
<i>Thinopyrum</i> ^{b,e,f,g}	Introduced	✓ (NSW, Vic., SA, WA)	Weed	✓*

* Hybrids produced under experimental conditions, no known occurrence of natural hybridization.

[?] Endemicity of the species is still discussed

Sources: ^a (Jacot et al. 2004); ^b (Simon & Alfonso 2014); ^c (Eastham & Sweet 2002), ^d (Barkworth & Jacobs 2011); ^e (ALA 2010); ^f (Bell et al. 2010); ^g (Sandercock & Schmucker 2006).

9.4 Artificial interspecific and intergeneric crossing

Artificial hybridization has been commonly used in wheat breeding (OECD, 1999). Hand pollination, use of phytohormones such as gibberellic acid or 2,4-D, *in vitro* anther cultivation, embryo rescue and artificial chromosome doubling using colchicine are routinely used (see section 2.4 for details). Some of the available studies have been reviewed by (Jacot et al. 2004). Wheat was crossed as a pollinator with *Agropyron*, *Aegilops*, *Elytrigia*, *Roegneria* and *Secale*. These studies showed that crosses under controlled conditions were more successful than natural hybridization (Jacot et al. 2004; Eastham & Sweet 2002). These crosses have been used for wheat improvement. In particular, wheat–*Aegilops* interspecific hybrids have been developed and useful agronomical traits such as disease resistance or salt tolerance have been incorporated in the wheat gene pool (Schneider et al. 2008; Colmer et al. 2006).

Hybrids between *H. vulgare* and *T. aestivum* have been produced, in order to transfer agronomical traits to wheat (such as drought resistance and salt tolerance) (Molnar-Lang et al. 2000; Islam et al. 1981; Koba et al. 1991). Hybrids were produced by hand pollination and embryo rescue, cultivated *in vitro* (due to their complete sterility) and backcrossed using the wheat parent. Increased chromosome arm associations have been observed in wheat-barley hybrids regenerated *in vitro* (Molnar-Lang et al. 2000). The authors suggest that this could be used to generate recombinant

progenies and transfer agronomic traits from barley to wheat. *H. marinum* - *T. aestivum* hybrids were recently assessed for their tolerance to salt and waterlogging, demonstrating the importance of wild related species for wheat improvement (Munns et al. 2011).

Two other examples of successful crosses under experimental conditions are triticale and perennial wheat. Triticale, the first successful human-made cereal grain, was first developed in 1888 when fertile hybrids were obtained by crossing wheat and rye (*Secale cereale*) (Ammar et al. 2004). The name triticale combines the names of the two *Triticum* and *Secale* genera involved in the crossing. *T. aestivum* was first used for these crosses, resulting in a sterile hybrid ($2n=28$, ABDR), which can be treated with colchicine to artificially double the chromosome number and create a fertile octaploid hybrid ($2n=56$, AABBDDRR). Most commercial triticales are derived from crosses between *T. turgidum* and rye, producing a hexaploid hybrid ($2n=42$, AABBRR) after chromosome doubling. Most wheat x rye hybrids are completely male sterile and highly female fertile (Hegde & Waines 2004). Wheat x triticale crosses have been performed using hand pollination and embryo rescue. Hybrids obtained were almost totally self-sterile and severe hybrid necrosis was observed in all crosses (Bizimungu et al. 1997).

Crosses between tetraploid/hexaploid wheat and wheatgrass species (such as *Thinopyrum* sp.) have been performed to produce perennial wheat, as a way to reduce the environmental impact of annual crops (Hayes et al. 2012; Bell et al. 2010). Trials in Australia using 81 hybrids have shown that a few of them (3/81) could be harvested over at least three years (Hayes et al. 2012). Several perennial relatives of wheat, such as the native *Elymus scaber* (a species of particular interest as it is widely distributed across Australia's cropping zones) are described as being highly resistant to diseases and/or tolerant to salt (Bell et al. 2010). Conversely, perennial wheat could be a "green bridge" for pathogens, where they could accumulate over several years as no annual crop rotation would take place (Bell et al. 2010).

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APPENDIX A WEED RISK ASSESSMENT OF WHEAT

Species: *Triticum aestivum* (wheat)

Relevant land uses:

1. Intensive⁶ uses (ALUM⁷ classification 5)
2. Production from dryland agriculture (ALUM classification 3.3)
3. Production from irrigated agriculture (ALUM classification 4.3)

Background: The Weed Risk Assessment (WRA) methodology is adapted from the Australian/New Zealand Standards HB 294:2006 National Post-Border Weed Risk Management Protocol. The questions and ratings (see table) used in this assessment are based on the South Australian Weed Risk Management Guide (Virtue 2004). The terminology is modified to encompass all plants, including crop plants.

Weeds are usually characterised by one or more of a number of traits, these including rapid growth to flowering, high seed output, and tolerance of a range environmental conditions. Further, they cause one or more harms to human health, safety and/or the environment. Although wheat has some traits associated with weeds, it is not considered as an invasive weed in Australia. Other than agricultural areas where it is cultivated, wheat is common along the sides of roads and railway lines that have acted as routes for its transportation. It is classified as being naturalised to agricultural areas in all states, except the Northern Territory, and in Western Australia has been recorded as a minor problem in some areas (Groves et al. 2003). Unless cited, information in this weed assessment is taken from this document *The Biology of Triticum aestivum* L. (*Bread Wheat*) v3 (OGTR 2015). This WRA is for **non-GM wheat volunteers** and includes non-GM herbicide tolerant varieties of this crop. Reference made to wheat as a cultivated crop is only to inform its assessment as a volunteer.

⁶ *Intensive use* includes areas of intensive horticulture or animal production, areas of manufacture or industry, residential areas, service areas (e.g. shops, sportsgrounds), utilities (e.g. facilities that generate electricity, electrical substations, along powerlines) areas of transportation and communication (e.g. along roads, railways, ports, radar stations), mine sites and areas used for waste treatment and disposal.

⁷ ALUM refers to the Australian Land Use and Management classification system version 7 published May 2010.

Invasiveness questions	Wheat
<p>1. What is wheat's ability to establish amongst existing plants?</p>	<p>Rating: Low in all relevant land uses</p> <p>Wheat is a domesticated crop that grows best under agricultural conditions. It prefers soils with high fertility and responds well to irrigation, especially during tillering and flowering. Wheat volunteers, mainly derived from seed that is shed at or before harvesting, readily establish in disturbed lands of <i>dryland and irrigated cropping areas</i>, especially along the margins of fields. Seed losses can also occur during harvesting itself, as well as in <i>intensive use areas</i> involved in transport, storage and processing. Volunteers also readily appear in subsequent cereal and non-cereal crops sown on the same land where wheat has been grown and harvested. However wheat has little dormancy and, subsequently, dispersed seed is likely to germinate early and die in unfavourable environmental conditions or be consumed by predators. Wheat does not compete well with other vegetation.</p>
<p>2. What is wheat's tolerance to average weed management practices in the land use?</p>	<p>Rating: Low in all relevant land uses</p> <p>Weed management practices (preventive, cultural and chemical) aim to reduce the presence of weeds and loss in yields due to weeds. In <i>dryland and irrigated cropping areas</i>, where wheat is grown in rotation with other crops, these practices effectively control wheat volunteers. Nevertheless, seeds may germinate after herbicides have been broken down and volunteers may become established. In <i>intensive use areas</i>, such as land adjacent to grain silos and along roadsides and railway tracks, weed management practices minimise the spread of volunteers.</p> <p>The degrees of susceptibility of the currently available wheat varieties to herbicides are available in the respective grower guides for each state⁸.</p>

⁸ Source: [Grains Research and Development website; accessed on 21 January 2016.](#)

3. Reproductive ability of wheat in the land use:	
3a. What is the time to seeding in the land uses?	<p>Rating: < 1 year in all relevant land uses</p> <p>Wheat is an annual crop that generally takes five to seven months to complete its lifecycle under standard agricultural conditions. Volunteer wheat behaves in a similar way.</p>
3b. What is the annual seed production in the land use per square metre?	<p>Rating: Low in all relevant land use areas (from volunteers)</p> <p>As a crop in <i>dryland and irrigated cropping areas</i>, wheat seed yields vary greatly between countries, averaging approximately 300 g/m² (FAO 2015b), or 7500 seeds/m², assuming a weight of 0.04g per seed. In Australia, using data for the 2012-13 crop year, the average yield was 1.76 T/ha or 176 g/m² or about 4400 seeds/m². At a recommended rate of about 100 plants/m² for a 2 T/ha harvest, the 2012-13 data represents a yield of about 44 seeds/plant. A 3% loss is assumed, therefore, approximately 132 seeds/m² would remain on a field post-harvest. One study in Australia indicated that 0.7, 5.6 and 5.3 volunteer wheat plants were present per square metre (measured as 70, 560 and 530 plants per 100 m²) a few months post-harvest in no-till, cultivated stubble-retained and cultivated stubble-burn systems, respectively (Wicks et al. 2000). However, these plants are unlikely to persist and generate seed as typical management practices for follow-on crops or fallow include control of weeds (including wheat volunteers) through herbicide sprays, grazing or cultivation.</p> <p>In <i>intensive use areas</i>, seed production per unit area is likely to be considerably less than that in <i>dryland and irrigated cropping areas</i>, due to suboptimal germination and growth conditions (e.g. lack of moisture and nutrients), and competition by other plants.</p>
3c. Can wheat reproduce vegetatively?	Wheat cannot reproduce by vegetative propagation.
4. Long distance seed dispersal (more than 100 m) by natural means in land uses:	
4a. Are viable plant parts dispersed by flying animals (birds and bats)?	<p>Rating: Occasional in all relevant land uses</p> <p>There is no evidence that flying animals play a major factor in the dispersal of wheat seeds. Some introduced species such as ring-necked pheasant, mallard duck and rock pigeon do not excrete viable</p>

	<p>wheat seeds, but may disperse viable seed from their crop/oesophagus or gizzard if they were killed shortly after consuming the grain. Viable seed can also be transported on the muddy feet/legs of birds (Cummings et al. 2008). Amongst Australian birds, corellas have been shown to excrete some viable wheat seeds after passage through the digestive tract. Corellas readily consume wheat seeds under laboratory conditions with 2% of consumed seeds surviving to germinate under laboratory conditions (Woodgate et al. 2011), thus they may have a minor role in seed distribution. It has also been reported that wheat seeds will germinate after passage through an emu's digestive system, although no experimental evidence was provided (Davies 1978).</p>
<p>4b. Are viable plant parts dispersed by land based animals?</p>	<p>Rating: Unlikely to Occasional in all relevant land uses</p> <p>Wheat seeds do not possess adaptations for dispersal on the exterior (fur) of animals (e.g. hooks or spines). Nonetheless, wheat seeds may be dispersed in the wool of sheep. Seed dispersal by ingestion and excretion by land based animals has been reported. Wheat seeds are known to survive digestion and germinate in the dung of cattle and sheep. Dispersal in the hooves of animals is also probable, but not well reported, thus the frequency is not known. Rodents which hoard seeds could disperse wheat seed from crop production areas (e.g. after harvest) or from volunteers.</p>
<p>4c. Are viable plant parts dispersed by water?</p>	<p>Rating: Unlikely to Occasional in all relevant land uses</p> <p>Dispersal by water is possible, but no data is available. Generally, the presence of a non-brittle (non-shattering) rachis reduces the opportunity for long distance seed dispersal by water. Wheat seeds/ears are heavy and not adapted for water dispersal.</p>
<p>4d. Are viable parts dispersed by wind?</p>	<p>Rating: Unlikely to Occasional in all relevant land uses</p> <p>Dispersal by high winds is possible, but no data is available. Wheat seeds are heavy and do not possess appendages that are designed to facilitate wind dispersal (e.g. they are not "winged"). Generally, the presence of a non-brittle (non-shattering) rachis reduces the opportunity for long distance seed dispersal by natural means.</p>
<p>5. Long distance seed dispersal (more than 100 m) by human means in land uses:</p>	

<p>5a. How likely is deliberate spread via people</p>	<p>Rating: Common in/from all relevant land uses</p> <p>Wheat is a crop species that is purposely transported and cultivated for the production of seed that is part of human food and animal feed. Where wheat is present as a volunteer, it is managed like other weeds. In those instances, wheat would not be spread deliberately.</p>
<p>5b. How likely is accidental spread via people, machinery and vehicles?</p>	<p>Rating: Occasional (to common) in/from all relevant land uses</p> <p>In <i>dryland and irrigated cropping areas</i>, where wheat is planted as a crop, it is common for wheat to be accidentally dispersed by people, machinery and vehicles. Seed is transported by humans after harvesting to silos, and further afield for processing, providing many opportunities for seed dispersal. Seed could be spread along roadsides and railway lines, as well as near storage facilities. Seed can remain on machinery after harvesting (e.g. in the header at the front of a combine harvester, reel, threshing drum, sieves). However, where wheat grows as a volunteer, it would be managed like other agricultural weeds. In those – suboptimal – growing conditions, fewer seeds are expected to be produced per plant than when wheat is cultivated as a crop. Therefore, accidental spread of volunteer seed is expected to occur occasionally. Accidental spread by people, machinery and vehicles may occur in or from <i>intensive use areas</i>. Practices such as the mowing of weeds along roadsides could lead to occasional spread of seeds by machinery.</p>
<p>5c. How likely is spread via contaminated produce?</p>	<p>Rating: Occasional in/from all land use areas.</p> <p>Wheat farming in <i>dryland and irrigated cropping areas</i> is characterised by rotation with other crops, such as canola, lupins and beans. The amount of wheat seed left in the field prior to the planting of a rotation crop will depend upon the efficiency of the wheat harvesting, seed cleaning of machinery, and general weed management procedures. Growth of wheat volunteers within a rotation crop depends on the weed management procedures of the latter crop, while the spread of this wheat depends on the processing of the harvested plant material from the rotation crop. Long distance dispersal via contaminated hay and forage may occur from cropping areas and in or from intensive use areas (such as along roadsides) if harvested for hay or forage.</p>

<p>5d. How likely is spread via domestic/farm animals?</p>	<p>Rating: Occasional in all relevant land uses</p> <p>If livestock are grazed in or adjacent to a wheat field, then it is possible that viable wheat seeds may be spread either in their hooves or fur. Wheat seeds can be dispersed in the wool of sheep. The separation of plant and animal farming minimises this possibility, but sometimes livestock are grazed on rotation crops such as legumes. Whole wheat, or that which has been processed (crushed or rolled), constitutes some livestock feeds (DPI NSW 2014). As noted above (4a & b), wheat seeds can germinate in the dung after passing through cattle and sheep, and can survive digestion by some bird species, but survival through other animals is not known. In the case of processed wheat (dry-milling or coarse grinding), it is expected that only a small amount of viable seed is present in the feed and this would further reduce survival of the seed during digestion.</p>
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Impact Questions	Wheat
<p>6. Does wheat reduce the establishment of desired plants?</p>	<p>Rating: Reduces establishment by < 10% in all relevant land uses</p> <p>Wheat is a domesticated and cultivated plant that typically establishes where land has been disturbed, most particularly in <i>dryland and irrigated cropping areas</i>. These areas are subject to standard weed management practices that would minimise the impact of any wheat volunteers on the establishment of desired crop plants.</p> <p>In <i>intensive use areas</i>, such as along roadsides, desired species may range from native flora to introduced trees, bushes and shrubs. Such areas are often managed, for either aesthetic or practical reasons (e.g. maintaining driver visibility) by the removal of larger trees and invasive weeds. As such, wheat would be treated as a weed and managed accordingly. If left untreated, wheat is not competitive and would struggle to survive and persist amongst other vegetation. Dispersed wheat seed (e.g. along transport routes) is likely to germinate in unfavourable environmental conditions or be consumed by predators.</p>

Impact Questions	Wheat
<p>7. Does wheat reduce the yield or amount of desired plants?</p>	<p>Rating: Reduces yield/amount by < 10% in all relevant land uses</p> <p>Wheat is typically used in rotation with other crops. The rationale behind crop rotation in <i>cropping areas</i> is the desire to break cycles of pest and pathogen infection, manage persistent weeds, and maintain soil moisture and quality. When used as a part of a rotation program, maximising the yield of the follow-on crop is of primary importance. Prior to planting the follow on crop, weeds (including wheat volunteers) would be managed by mechanical or chemical means, thus greatly reducing the density of wheat volunteers. Wheat plants are not competitive amongst other vegetation, are easily managed in follow-on crops and volunteers are effectively controlled in all relevant land use areas (see question 2, above).</p>
<p>8. Does wheat reduce the quality of products or services obtained from the land use?</p>	<p>Rating: Low in all relevant land uses</p> <p>As discussed in questions 6 and 7 above, wheat (as a weed or volunteer) has a low impact on both the establishment and yield/amount of desired species (e.g. the follow on crop in a rotation or desired species along roadsides). Generally, because wheat volunteers are not competitive, their density is expected to be low and they are effectively controlled (see question 2), there is a low expectation that wheat would reduce the quality or characteristics of products, diversity or services available from any land use areas. However, for some follow on crops (e.g. red lentils) even a small amount of wheat seeds (2 seeds per 200 g of lentils) can lower the quality of the crop (Pulse Australia 2014).</p>
<p>9. What is the potential of wheat to restrict the physical movement of people, animals, vehicles, machinery and/or water?</p>	<p>Rating: Low in all relevant land uses</p> <p>As a densely planted mature crop, wheat is never impenetrable and is unlikely to inhibit the passage of people, animals, vehicles, machinery and water. Standard management practices as well as environmental conditions would keep the density of wheat volunteers very low. Thus, the potential for wheat to restrict the physical movement of people, animals or water would be low.</p>
<p>10. What is the potential of wheat to negatively affect the health of animals</p>	<p>Rating: Low in all relevant land uses</p>

Impact Questions	Wheat
and/or people?	There is no evidence that wheat is toxic to humans. A minority of people do suffer from wheat induced allergies, chiefly caused by α -amylase inhibitors and seed storage proteins. Coeliac disease (gluten intolerance), characterised by damage to the intestinal wall and a failure to absorb the nutrients found in food, is an autoimmune disorder induced by an intolerance to cereal storage proteins. Like many plants, excess production of nitrate can occur in wheat, which upon digestion by animals (in particular ruminants) can be converted to nitrite, an ion that is tenfold more toxic than nitrate. Elevated levels of phytic acid in wheat can also be a problem, chelating minerals and preventing their dietary use after digestion by animals. Standard management practices as well as environmental conditions would keep the density of wheat volunteers very low. The proportion of volunteer wheat in animal feed (e.g. hay) is unlikely to be great enough to cause toxicity. Thus the potential for wheat to negatively affect the health of animals or people is considered low.
11. Major positive and negative effects of wheat on environmental health in each relevant land use:	
11a. Does wheat provide food and/or shelter for pathogens, pests and/or diseases in the land use?	<p>Rating: Minor or no effect in all land uses</p> <p>In crop rotation regimes, wheat can provide a disease break, resulting in a decline in the numbers of any pathogen, pest or disease that attacks the follow on crop. However, wheat is associated with a number of insect pests that infect multiple crops. Wheat is susceptible to a range of pathogens, such as bunt, rusts, and nematodes. Infected wheat volunteers could act as a reservoir of these pathogens that can infect crops in subsequent years. Most of these pathogens are specific to wheat or cereals in general, and do not infect plants that are more distantly related.</p> <p>However, the density of wheat volunteers is expected to be low and thus may have only minor or no effect.</p>
11b. Does wheat change the fire regime in the land use?	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to affect fire regimes.</p>

Impact Questions	Wheat
11c. Does wheat change the nutrient levels in the land use?	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to affect nutrient levels.</p>
11d. Does the species affect the degree of soil salinity in the land use?	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to affect soil salinity.</p>
11e. Does the species affect the soil stability in the land use?	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to affect soil stability.</p>
11f. Does the species affect the soil water table in the land use	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to affect the soil water table.</p>
11g. Does the species alter the structure of nature conservation by adding a new strata level?	<p>Rating: Minor or no effect in all relevant land uses</p> <p>The number and density of wheat volunteers is expected to be low for all relevant land uses, and would not be expected to add a new strata level.</p>