Australian Government
Department of Health
Office of the Gene Technology Regulator

The Biology of *Hordeum vulgare* L. (barley)


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Version 2: April 2017

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 has been updated from Version 1 (February 2008) and includes an appendix containing a weed risk assessment of barley volunteers based on the National Post-Border Weed Risk Management Protocol.

For information on the Australian Government Office of the Gene Technology Regulator visit [OGTR website]

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Preamble

This document describes the biology of *Hordeum vulgare* L., with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *H. vulgare*, general descriptions of its morphology, reproductive biology, biochemistry, and 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 *H. vulgare* that may be released into the Australian environment.

Barley is one of the founder crops of Old World agriculture and was one of the first domesticated cereals. It is also a model experimental system because of its short life cycle and morphological, physiological, and genetic characteristics. Barley ranks fourth in world cereal crop production and is used for, in order of importance, animal feed, brewing malts and human food. Barley is a short season, early maturing grain found in widely varying environments globally. In Australia, barley is the second largest field crop (after wheat), and is grown in wheat production areas of all states.

H. vulgare is divided into two subspecies: *Hordeum vulgare* L. ssp. *vulgare* and *H. vulgare* L. ssp. *spontaneum* (C. Koch.) Thell. *H. vulgare* ssp*. vulgare* is cultivated barley, and both this term and the species name will be used in this document. *H. vulgare* ssp. *spontaneum* is the wild progenitor of cultivated barley and will be referred to as wild barley or by the species name.

Section 1 Taxonomy

Barley belongs to the genus *Hordeum* in the tribe Triticeae of the grass family, Poaceae (also known as Gramineae). The Triticeae tribe is a temperate plant group containing several economically important cereals and forages as well as about 350 wild species. The genus *Hordeum* is unusual among the Triticeae as it contains both annual species, such as *H. vulgare* and *H. marinum*, and perennial species, such as *H. bulbosum* (Von Bothmer 1992).

There are 32 species within the *Hordeum* genus, all with a basic chromosome number of x=7. Cultivated barley, *Hordeum vulgare* L. ssp. *vulgare*, and its wild progenitor *H. vulgare* L. ssp. *spontaneum* (C. Koch.) Thell.[1] are diploid species with 2n=2x=14 chromosomes. Other *Hordeum* species are diploid, tetraploid (2n=4x=28) or hexaploid (2n=6x=42) (Komatsuda et al. 1999).

The two species *H. vulgare* and *H. bulbosum* are considered to share a common basic genome, I, which is not related to any other genome in the genus. The genomes of the two annual Mediterranean species, *H. marinum* and *H. murinum*, seem not to be closely related to the other genomes in *Hordeum* and have been designated as X and Y, respectively. The remaining diploid *Hordeum* species are all closely related and share the H genome (Von Bothmer 1992).

Section 2 Origins and Cultivation

2.1 Centre of diversity and domestication

The genus *Hordeum* has centres of diversity in central and south western Asia, western North America, southern South America, and in the Mediterranean (Von Bothmer 1992). *Hordeum* species occur in a wide range of habitats. The majority of the wild perennial species grow in moist environments whereas the annual species are mostly restricted to open habitats and disturbed

[1] In traditional nomenclature, *Hordeum vulgare* ssp. *vulgare* and *H. vulgare* ssp. *spontaneum* are considered separate taxa *(H. vulgare* and *H. spontaneum).*

areas. Many species have adapted to extreme environments and many have tolerance to cold and saline conditions (Von Bothmer 1992).

Cultivated barley is grown in a range of diverse environments that vary from sub-Arctic to sub-tropical, with greater concentration in temperate areas and high altitudes of the tropics and subtropics. Other than the cool highlands, barley is rarely grown in the tropics as it is not suited to warm humid climates (Nevo 1992).

Barley was first domesticated about 10,000 years ago from its wild relative, *H. vulgare* ssp *spontaneum*, in the area of the Middle East known as the Fertile Crescent (Badr et al. 2000). *H. vulgare* ssp. *spontaneum* still grows in the Middle East and adjacent regions of North Africa, in both natural and disturbed habitats, such as abandoned fields and roadsides. In the Fertile Crescent, central populations are often continuously and massively distributed. Peripheral populations become increasingly sporadic and isolated and are largely restricted to disturbed habitats (Nevo 1992).

Until the late nineteenth century, all barleys existed as highly heterogeneous landraces adapted to different environments. Over the past 100 years, the landraces have mostly been displaced in agriculture by pureline varieties with reduced genetic diversity (Nevo 1992). Extensive cultivation, intensive breeding and selection have resulted in thousands of commercial varieties of barley. For commercial purposes, barley varieties are classified into broad classes that are used as a basis for world trade. The major factors used to distinguish barley varieties are feed or malting barley, winter or spring growth habit, starch amylose/amylopectin ratio, hulled or hull-less barley, and six-, four- or two-row varieties (OECD 2004). In two-row (*distichum*[2]) varieties, only one spikelet at each node is fertile. In six-row (*vulgare*) varieties, all three are fertile (see Section 3.2).

The progenitor of cultivated barley, *H. vulgare* ssp. *spontaneum,* has a brittle two-row spike and a hulled grain. Six-row barley appeared about 8000 years ago (Komatsuda et al. 2007). The small, one seed arrow-like spikelets of *H. vulgare* ssp *spontaneum* are adapted to reach the soil through stones and pebbles. However, the spontaneous six-row mutants, which produce larger three seed spikelets, do not have this evolutionary advantage and do not reach the soil as easily therefore they are naturally eliminated from wild barley populations. Thus, six-row barley occurs primarily as cultivars or weeds in agricultural systems (Komatsuda et al. 2007).

In cultivated hull-less barley, which also appeared 8000 years ago, the husks do not adhere to the grain, which falls free on threshing. Other traits improving seed recovery and yield were also selected during domestication of barley. As a result, in cultivated barley the spike is tough and the grains persist, compared to wild barley in which the brittle spikes fragment at maturity and the grains fall. Cultivated barley has also been selected to have low seed dormancy.

2.2 Commercial uses

Barley is the fourth most important cereal crop in the world after wheat, maize, and rice, and is among the top ten crop plants in the world (Akar et al. 2004). Globally, over 148 million tonnes of barley is produced annually on about 50 million hectares. Countries producing the most barley in 2015-16 are summarised in Table 1. Leading exporters of barley include Australia, Ukraine, EU,

[2] Also known as *Hordeum distichum* or *H. vulgare* ssp. *distichum*. Referred to here as a variety based on Briggs (1978).

Argentina and Russian Federation (see Table 1), while the principal markets for importing barley are Saudi Arabia, Iran and China[3].

Table 1: Barley production, area and export, 2015-16[3]

Country	**Production ('000 tonnes)**	**Area harvested ('000 hectares)**	**Trade Year Exports ('000 tonnes)**
European Union	61,517	12,192	8,603
Russian Federation	17,083	8,942	3,738
Ukraine	8,751	3,000	4,673
Australia	8,593	4,105	5,400
Canada	8,226	2,354	1,146
Turkey	7,400	3,400	0
Argentina	4,940	1,250	2,836
United States	4,750	1,278	161
Morocco	3,500	1,600	0
World	148,652	50,069	27,490

Originally, barley was mainly cultivated and used for human food, but it is now used primarily for animal feed and to produce malt, with smaller amounts used for seed and direct human consumption. Barley is also used to produce starch, either for food or for the chemical industry (OECD 2004). In addition, barley has some useful by-products, the most valuable being the straw which is used mainly for animal bedding in developed countries, but also for animal feed in developing and under-developed countries (Akar et al. 2004).

Animal Feed

Globally, up to 85% of barley produced is used for feeding animals, including cattle (beef and dairy), swine and poultry (OECD 2004; Akar et al. 2004). In most cases, the whole barley kernel is rolled, ground, or flaked, prior to being fed, to improve digestibility (OECD 2004).

Barley is considered to have a poorer nutritive value than wheat because its high fibre content means the energy is not easily utilised by animals. Although it has a higher protein content than maize, the diet of high-performing monogastric animals usually needs to be supplemented with other protein sources due to the low content and quality of protein in the barley grain (OECD 2004).

Malt

The second most important use of barley is for malt, which is used mostly in beer, but also in hard liquors, malted milk and flavourings in a variety of foods. Barley malt can be added to many food stuffs such as biscuits, bread, cakes and desserts. Brewer's and distiller grains and sprouts from malting barley also have desirable protein content for animal diets (Akar et al. 2004).

When barley is used for malt, it involves steeping in water, under controlled conditions, allowing the barley grain to germinate or sprout. It is then dried or roasted in a kiln, cleaned, and can be stored

[3] Data: USDA Foreign Agricultural Service's Production, Supply and Distribution (PSD) online database queried 21 March 2017.

for extended periods. Malt itself is primarily an intermediate product and requires further processing, such as fermentation in beer and whisky production (OECD 2004).

In general, two-row barley varieties are preferred for malt production (Australian Bureau of Statistics 2007), although six-row barley is common in some American style lager beers. Malting barley varieties show more uniform germination, need shorter steeping, and have less protein (8–10.5% dry matter) in the extract than feed barleys. In Australia, the best malting barley comes from more southern areas, such as South Australia (SA) and Victoria (Vic), due to climatic conditions (Sims 1990).

Human Food

Traditionally, barley was one of the dominant food grains, but has been surpassed by rice and wheat in many countries. Barley is still an important food grain in several regions of the world, including Morocco, India, China and Ethiopia (OECD 2004). For example, barley as flatbread or porridge is widely consumed in North Africa and parts of Asia. Food barley is generally found in regions where other cereals do not grow well due to altitude, low rainfall, or soil salinity (FAO 2002).

In Western countries, barley is increasing in popularity as a food grain and is used in flours for bread making or other specialties such as baby foods, health foods and thickeners. It is preferred by some food manufacturers due to its lower price compared to wheat and its nutritional value (Akar et al. 2004). There is also a market for Australian barley for shochu (a Japanese alcohol made from barley, sweet potato or rice) production in Japan. Barley starch is used in both the food industry as a sweetener and binder, and the brewing industry, in the production of beer and alcohol (OECD 2004).

Barley must have its fibrous outer hull removed before it can be eaten. Alternatively, hull-less barley varieties, which require minimal processing, have been developed for food applications (National Barley Foods Council 2017). Pearl barley is dehulled barley that has been pearled or polished further, removing some of the bran. Dehulled or pearl barley may be processed into a variety of barley products, including flour and flakes.

2.3 Cultivation in Australia

2.3.1 Commercial propagation

In Australia, growers can either sow barley seed saved from a previous season if it is known to be pure and of good quality, or they can purchase seed. Seed may be bought from neighbouring farms, but only some varieties are permitted by law to be traded amongst growers, and some varieties must also be accompanied by a seed analysis statement.

Seed purchased from a commercial distributor should be certified. Barley 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, for example basic and certified barley seed must be separated from other cereals by a 2 metre wide strip or a physical barrier (fence) (Smith & Baxter 2002). These standards are designed to reduce contamination with seed from other sources in the final certified seed. Standards also set out the allowed contaminant levels in the seed after harvest. The standards in use by the Australian Seeds Authority Ltd were designed to comply with the OECD Seed Certification Guidelines (Australian Seeds Authority Ltd. 2006).

2.3.2 Scale of cultivation

Barley is the main coarse grain (excluding wheat) grown in Australia, with an estimated gross value of $2.4 billion in 2014-15 (Australian Bureau of Statistics 2016). It is grown in wheat production areas in New South Wales (NSW), Vic, Queensland (Qld), Western Australia (WA) and SA (Figure 1). A small amount of barley is also grown in Tasmania (Tas). The area sown to barley in Australia is forecast to be around 4 million hectares for 2016-17 , with production forecast to increase in 2016-17, to a record high of 10.6 million tonnes (Australian Bureau of Agricultural and Resource Economics and Sciences 2016).

While Australia only produced about 6% of the world's barley in 2014-15, it provided about 18% of world barley exports[4] and this is likely due to a relatively small domestic market. For 2014-15, about 68% of Australia's barley crop was exported, primarily for use as animal feed (52%) and malting barley (36%), with about 12% used as malt. The remaining 32% of barley produced in Australia was used domestically, with about 7% used for seed (Australian Bureau of Agricultural and Resource Economics and Sciences 2016). The remaining domestic use is about 30% malting barley and 60% for animal feed[5].

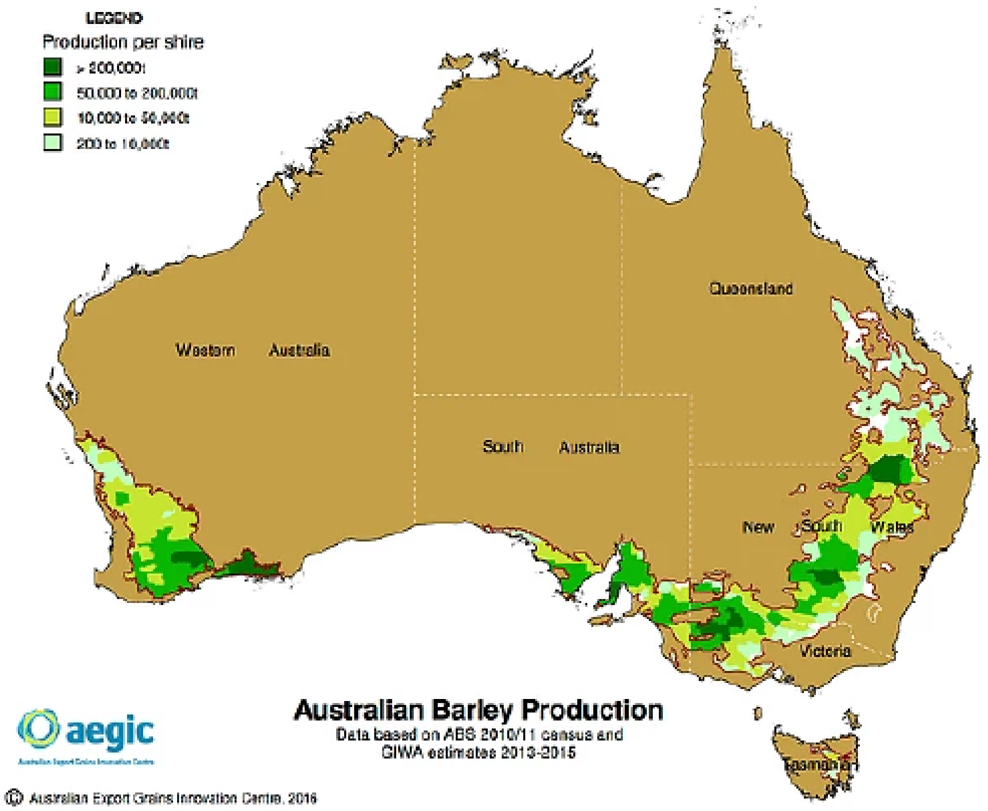

Figure 1: Barley growing shires of Australia (used with permission from Australian Export Grains Innovation Centre, South Perth, WA).

[4] Data: USDA Foreign Agricultural Service's Production, Supply and Distribution (PSD) online database queried 21 March 2017.
[5] Barley Australia website, accessed 21 March 2017.

2.3.3 Cultivation practices

Over 90% of the area sown to barley in Australia is sown to two-row cultivars (Sims 1990). Most of these are spring barleys, but they are predominantly grown as a winter crop. Different barley varieties are suited to, and grown in, different areas of Australia, depending on soil type, climate, end use (malt or feed), and the incidence of pests and diseases. Agronomic information is available online from various State Departments of Agriculture (see Barley Australia website). Additionally, the Grains Research and Development Corporation (GRDC) has published barley production guides for the Northern, Southern and Western regions of Australia (see GRDC website). Specific cultural practices presented in this section are for the Southern Region, encompassing central and southern NSW, Vic, Tas and south-east SA.

Barley is grown mainly as a grain crop, although in some areas it is used as a fodder crop for grazing, with grain being subsequently harvested if conditions are suitable (Australian Bureau of Statistics 2007). Barley being grown for fodder is sown in higher rainfall areas in February and March, and as late as August in the case of spring forage. Grain barley is sown from April to July, depending on variety and location (Sims 1990). In southern Australia, barley is generally harvested from October to December (GRDC 2016b).

Barley is ideally sown at a depth of 3–6 cm into moist soil and a plant density of 80–120 plants/m^2. Sowing depth into dry soils would be 3–4 cm. Densities of less than 80 plants/m^2 can result in reduced yield, and above 120 plants/m^2 can lead to a reduction in seed weight (GRDC 2016b) In Australia, barley is often grown in rotation with wheat, oats and pasture (Australian Bureau of Statistics 2007). Malting barley is best grown after a non-legume crop, to avoid the presence of too much nitrogen in the soil leading to high levels of grain protein. Similarly, nitrogen fertiliser should be applied to achieve optimum levels of grain protein for the end use (see Section 2.2).

There are a number of pests and diseases of barley, which may require management (e.g. application of herbicide or pesticide) during the growing season (see Section 7.2). Integrated weed management practices are used to control weeds in barley crops. Techniques employed include the use of weed-free seed, increasing seeding rates, rotation cropping, and herbicides (see GRDC website: Integrated Weed Management Hub, accessed 17 March 2017) Weed control using specific classes of herbicides may involve a pre-, early post- or late post-emergence application. A number of herbicides can cause a reduction in yield in some barley varieties (GRDC 2016b).

Cultivation options for barley include zero-till, no-till, direct drilling, reduced tillage, or conventional cultivation, with the latter becoming less common over the last 20 years. In most major grain growing regions, no-till farming systems were used by 90% of the growers (Llewellyn & D'Emden 2010). In combination with no- or reduced tillage, stubble can be retained (left standing or cut and spread for mulch), or removed, for example by grazing, burning or cultivation.

Barley dries down well and the use of desiccants is generally not required unless late weed growth needs to be controlled (GRDC 2016b). Barley is usually harvested directly after the grain has ripened and dried to a moisture content of 12%. In some conditions, barley is harvested at higher moisture contents (up to 20%) and then aerated or dried (GRDC 2016b). Alternatively, barley can be cut when the grain is physiologically mature (20 – 30% moisture) and allowed to dry in rows held together by straw (swathes). This method is more frequently used in areas with high likelihood of rain during harvest (Western Australian Department of Agriculture and Food 2017).

2.4 Crop Improvement

2.4.1 Breeding

Barley has been intensively bred for improved performance and quality, resulting in reduced genetic diversity in the elite cultivars. Since 1927, ionising radiation and chemical mutagens have been used to increase mutation rates in barley breeding programs (Horvath et al. 2001). Recently a herbicide tolerant barley line (Scope CL), developed through a mutagenesis-based (non-GM) breeding program was released for commercial production. Scope has tolerance to the broad spectrum herbicide Intervix, a group B herbicide with active ingredients imazox and imazapyr (see Seednet website, accessed 31 March 2017).

Until the mid 1900s, breeders concentrated on conventional crossing to develop new cultivars (Pickering & Johnston 2005). In these programs, hundreds of thousands of lines are often required to produce a new variety.

However, since the 1950s, significant yield improvements have resulted from the application of more advanced plant gene technologies (Pickering & Johnston 2005; Thomas 2003). An extensive catalogue of genetic stocks, such as aneuploid lines, deletion stocks and translocation lines, is available for barley (Varshney et al. 2007). A number of high-density genome-wide profiling techniques are now available for barley breeding, including sequencing of the genome, high-density mapped single nucleotide polymorphism (SNP) arrays, and exome (the gene coding part of the genome) capture arrays (Dawson et al. 2015). High density molecular genetic maps are being used in marker assisted selection (MAS) for breeding as well as for map based cloning and comparative mapping studies. Marker assisted backcrossing used in combination with the production of doubled haploids can halve the time between the first cross and release of a variety compared to conventional breeding (Varshney et al. 2007).

Most of the proposed targets for marker assisted breeding in barley relate to disease resistance genes, with malting quality representing another important target (Varshney et al. 2007). Several new Australian barley varieties have been developed using this technology (Varshney et al. 2007) and MAS continues to be applied to breeding barley to enhance disease resistance (Miedaner & Korzun 2012). Whole genome breeding, in which large numbers of genes are targeted at once, is also being used in Australian breeding programs to develop new varieties, for example the variety “Flagship” released in 2004 (Varshney et al. 2007).

Molecular techniques such as embryo rescue have allowed the exploitation of wild relatives of barley as a source of genetic variation in crossing programs (Pickering & Johnston 2005). There are three genepools in the genus *Hordeum* (see Section 9). Wild barley belongs to the primary genepool, has no crossability barriers with cultivated barley, and has been used extensively in barley breeding for disease resistance and abiotic stress tolerance (Pickering & Johnston 2005). *Hordeum bulbosum*, the only member of the secondary genepool, has been used widely for the production of homozygous haploid lines (doubled haploids). The tertiary genepool of barley comprises about 30 *Hordeum* species, but strong crossability barriers have hindered successful crossing between these species and *H. vulgare* (Pickering & Johnston 2005).

2.4.2 Genetic modification

Particle bombardment and *Agrobacterium*-mediated DNA delivery are the two main methods used for stable transformation of barley plants (Hensel et al. 2008; Travella et al. 2005; Wan & Lemaux 1994; Tingay et al. 1997). Other barley transformation methods are based on androgenetic pollen cultures or isolated ovules as gene transfer target (Hensel et al. 2008). Although transformation techniques have been developed for a range of barley cultivars (Hensel et al. 2008; Chang et al. 2003), transformation efficiency of barley is strongly genotype dependent (Finnie et al. 2004). The spring cultivar Golden Promise, and the winter cultivar Igri, have been widely used for transformation due to their high regeneration rate (Dahleen & Manoharan 2007). Golden Promise is salt tolerant but susceptible to several fungal pathogens, and it is no longer widely grown commercially (Finnie et al. 2004).

GM barley plants aimed at commercial applications have been produced (for review, see Dahleen & Manoharan 2007). However, to date, there are no commercial genetically modified (GM) barley varieties available[6].

Field trials of GM barley have been previously approved in Australia (see OGTR website for details). These trials examined introduced traits such as increased tolerance to drought, salinity, cold, boron, and aluminium; altered grain starch composition; increased dietary fibre; and enhanced nitrogen utilisation.

SECTION 3 MORPHOLOGY

3.1 Plant morphology

Barley is an annual grass that stands 60–120 cm tall. Barley has two types of root systems, seminal and adventitious. The depth the roots reach depends on the condition, texture and structure of the soil, as well as on the temperature. The deepest roots are usually of seminal origin and the upper layers of the soil tend to be packed with the later developing adventitious roots. If the grain is deeply planted a 'rhizomatous stem' is formed, which produces leaves when it reaches the surface. The 'rhizome' may be one or several internodes in length, and may carry adventitious roots (Briggs 1978).

The stems are erect and made up of hollow, cylindrical internodes, separated by the nodes, which bear the leaves (Gomez-Macpherson 2001). A mature barley plant consists of a central stem and 2–5 branch stems, called tillers. The apex of the main stem and each fertile tiller carries a spike. At, or near, the soil surface, the part of the stem carrying the leaf bases swells to form the crown. It is from the crown that the adventitious roots and tillers develop (Briggs 1978).

Barley leaves are linear, 5–15 mm wide, and are produced on alternate sides of the stem. The leaf structure consists of the sheath, blade, auricles and ligule. The sheath surrounds the stem completely. The ligule and auricles distinguish barley from other cereals as they are smooth, envelope the stem and can be pigmented with anthocyanins (Gomez-Macpherson 2001).

3.2 Reproductive morphology

The inflorescence of barley is referred to as the ear, head or spike. The flowering units, the spikelets, are attached directly to the central axis, or rachis, which is the extension of the stem that supports the spike (Figure 2). There are three spikelets at each node, called triplets, alternating on opposite sides of the spike. Each spikelet is made up of two glumes, which are empty bracts, and one floret that includes the lemma, the palea, and the enclosed reproductive components. Depending on variety, each lemma is extended as an awn, or more rarely a hood. The sterile glumes in some varieties can also be awned. Awnless varieties are also known. In hulled or husked varieties, the palea and lemma adhere to the grain. In hull-less or naked varieties, the palea and lemma are not attached and separate from the grain on threshing (Briggs 1978).

[6] CERA (2012) GM Crop Database. Center for Environmental Risk Assessment (CERA), ILSI Research Foundation, Washington D.C. Accessed 21 March 2017.

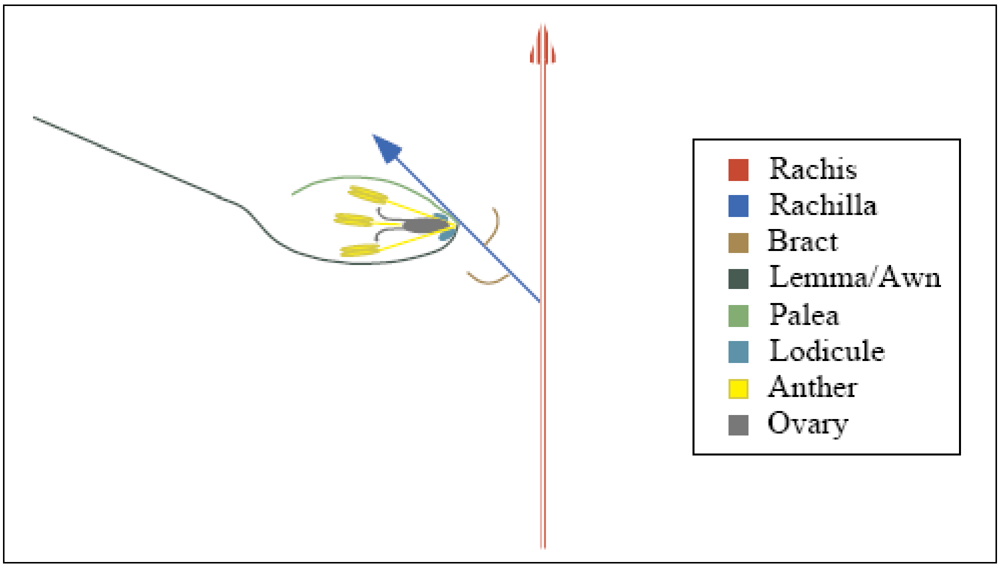

Figure 2: Depiction of the barley spikelet (Williams-Carrier et al. 1997). Reproduced with permission of the Company of Biologists.

In six-row barley, all of the spikelets in a triplet are fertile and able to develop into grains. The central seeds are round and fat, but the lateral seeds tend to be slightly asymmetric and, in some varieties (*intermedium* forms), they are also smaller than the central grain. In two-row barley, however, only the central spikelet is both male and female fertile. The two lateral spikelets are smaller with reduced stamens and a rudimentary ovary and stigma. Therefore, the lateral spikelets of two-row barley are sterile, and only a single seed is produced at each node of the spike, giving it a flat appearance (Komatsuda et al. 2007). Each spike may carry 25–60 kernels in six-rowed varieties or 15–30 kernels in two-rowed varieties (Briggs 1978).

SECTION 4 DEVELOPMENT

4.1 Reproduction

4.1.1 Asexual reproduction

The production of rooted tillers has occasionally been described as a form of vegetative reproduction, as tillers separated from the plant can grow supported by the adventitious roots only (Briggs 1978). Otherwise, barley is not capable of vegetative spread (Ellstrand 2003).

4.1.2 Sexual reproduction

Winter barley varieties require a period of cold stimulus (vernalisation) to initiate floral development. Spring barleys do not require vernalisation. Most barley varieties grown in Australia are spring barleys that are grown as a winter crop. Sowing usually occurs between early May and early June, depending on variety and location, so that flowering occurs close to the ideal time, which ranges from September to early October. Flowering in many barley varieties responds to day length as well as temperature, so development patterns can vary with latitude.

After a number of leaves have initiated the stem apex gives rise to spikelet initials which form the inflorescence or spike. The oldest spikelets are at the base of the spike, which terminates with the formation of one or more sterile florets. Initially, the spike is contained within the sheath of the flag leaf, which swells and is called the boot. In most varieties the spike eventually becomes clear of the boot, and flowering generally occurs in the newly emerged spike. Flowering usually begins in the florets around the middle of the ear and spreads upwards and downwards, taking 1–4 days to complete. Ears on different tillers may mature at varying times (Briggs 1978).

The pollen and ovules in each floret mature together (Briggs 1978). Barley pollen viability estimates range from a few hours to at least 26 hours (see Section 4.2), while stigma are receptive and able to be fertilised for a period of 6 to 8 days following the first flower opening (Riddle & Suneson 1944). Cereals can be either closed-flowering (cleistogamous) or open-flowering. In closed-flowering types the anthers remain inside each floret, thus self-pollination occurs. In open-flowering types, the lodicules become turgid and push the palea and lemma apart, so that the anthers may emerge (Briggs 1978). In the latter case, pollen shedding starts before the spikelet opens and continues after it opens, thus outcrossing is possible (Turuspekov et al. 2005). Nevertheless, most pollen is shed before the spikelet opens, so that self-fertilisation is usual (Briggs 1978).

Floral traits such as high anther extrusion, large anthers and vigorous stigmas may increase the level of outcrossing in barley plants. Such traits are influenced by both genetic and environmental factors (Abdel-Ghani et al. 2005).

4.2 Pollination and pollen dispersal

Barley pollen is small and relatively light (Eastham & Sweet 2002). Pollen grains are 35–45 µm in diameter and of spheroidal-ovoid shape. Within about five minutes of adhering to the stigma, pollen grains take up moisture and germinate. The rates of pollen tube growth, cell division and other aspects of grain development are strongly temperature dependent, but generally the pollen tube takes about 45 minutes to grow (Briggs 1978).

Pollen production in barley per spike is about 10% of that of rye (Eastham & Sweet 2002). Few studies of barley pollen viability have been done. Earlier work suggests that barley pollen is extremely sensitive to drying and remains viable for only a few hours after dehiscence (Bennett et al. 1973; Pope 1944). In addition, pollen viability was found to fall to 54% at distances of 1.5–3 m from the parent plants (Giles 1989). In a more recent study, pollen viability remained above 80% after 4 hours at up to 23°C and 75% humidity (Gupta et al. 2000). Similarly, pollen viability remained above 80% after 8 hours at temperatures of up to 40°C (Parzies et al. 2005). In this study, pollen viability differed significantly with genotype, temperature and duration of the temperature treatments, being higher at 20°C than at 40°C. After a 26 hour treatment of high/low/high temperatures, pollen viability fell below 60% for some genotypes but remained high (>80%) in others. Humidity was not controlled and was therefore variable in these experiments. The authors concluded that pollen viability of barley remains high enough to allow cross fertilisation over a period of at least 26 hours and at temperatures of up to 40°C (Parzies et al. 2005).

Annual *Hordeum* species are mainly inbreeders, although none are obligate inbreeders (Von Bothmer 1992). Cultivated barley and its wild progenitor both reproduce almost entirely by self-fertilisation (~99%) (Ellstrand 2003; Wagner & Allard 1991; Von Bothmer 1992), and gene flow in barley is low (Ritala et al. 2002).

Barley is not generally pollinated by insects (USDA-APHIS 2006), so any outcrossing occurs by wind pollination and distance is the most important factor that affects rates of outcrossing as a result of pollen migration in barley. Gene flow rapidly decreases at distances beyond a few metres (Gatford et al. 2006), and most outcrosses that have been detected in cultivated barley result from pollen migrations between closely adjacent plants (Wagner & Allard 1991).

The extent of outcrossing also varies with ecology, genotype and weather conditions (Ritala et al. 2002). In general, cool and moist conditions promote outcrossing in barley (Gatford et al. 2006;

Abdel-Ghani et al. 2004; Parzies et al. 2000; Chaudhary et al. 1980), possibly because pollen viability may be extended under these conditions.

Prevailing wind direction has also been suggested to influence pollen migration, but differences observed are often small (for example, see Wagner & Allard 1991; Berns 1984). Interestingly, prevailing winds were mostly opposite to the direction of gene flow in an Australian study of wheat and barley (Gatford et al. 2006).

The extent of outcrossing in *H. vulgare* ssp. *spontaneum* was estimated as varying from 0–9.6%, with a low overall average of 1.6% (Brown et al. 1978). Outcrossing rates for cultivated barley are very similar, with frequencies of 0–10% being reported, as detailed below.

Average outcrossing rates in barley landraces in Jordan and Syria have been estimated at 0.2% (plants collected about 1 m apart and within 2 to 3 km of cultivated barley landraces) and 1.7% (plants collected at least 2 m apart), respectively (Abdel-Ghani et al. 2004; Parzies et al. 2000). Outcrossing rates in barley populations in Canada ranged from 0–0.8%, with a mean of 0.35% (Chaudhary et al. 1980).

Doll (1987) reported outcrossing rates in autumn and spring sown-barley of 5% and less than 0.5%, respectively. Interestingly, particular lines sown in both autumn and spring showed different levels of outcrossing and the author suggested this was due to the fact that the sex organs of the autumn-sown barley were more exposed during flowering than spring-sown barley, which tend to flower even before spikes emerge from the sheath. Gorastev and Popova (1977, as reported in Doll 1987) also noted stamen extrusion and relatively high rates of outcrossing in their study of winter barley varieties. In Doll's study (1987), for about one third of the outcrosses, the pollen may have come from neighbouring plots, but for another one third the nearest pollen donor was at least 10 m away. One of the autumn sown lines had about 10% outcrosses, possibly due to the early flowering of this variety, its genetic background, or a combination of the two.

In a study using male sterile barley at a distance of 1 m as the recipient, viable pollen flow resulted in an average of less than half a seed to one seed per head, and seed set diminished with distance (Ritala et al. 2002). In normal fertile barley, the cross pollination frequency was between 0 and 7% at a distance of 1 m. This study used open flowered barley as the recipient and outcrossing would be expected to be lower in most cultivated barley varieties (Ritala et al. 2002).

Under Australian field conditions, gene flow from GM barley occurred at a frequency of only 0.005% over a maximum distance of 10 m. However, gene flow was not measured beyond this distance and therefore the amount of gene flow may be higher (Gatford et al. 2006).

In experiments designed to measure outcrossing rates plants in physical contact with each other, the average rate of outcrossing was about 0.8% (Allard unpublished, discussed in Wagner & Allard 1991). The rate of outcrossing fell to 0.2% when physical contact was virtually eliminated by spacing plants 30 cm apart, and when plants were 60 cm or 90 cm apart, the pollen migration rate fell to approximately 0.1%. Pollen migrants were only detected sporadically when pollen donor and recipient plants were separated by 3 m, and no outcrossing was detected when plants were separated by 10 m.

In observations of pollen migration between commercial barley fields, outcrossing rates were 0.05% and 0.01% for distances of 1 m and 10 m, respectively. No pollen migrants were observed in these studies at distances of 20 m or 50 m (Allard unpublished, discussed in Wagner & Allard 1991). However, cross fertilisation with very low frequencies has been observed at distances of up to 50 m

(Ritala et al. 2002) and 60 m (Wagner & Allard 1991), although cross pollination at such distances is rare.

To certify both basic and certified barley seed through Seed Services Australia in SA, the crop must be separated from other cereals by at least a two metre strip or a physical barrier such as a fence to prevent any mixture of seed during harvest (Smith & Baxter 2002). The Canadian Seed Growers' Association and the California Crop Improvement Association require a three metre isolation distance between barley and other cereals (Canadian Seed Growers' Association 2005; California Crop Improvement Association 2003).

4.3 Fruit/seed development and seed dispersal

Double fertilisation occurs in barley and results in a diploid embryo with equal nuclear contributions from the male and female gametes, and the triploid endosperm, which is derived from a second fusion between one male gamete from the pollen and two polar nuclei from the embryo sac (Briggs 1978). The total number of cells in the endosperm is higher than in wheat or rice, which is why barley grains contain more cell wall material such as β-glucans than these cereals (Gomez-Macpherson 2001).

In addition to varieties being awned or hooded and husked or husk-less, grain shapes and sizes can vary widely. Grain development progresses through a number of stages; watery ripe, milk, soft dough, hard dough, grain hard and harvest ripe (NSW Department of Industry and Investment 2010).

During domestication a strong selection for tough rachis was made for easier reaping, threshing and sowing, with the result that cultivated barley is not prone to shattering. Instead, the single seed is broken off at the base at maturity (Von Bothmer 1992). Some *Hordeum* species, including *H. lechleri* and *H. jubatum*, have small, light seeds and spikelets that serve as an elegant flying aparatus for wind dispersal. Other species, including *H. vulgare, H. bulbosum* and *H. murinum,* have large, heavy seeds and special bristles on the spikelets which make them adhere well to the furs of larger animals, the feathers of birds and the clothing of people, and the seeds may get dispersed in this way (Von Bothmer 1992; Von Bothmer et al. 1995). Viable seed may also be transported on the muddy feet/legs of birds (Cummings et al. 2008; Sorensen 1986).

Approximately 15% of the faecal dry matter from cattle fed whole barley seeds was composed of whole and undamaged barley seeds (Beauchemin et al. 1994). Although the viability of the intact seeds was not determined, this study suggests there is the potential for livestock to disperse viable barley seed after consumption. In feeding studies with corellas, galahs, house sparrows, mallard ducks, pheasants, red-winged black birds and rock pigeons fed whole barley seeds did not excrete any intact barley seeds (Cummings et al. 2008; Woodgate et al. 2011).

However, viable seed from other cereal crops has been reported to survive passage through the digestive tract of some birds. Viable oat seeds, a grass from the same subfamily as barley (Pooideae), were detected in emu droppings (Calvino-Cancela et al. 2006). 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). Corellas have been shown to excrete some (about 3%) viable wheat seeds after passage through the digestive tract (Woodgate et al. 2011).

4.4 Seed dormancy and germination

Dormancy is defined as the inability of viable seed to germinate under favourable conditions. Dormancy of the barley grain is typically imposed by the seed covering structures (lemma, palea, pericarp and seed coat). Primary dormancy is intrinsic, whereas secondary dormancy arises as a result of external factors. Water sensitivity is a form of secondary dormancy in which germination is reduced under excessive moisture conditions (Briggs 1978). Australian barley crops do not generally show strong dormancy due to the favourable conditions and the varieties grown (Woonton et al. 2001).

Long dormancy is not desirable in malting barley as the malting process requires grain to germinate rapidly and uniformly; at least 50% in 1–2 days and 95–100% in 3 days (Briggs 1978). Therefore, during domestication, non-dormancy of seeds was selected for, so that in cultivated barley more that 90% of all seeds germinate within 4 days of imbibition, whereas in the wild form, ssp. *spontaneum*, seed germination is highly irregular (Von Bothmer 1992). Barley varieties developed for animal feed have not undergone such strong selection for low dormancy, and many six-rowed varieties have variable to high levels of dormancy (Oberthur et al. 1995).

While low dormancy is desirable in malting barleys, too little dormancy can lead to pre-germination or pre-harvest sprouting, where germination of the grain begins on the mother plant in rainy conditions before harvest. Both pre-germination and pre-harvest sprouting trigger the hydrolysis of the endosperm and can have adverse effects on the yield, malting quality and storage life of the grain. Pre-harvest sprouting susceptibility is determined mainly by genotype; some varieties are resistant due to deep dormancy, others are highly susceptible, and a third group are intermediate (Rodriguez et al. 2001). Traditionally, Australian malting barley varieties have relatively good tolerance to pre-harvest sprouting. However, Harrington barley, which has been widely used in Australian breeding programs, is highly susceptible to pre-harvest sprouting (Li et al. 2003).

In addition to the influence of variety, dormancy varies with grain maturity and with the conditions during grain ripening, harvest and storage. Freshly harvested grain is the most dormant, and dormancy declines as the grain ripens (Briggs 1978). Cool, moist conditions during ripening encourage the expression of dormancy, while low dormancy is generally associated with high temperatures, short days, low moisture and high nitrogen levels (Rodriguez et al. 2001).

In the natural environment, the release of seed dormancy is promoted by factors including after-ripening (exposure of the seed to hot, dry conditions) and stratification (imbibition at low temperature) (Gubler et al. 2005). In cultivation practices, dormancy is commonly relieved by after-ripening, which is achieved by post-harvest storage in warm temperatures and low humidity (Leymarie et al. 2007). Coat imposed dormancy in barley may last 0.5–9 months in dry storage (Pickett 1989). In contrast, storing grain in cold and moist conditions can maintain dormancy, and barley seeds have remained dormant for 3 years at 2°C under high humidity (Pickett 1989).

Shed grain may exhibit more prolonged dormancy than grain in dry storage, possibly because wet periods following harvest encourage retention of dormancy, so that self-sown grain often germinates just before the following crop (Pickett 1989).

In a study in Germany, seeds and spikes of freshly-ripened barley kernels were incorporated into the ground at depths of 1-15 cm and 15-30 cm directly after harvest in the summer of 1981 and again after harvest in 1982. Chopped straw was added to half of the plots. Depth of incorporation, application of straw and incorporation as seed or as spikes had no consistent effect on seed viability. A small proportion of seed, 1% for the 1981 trial and 0.02% for the 1982 trial, remained viable after 15 months. The different seed viability rates for the two trials was attributed to lower temperatures while the seed was developing and maturing in 1981 compared to 1982. The cooler temperatures lead to greater dormancy as demonstrated by the germination rates immediately after harvest which were only 10% in 1981 compared to 59% in 1982 (Rauber 1988).

In a Scottish study, winter barley was buried in the autumn to depths of 5, 10, 15 and 20 cm and emergence was measured in the following three years. In the first season following burial, emergence occurred from seed buried from all depths, and was highest from seed buried at 5 cm and lowest from seed buried at 20 cm. No plants emerged in the second or third year after burial. No data as to the initial viability of the buried barley seeds in this trial were provided (Davies & Wilson 1993).

In a Scottish survey, volunteer winter barley was reported to persist for up to five years in some rotations (Davies & Wilson 1993). For a trial of GM barley, the USDA/APHIS categorised barley seed dormancy as less than 2 years (USDA-APHIS 2006).There is a difference in germination rates between buried grain and grain lying on the surface. Cereal seeds remaining on the surface can generally easily germinate and become established (Ogg & Parker 2000). Exposure to periods of rain interspersed with dry conditions may encourage germination in grains on the soil surface. On the other hand, deep cultivation soon after harvest encourages dormancy by placing the grain in a cool, moist environment (Pickett 1989).

While low temperatures during grain development can induce deeper dormancy, low temperatures during germination can break dormancy of freshly harvested seeds (Nyachiro et al. 2002). Germination can occur at temperatures between 5°C and 38°C, with 29°C being optimal. Successful germination also requires both water and oxygen. Germination begins with the grain absorbing moisture and swelling. The rate of grain imbibition increases rapidly with increasing temperature (Briggs 1978).

Soil type and condition, including pH level, can also affect germination of barley seeds. Deep cultivation in certain soil types can prevent emergence by encouraging prolonged dormancy in seeds as a result of low oxygen availability (Pickett 1989; Ogg & Parker 2000). By delaying germination, deep burial can reduce the viability of shed seeds. Shed cereal seeds are generally short lived, and therefore it may be possible to leave shed seed ploughed under until non-viable. Even if germination at depth could be stimulated, emergence of the resultant seedlings would be unlikely (Pickett 1989).

4.5 Vegetative growth

Cultivated barley is a grass that may be either a winter or spring annual. Barley growth can be divided into a number of stages; germination, seedling development, tillering, stem elongation, heading (ear emergence), flowering and ripening (Figure 3).

The duration of the different developmental stages varies widely. Growth rate depends on the weather, water supply, soil fertility, the degree of competition with other plants, the presence of pests and diseases, and the time of planting. Initially growth is slow while the seedlings establish and the tillers form. Total time to maturity depends on variety, location and planting date. In south-east Qld, barley plants take between 105 and 157 days to reach maturity (Thomas & Fukai 1995).

Roots

The seminal rootlets of barley emerge when the seed germinates and form a fibrous branched mass of roots, some of which extend deeply downwards. Later, at the tillering stage, the adventitious root system arises from the crown, and this tends to be thicker and less branched. Under some conditions such as drought, the adventitious roots may not develop at all. In other cases, the seminal roots cease functioning during the life of the plant. Different barley varieties can vary significantly in rooting system, and this can impact on their competitive ability (Briggs 1978).

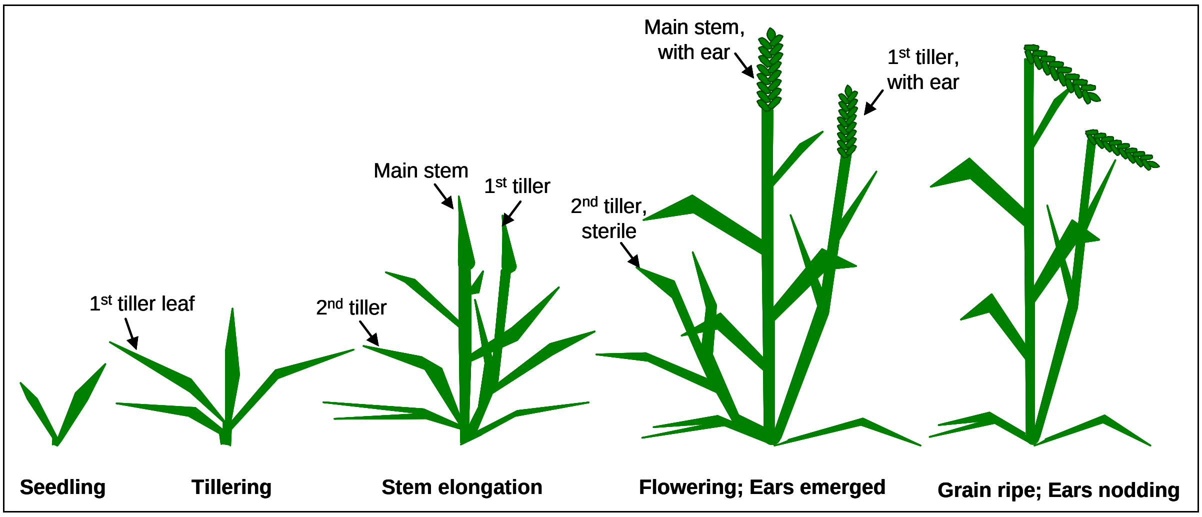

Figure 3: Schematic diagram of barley plants at successive stages of development.

Leaves

After germination, the coleoptile (a leaf sheath that encloses the embryonic plant) reaches the surface and the first leaf emerges at its tip. The leaves grow rolled up from the tube formed by the bases of earlier leaves, unrolling once emerged (Briggs 1978). Leaves emerge continuously on the main stem and tillers until the final (flag) leaf emerges. Emergence of the flag leaf is an important growth stage for timing the application of certain growth regulators. The mature leaves progressively senesce and gradually the whole plant dries out until full maturity, when the grain is ripe (Briggs 1978).

Stems and Tillers

Stem elongation usually starts when the plant is about 5 cm in height and coincides with leaf emergence, tillering and spike formation (Briggs 1978). During stem elongation the developing spike is carried upwards.

Tillers start to develop at about the 3-leaf stage (Figure 3). The number of tillers and duration of tillering vary with variety and growth conditions (Briggs 1978). Some older genotypes produce many tillers but develop few spikes, while most modern genotypes have a higher percentage of tillers that develop spikes (Gomez-Macpherson 2001). In addition, winter varieties usually produce more tillers than spring varieties during the vegetative growth period over winter. In general, field grown barley plants typically produce 2–5 tillers (Briggs 1978; Gomez-Macpherson 2001). Most tillers initiate adventitious roots, although later appearing tillers often remain unrooted and die prematurely (Anderson-Taylor & Marshall 1983).

SECTION 5 BIOCHEMISTRY

5.1 Toxins

Barley is generally not considered toxic. However, a number of allergens and anti-nutritional factors occur in barley and in extreme cases may have a toxic effect. These are described in Sections 5.2 and 5.3.

5.2 Allergens

Barley, like wheat, is a common allergenic food in the human diet and is associated with several adverse reactions. Inhalation of barley flour can cause baker's asthma, an occupational allergy. Glycosylated forms of proteins from the cereal trypsin/alpha-amylase inhibitor family have been identified as major allergens associated with baker's asthma (Sanchez-Monge et al. 1992).

Ingestion of barley may induce symptoms of food allergy in sensitive individuals, especially children. Symptoms include gastrointestinal complaints, atopic dermatitis and anaphylaxis, (Armentia et al. 2002). Contact dermatitis and anaphlaxis can also be induced by barley proteins present in beer. Two proteins were identified from a crude protein preparation of beer which gave positive sera and contact test results in some sensitive individuals (Garcia-Casado et al. 2001).

Barley pollen expresses proteins capable of cross reactivity with known anti-allergen antibodies and therefore the pollen may represent a potential source of aeroallergenic proteins for individuals near agricultural sites (Astwood et al. 1995).

<u>Coeliac disease</u>

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).

Release of the first gluten-free barley variety which should benefit coeliac and gluten-intolerant people has been reported (Tanner et al. 2016). The variety, Kebari™, contains less than 5 ppm hordeins, the type of glutens found in barley, which is well below the 20 ppm level recommended by the World Health Organization for classification as gluten-free[7]. Kebari has recently been used in Germany in the commercial production of gluten-free beer[8].

[7] CSIRO website, accessed 21 March 2017.
[8] CSIRO website, accessed 21 March 2017.

5.3 Other undesirable phytochemicals

Enzyme Inhibitors

Both protease and alpha-amylase inhibitors are present in the barley grain. 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), although members of the trypsin/alpha-amylase inhibitor protein family are major allergens associated with baker's asthma (see Section 5.2).

The most common barley protease inhibitors are inhibitors of trypsin, chymotrypsin and microbial proteases (Casaretto et al. 2004). However, due to the low levels of protease inhibitors in the barley grain, it is unlikely that they have a significant negative influence on protein digestibility (Newman & Newman 1992).

Lectins

Lectins are glycoproteins that bind to specific carbohydrate groups on cell surfaces, causing lesions to form. In the intestinal tract, these lesions can seriously impair the absorption of nutrients (OECD 2003). Although more commonly associated with legumes, cereal grains including barley are also known to contain lectins, although their possible physiological significance is unknown (OECD 2004). As lectins are usually inactivated by heat treatment, they are really only of interest when raw or inadequately cooked food or feed is consumed (OECD 2003). Therefore, in the case of barley, they are more likely to be an animal feed concern.

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. This anti-nutrient is of particular importance to monogastric animals, whereas ruminants possess digestive enzymes which degrade phytate and release the chelated minerals (OECD 2003). Mature seeds of most traditional crops contain about 75% of total phosphorus as phytic acid (Raboy 2000). The excretion of feed phytic acid phosphorus by livestock (e.g. poultry, swine, and fish) contributes to water pollution and is a major environmental issue (Raboy 2000).

Low phytic acid mutants, with reduced phytic acid accumulation and increased inorganic phosphorous, have been identified in barley (Larson et al. 1998; Raboy 2000), but typically have an associated yield penalty (Raboy 2000; Raboy et al. 2014). Recent studies indicate that the low phytic acid 1-1 trait in barley is a seed-specific or filial determinant of barley endosperm total phosphorus, suggesting low phosphorus varieties with good agronomic performance could be developed (Raboy et al. 2014). A hulless, low phytate barley with improved feed conversion and nutrient digestibility compared to a regular-hulled barley has been released in Canada (Woyengo et al. 2012).

Phenolic compounds

The phenolic compounds proanthocyanidins and catechins are found in barley seed coats, and these can form insoluble complexes with proteins inhibiting nutrient utilisation (Newman & Newman 1992). Proanthocyanidins also cause haze formation in beer, an undesirable characteristic for most breweries (von Wettstein 2007). Although proanthocyanidin-free barley has been produced and released commercially (von Wettstein 2007), only one report was found indicating its use for brewing beer[9].

5.4 Beneficial phytochemicals

Barley is an excellent source of dietary fibre, protein, and complex carbohydrates, and is a good source of certain vitamins and minerals. Barley composition varies markedly in different environments and between varieties (OECD 2004). The concentration of starch is inversely related to the content of total dietary fibre and protein. In malting barley, lower protein content (8–10.5% dry matter) and corresponding high starch content is preferred. In feed barley, grains with low fibre, higher protein (10–15%) and higher starch content are preferred (OECD 2004).

Carbohydrates, including starches, sugars and non-starch polysaccharides, comprise about 80% of the barley grain (Newman & Newman 1992). Most of the carbohydrates is starch, which makes up 60% of the grain and provides energy for germination (OECD 2004). Starch is the major source of readily available energy for food and feed. In most barleys, the predominant starch is amylopectin and the remainder is amylose (Newman & Newman 1992).

The non-starch polysaccharides are collectively called total dietary fibre and include ß-glucans and arabinoxylans. The fibre content of barley is relatively high, and the benefits of dietary fibre on human health are well known. The soluble fibre ß-glucan, for example, can lower both post-prandial blood glucose levels and blood cholesterol (OECD 2004; McIntosh et al. 1991). In contrast, arabinoxylans and ß-glucans can have a deleterious effect on digestion in monogastrics (OECD 2004). In addition, ß-glucans are known to negatively impact poultry, especially young birds, by reducing the intestinal viscosity (Newman & Newman 1992).

Protein is the second major component of the barley grain. Protein content of barley grains is strongly affected by the growth conditions and nitrogen fertilisation regime, but is usually about 10–12%. Barley proteins can be classified by solubility as albumins, globulins, prolamins and glutelins (Newman & Newman 1992). Prolamins (or hordeins) are the major storage protein and account for up to half of the total nitrogen in the grain. The other groups consist mainly of structural and metabolic proteins (OECD 2004).

Barley contains 2–3% minerals, although the mineral content can vary markedly with variety, growing conditions and fertiliser application. The major minerals are magnesium, phosphorus, potassium, calcium and sodium. Although much of the phosphorus is unavailable to monogastric animals, barley contains more phosphorus and has higher phosphorus bioavailability than other grains (OECD 2004).

Barley also contains 2–3% lipids, including several with health promoting activities such as carotenoids and tocopherols (Newman & Newman 1992). Vitamin E, a mixture of tocopherols, is present in barley oil. Barley grains also contain B vitamins (OECD 2004).

Barley contains a number of other compounds, some of which may have a role in protection against diseases when ingested at high levels. These include simple phenolic acids, flavenoids and lignans, all of which have good antioxidant properties (OECD 2004).

[9] CRISP malting Group website, accessed 21 March 201.7

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic stresses limiting growth

6.1.1 Nutrient stress

The main nutrients typically deficient for the successful production of a barley crop are nitrogen, potassium and phosphorus, and zinc. In some soil types and growing areas, sulphur, copper, manganese and molybdenum may also be lacking (GRDC 2016b).

Nitrogen is needed for early tiller development and high yield, and determines the protein concentration in the grain. The amount of nitrogen required varies with the cultivar, growth conditions, soil type and rotational history of the field. Nitrogen fertilisers are applied between sowing and early to mid-vegetation. Delaying nitrogen application to later in the season can affect protein levels (GRDC 2016b). In malting barley, the requirement for nitrogen must be balanced to maximise yield without increasing the protein level in the grain (Queensland Department of Agriculture and Fisheries 2017).

Potassium deficiencies can lead to poor root growth and leaf development, and to fewer and smaller grains. In addition, potassium deficiency can reduce tolerance to environmental stresses and increase susceptibility to leaf diseases. The occurrence of potassium deficiency depends on soil type, cropping practices and rainfall. Generally in the Southern Region, additional potassium is not required. Light soils with high rainfall, especially where hay is regularly cut and removed, are more likely to be deficient in potassium. Potassium fertilisers can be applied at planting (side-banded), drilled in pre-planting, broadcast and cultivated in fallow or applied to a preceding crop (GRDC 2016b).

Phosphorus is essential for two distinct phases of growth: during early development (emergence to end of tillering) and for seed formation and grain filling. Potassium deficiency can reduce head and grain number. Phosphate fertiliser is generally applied with the seed during sowing to meet the requirements during the early development phase. Considerably more phosphorus is needed during seed formation and grain filling, and this is primarily obtained from the soil profile (GRDC 2016b).

Zinc is a micronutrient, essential for protein shape and thus important for enzyme function in the plant. Deficiencies manifest as stunted plants with short, thin stems and pale green leaves with yellow patches. Severe deficiencies result in reduced tillering, delayed maturity and little or no grain production. Zinc can be applied with outer nutrients at planting or as a foliar application (Norton 2014).

6.1.2 Temperature stress

Barley can grow in a wide range of environments, including extremes of latitude and longitude. The optimum temperature for growth depends on the developmental stage (van Gool & Vernon 2006). In general, barley is a cool season crop and grows best in temperatures of 15–30 °C, but it can tolerate high temperatures if the humidity is low (Nevo 1992). High temperatures post-anthesis, however, can reduce grain weight and change malting performance (van Gool & Vernon 2006). Barley is not as cold hardy as wheat, and is more susceptible than wheat is to frost at the early seedling stage (Gomez-Macpherson 2001).

6.1.3 Water stress

Barley grows best in coarse-textured, well drained soils. In Australia, barley is grown in wheat production areas receiving 750 mm to less than 325 mm annual rainfall (van Gool & Vernon 2006).

These areas 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 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 Vic and southern NSW, and the summer-dominant rainfall of the northern wheat growing areas (Cramb et al. 2000).

Barley has a number of good agronomic attributes (e.g. shorter growing season, high water use efficiency) compared to other cereals, and can be grown on limited irrigation (GRDC 2016b). Compared to other cereals, barley is well adapted to drought through water use efficiency. Nevertheless, drought is an important abiotic stress for barley, which is often grown in environments where drought is common (Stanca et al. 1992).

Waterlogging is also an important constraint to barley production, and is the major limiting factor in the high rainfall zone of south-west WA (van Gool & Vernon 2006). Barley is more susceptible to waterlogging than wheat or oats (GRDC 2016b).

6.1.4 Other stresses

Barley is particularly sensitive to soil acidity compared to other cereals, and this can be a major constraint to crop growth. Barley is also sensitive to aluminium toxicity, which is linked to acidic soils, and boron toxicity (van Gool & Vernon 2006).

6.2 Abiotic tolerances

Barley is well adapted to a wide range of soils and is the most tolerant cereal to salinity. Therefore, it is often the cereal crop preferred for sodic soils. Barley is also more tolerant of alkalinity than other cereals (van Gool & Vernon 2006).

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

Barley is more competitive with weeds than wheat, canola and pulses when sown at recommended seeding rates because of its greater tillering ability and below ground root competition. However, yield can be reduced by weeds and integrated weed management practices are employed to control weeds in barley crops (see Section 2.3.3). In the winter cropping system (which includes barley), weeds cost Australian agriculture $1.3 billion annually (GRDC 2016b).

Weeds that can be a problem in barley crops in the Southern Region include the broad-leaved weeds wild mustard (*Sisymbrium officinale*) and wild radish (*Raphanus raphanistrum*), and the grass weeds annual ryegrass (*Lolium rigidum*), brome grass (*Bromus* spp.) and wild oats (*Avena fatua* and *A. ludoviciana*).The most damaging of these crops weeds, annual ryegrass, wild oats, brome grass and wild radish are all capable of establishing large persistent seedbanks (GRDC 2016b).

7.2 Pests and pathogens

Damage to cereal crops by birds has been noted in Australia and around the world (Bomford & Sinclair 2002; Coleman & Spurr 2001; Brodie 1980). In Australia, the main bird pests of winter wheat, barley, oats and pulse crops (various species of grain legumes) are the galah (*Eolophus roseicapilla*) (Temby & Marshall 2003; Jarman & McKenzie 1983), little corella (*Cacatua sanguinea*) (Bomford & Sinclair 2002), long-billed corella (*Cacatua tenuirostris*) (Temby & Marshall 2003), cockatiel

(*Nymphicus hollandicus*) (Jones 1987), sulphur-crested cockatoo (*Cacatua galerita*) (Temby & Marshall 2003; Massam 2001), tree sparrow (*Passer montanus*) and house sparrow (*Passer domesticus*) (Massam 2000), and emu (*Dromaius novaehollandiae*) (Davies 1978). Birds such as cockatoos damage the cereal crop most during germination in autumn, but may feed on the crop at different times including grain ripening (Temby & Marshall 2003). When feeding on seed, cockatiels appear to prefer softer, younger seed to harder, mature seed (Jones 1987). Emus feed on a great variety of plant material, but prefer succulent foods, such as fleshy fruits, rather than drier items (Davies 1978).

Kangaroos are reported to damage grain crops by feeding on seedlings or trampling mature plants. Eastern grey kangaroos (*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). Like kangaroos, rabbits (*Oryctolagus cuniculus*) 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 agricultural crops is the house mouse (*Mus domesticus*), causing average annual losses to Australian agricultural crops of US$10 million (ACIAR 2003). Changes to farming practices over the past 30 years have seen an increase in the frequency of mouse plagues. Reduced tillage, stubble retention, more diverse crops and fewer livestock have provided mice with abundant food, crop cover and favourable breeding conditions (GRDC 2012). Rodents are opportunistic feeders and their diet can include seeds, the pith of stems and other plant materials (Caughley et al. 1998). Rodents may eat seeds, thus destroying them, at the seed source or they may hoard seed (AGRI-FACTS 2002). Caughley et al. (1998) indicate that the average territory size of mice varies between breeding and non-breeding seasons, from 0.015 to 0.2 hectares respectively, whereas others have suggested a much smaller territory of 3 to 10 m in diameter (AGRI-FACTS 2002). In addition, mice are reported to travel 300 m or more in a night (GRDC 2012). Reduced plant cover has been reported to be a deterrent to the movement of mice (AGRI-FACTS 2002).

Damage from field insects and other arthropod pests is not generally a major factor for barley crops, although significant damage can occur if conditions favouring the build-up of pest populations occur. Potential insect and arthropod pests of barley in Australia include: blue oat mite (*Penthaleus* spp.), redlegged earth mite (*Halotydeus destructor*), Bryobia mites (*Bryobia* spp.), Balaustium mite (*Balaustium medicagoense*), cutworms *(Agrotis* spp.), aphids (*Rhopalosiphum padi, R. maidis* and *Metopolophium dirhodum*), earwigs (*Nala lividipes*), common armyworm (*Leucania convecta*), *Helicoverpa* spp., pasture webworm (*Hednota* spp.), pasture cockchafers (*Acrossidius tasmaniae*), grass anthelids (*Pterolocera* sp.), lucerne flea (*Sminthurus viridis*), leaf hoppers (family: *Cicadellidae*), millipedes (*Ommatoiulus moreleti*), slaters (*Porcellio scaber*, *Armadillidium vulgare* and *Australiodillo bifrons*) and locusts (*Chortoicetes terminifera, Austroicetes cruciata* and *Phaulacridium vittatum*). Management of insects in barley crops is similar to that of wheat and involves cultivation, good weed control and the use of insecticide sprays. Slugs (*Deroceras reticulatum*, *D. invadens,* and *D. laeve*) and snails (*Cernuella virgate, Cochlicella acuta, Theba pisana* and *Prietocella barbara*) can also cause damage to barley crops, especially in the early seedling stage (GRDC 2016b).

Nematodes are microscopic, worm-like animals that can cause yield loss to crops. Two important nematodes affecting barley and other cereals are the root-lesion nematodes (*Pratylenchus* spp.) and the cereal cyst nematode (*Hererododera avenae*). The cereal cyst nematode can cause yield losses of up to 80%. Nematode management includes cultivation of tolerant or resistant cereal varieties and rotation with resistant crops to reduce nematode populations (GRDC 2016b).

Pathogens, particularly fungi and viruses, can reduce grain yield and quality in barley. Disease management strategies include using resistant varieties and rotation with non-host crops. The main diseases that affect barley in Australia are: barley yellow dwarf virus, cereal yellow dwarf virus, Fusarium head blight (*Fusarium graminearum*), covered smut (*Ustilago segetum var. hordei*), loose smut (*U. nuda*), leaf rust (*Puccinia hordei*), barley grass stripe rust (*Puccinia striiformis*), net blotch net form (*Pyrenophora teres f. teres*), net blotch spot form (*P. teres f. maculate*), powdery mildew (*Blumeria graminis f.s.p. hordei*), scald (*Rhynchosporium secalis*), stem rust (*Puccinia graminis*), crown rot (*Fusarium pseudograminearum*), common root rot (*Bipolaris sorokiniana*), take-all (*Gaeumannomyces graminis var. tritici*), rhizoctonia root rot (*Rhizoctonia solani*), pythium root rot (*Pythium sp.*), wirrega blotch (*Drechslera wirreganensis*), and ringspot (*Drechslera campanulata*) (GRDC 2016b; GRDC 2016a; DAFWA 2017).

7.3 Other biotic interactions

Endophytic actinobacteria, belonging to the genera *Streptomyces, Microbispora*, *Micromonospora* and *Nocardioidies*, have been isolated from surface sterilised healthy wheat and barley plants (Coombs et al. 2004). Actinobacteria are recognised as prolific producers of bioactive compounds and may have a role in disease resistance and maintaining the health of the plants (Conn & Franco 2004; Coombs et al. 2004).

Arbuscular mycorrhizal fungi and endophytic fungi have also been associated with barley (Hause et al. 2002; Waller et al. 2005). Such symbioses can improve the plants nutrient uptake and can protect the plant from disease resistance and abiotic stress.

SECTION 8 WEEDINESS

Barley shares some characteristics with known weeds, such as self-compatibility, wind-pollination (although it is predominantly self-pollinating, see Section 4.2) and the ability to germinate or to produce some seed in a range of environmental conditions (Section 2.1). However, it lacks most characteristics that are common to many weeds, such as long lived seed (Section 4.4), rapid growth to flowering (Section 4.5), continuous seed production as long as growing conditions permit (Section 4.1.2), very high seed output (Section 3.2), high seed dispersal and long-distance seed dispersal (Section 4.3) (Baker 1965; Keeler 1989).

During domestication of the modern barley plant, characteristics that benefited farmers were selected. Non-shattering heads were favoured because of ease of harvest and this trait placed barley plants at a competitive disadvantage to other species which could more efficiently distribute seed. Cultivated barley has also been selected to have low seed dormancy (see Section 4.4).

All cereals, especially barley, have been reported to be allelopathic (Bertholdsson 2004). However, 100 years of breeding has resulted in a decrease in allelopathic activity in barley and the gradual loss of barley's ability to interfere with weed growth in the field (Belz 2007; Bertholdsson 2004).

8.1 Weediness status on a global scale

An important element in predicting weediness is taxonomic relationships, considering weediness within a taxon, including its history of weediness in any part of the world (Bergelson et al. 1998; Panetta 1993; Pheloung 2001). Three *Hordeum* species have particularly developed as noxious weeds in many parts of the world: *H. murinum* and *H. marinum* are annual, originally Mediterranean species, and *H. jubatum* is a perennial North American species (Von Bothmer 1992).

H. vulgare is categorised as an economic weed that is unlikely to persist, but may be naturalised, in regions including Australia, New Zealand, UK, Finland, North America, South America and Mexico (Randall 2002). In an environmental assessment done by the USDA/APHIS in 1994, it was stated that barley occasionally escapes and becomes weedy or naturalised. However, barley is not reported as a serious or principal weed and there are no reports of barley becoming a significant weed in the US (USDA-APHIS 1994).

8.2 Weediness status in Australia

H. vulgare occurs as an escape from cultivation and is present throughout Australia[10]. It is listed as a naturalised non-native species present in all Australian states and territories with the exception of the Northern Territory (Groves et al. 2003). Barley is considered a minor weed in natural ecosystems, but is primarily a problem in agricultural or ruderal environments (Groves et al. 2003). Barley is likely to occur anywhere seed is dropped and often grows on roadsides, but seldom persists (Eastham & Sweet 2002; Harden 1993; Harden 1993; Walsh & Entwisle 1994). Barley crop derived seed can develop into volunteers, but only at a very low frequency (Flannery et al. 2005).

Other related species present in Australia include *Hordeum glaucum, H. hystrix, H. leporinum, H. marinum, H. murinum, H. secalinum, Secale cereale* and *Triticum aestivum* (Groves et al. 2003). Although some of these are weedy, none can cross with cultivated barley under natural conditions (see Section 9.2).

8.3 Weediness in agricultural ecosystems

Barley is recognised as a volunteer weed in agricultural fields (for example, see Pickett 1989; O'Donovan et al. 2007). Groves et al. (2003) do not give barley a rank in agricultural ecosystems in any Australian state or territory, indicating it is either not a problem or does not occur in agricultural environments (Groves et al. 2003). The exception is WA where barley receives the rank of '5c'. This rank indicates it is a naturalised species known to be a major problem at four or more locations and that it is currently under active control in part of the state (Groves et al. 2003).

8.4 Weediness in natural ecosystems

Groves et al. (2003) categorise barley as a minor weed in natural ecosystems warranting control at four or more locations within a State or territory.

8.5 Control measures

Small grains such as barley can interfere with subsequent crops. Shallow tillage after harvest, followed by irrigation, will germinate much of the small grain seed lying on the surface. After germination, shallow tillage or the application of herbicide (e.g. glyphosate) will kill volunteer plants (Ogg & Parker 2000).

During the growing season, volunteer barley contaminating non-cereal crops can generally be controlled with herbicides (for example fluazifop and sethoxydim (Ogg & Parker 2000)). Volunteer cereals contaminating wheat crops can be a serious problem (Pickett 1989), however the impacts can be reduced by seeding wheat at a high rate (O'Donovan et al. 2007). In the US, the herbicide sulfosulfuron (MON 37500) provides reasonable control of volunteer barley in wheat, but can also damage the wheat crop (O'Donovan et al. 2007).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

There are three genepools in the genus *Hordeum* based on several criteria including ease of interspecific hybridisations and molecular and cytogenetic analyses (Zhang et al. 2001). The primary genepool comprises *H. vulgare* ssp. *vulgare* and *H. vulgare* ssp. *spontaneum*, the secondary

[10] Australia's Virtual Herbarium website, accessed 21 March 2017.

genepool consists of *H. bulbosum* L., and the tertiary genepool includes the remaining *Hordeum* species (Pickering & Johnston 2005).

9.1 Intraspecific crossing (primary genepool)

In studies looking at possible hybrid combinations among the *Hordeum* species, intraspecific hybrids are generally fully fertile (Von Bothmer 1992). *H. vulgare* ssp. *spontaneum* is the only wild *Hordeum* species that is cross-compatible and fully interfertile with cultivated barley. *H. vulgare* ssp. *vulgare* and *H. vulgare* ssp. *spontaneum* are morphologically similar and hybrids of the two subspecies show normal chromosome pairing and segregation in meiosis and are fully fertile. When *H. vulgare* ssp. *vulgare* and *H. vulgare* ssp. *spontaneum* grow together, spontaneous hybridisation occurs sporadically (Nevo 1992). *H. vulgare* ssp. *spontaneum* is not known to be present in Australia.

9.2 Interspecific and Intergeneric crossing

9.2.1 Interspecific

With a few exceptions the isolation barriers (usually hybrid sterility) are very strict between the *Hordeum* species and there is little or no genetic exchange in nature due to a lack of chromosome pairing, even where two taxa have sympatric distribution (Von Bothmer et al. 1995).

9.2.2 Intergeneric

Intergeneric crosses invariably require the application of growth regulators during crossing, followed by embryo rescue (Fedak 1992).

9.3 Crossing under experimental conditions

There are a number of problems associated with manipulation of barley including; hybrid instability and chromosome pairing, endosperm degeneration and hybrid infertility (Pickering & Johnston 2005). Nonetheless, several interspecific crosses between *H. vulgare* and wild *Hordeum* species have been performed using tissue culture techniques (see below and Table 2). Both ploidy level and taxonomic group are important for crossability. Seedling lethality is common in the resulting hybrids and the majority are seed and pollen sterile (Von Bothmer & Jacobsen 1986; Ellstrand 2003).

Intergeneric crosses have also been performed with *in vitro* techniques between barley and various species from the genera *Triticum*, *Aegilops*, *Elymus* and *Secale*, plus *Psathyrostachys fragilis* and *Thinopyrum intermedium* (see Table 2). Intergeneric hybrids are usually sterile, very few respond to colchicine doubling and backcrossing can be difficult. To transfer genetic material, recombination must be induced to overcome the strong meiotic pairing control mechanisms (Fedak 1992).

9.3.1 H. bulbosum *(secondary genepool)*

Hordeum bulbosum is a highly self-incompatible species that occurs as both a diploid and an autotetraploid. The genomes of *H. vulgare* and *H. bulbosum* are genetically very closely related and the two can be readily crossed under artificial conditions. However, seed setting on crosses between some *H. vulgare* varieties and *H. bulbosum* can be very low due to incompatibility, which manifests as pollen tube bursting within stylar tissue (Pickering & Johnston 2005).

After successful fertilisation in crosses between diploid *H. bulbosum* and *H. vulgare*, the *H. bulbosum* genome is usually completely eliminated, resulting in haploid barley embryos (Zhang et al. 1999). Homozygous barley lines can be produced from the haploid plants through application of colchicine

(Von Bothmer et al. 1995). Chromosome elimination is strongly influenced by the parental genotypes and temperature during embryo formation, and true hybrids can be still obtained. However, due to endosperm degeneration, embryos must be rescued to regenerate plants. In addition, infertile diploid hybrids must be treated with colchicine to double the chromosome number and restore fertility. Seeds can then be obtained from the tetraploid hybrids by self-fertilisation. Triploid hybrids can be produced by crossing *H. vulgare* with tetraploid *H. bulbosum.* These are generally infertile, although partially fertile triploid hybrids exist and have been used in crossing programs (Pickering & Johnston 2005).

H. vulgare x *H. bulbosum* hybrids show variation in chromosome number, stability and pairing, and only hybrids with stable chromosome numbers and high intergenomic pairing are suitable for introgression. "High-pairing" hybrids can be produced from selected superior genotypes, but even in these hybrids recombination rates are low (Pickering & Johnston 2005). Successful introgression of genes from *H. bulbosum* into *H. vulgare* has been achieved mainly through backcrossing partially fertile triploid hybrids to *H. vulgare* (Zhang et al. 2001).

9.3.2 Other interspecific hybrids (tertiary genepool)

H. vulgare has been crossed to numerous other *Hordeum* species using tissue culture and embryo rescue techniques (see Table 2). The hybrids are almost totally sterile, and the genome of cultivated barley does not readily recombine with the genome of the other species, therefore genetic material is generally not exchanged (Jorgensen et al. 1986). In several interspecific combinations involving various wild *Hordeum* species and either *H. vulgare* or *H. bulbosum*, chromosome elimination occurs, resulting in haploids of one of the parents (Von Bothmer & Jacobsen 1986). Plant regeneration from calli of hybrids has been used in some studies to induce karyotypic variations and subsequent transfer of genetic material (Jorgensen et al. 1986; Jorgensen & Andersen 1989).

Triticum

Intergeneric hybrids can be obtained between barley cultivars and diploid, tetraploid and hexaploid wheats (see Table 2) (Fedak 1992), but only with extensive intervention such as hormone applications, chemical treatment and embryo rescue (Molnar-Lang et al. 2000; Koba et al. 1991; Molnar-Lang & Sutka 1994). There is no evidence that cultivated wheat x barley hybrids exist naturally (Eastham & Sweet 2002). Barley and wheat chromosomes normally do not pair in the hybrids, which are sometimes referred to as *Tritordeum* (Shepherd & Islam 1992). Crosses between diploid barley and hexaploid wheat (*Triticum aestivum* L.) are most common, and this combination forms the focus of the following discussion.

Wheat x barley hybrids are usually wheat-like in morphology and completely self-sterile, but female fertile (Fedak 1992). Many wheat x barley hybrids have been produced with barley as the female parent. The chromosome numbers of most of the resulting hybrids are 2n=28 and the chromosomes are somatically stable. Chromosome number at meiosis is more variable, and meiotic chromosome pairing is generally low. In addition, backcross lines are difficult to produce because of pistilloidy (the conversion of other floral parts into pistils) and/or male and female sterility in the backcross plants (Fedak 1992).

Hybrids with wheat as the maternal parent are more difficult to obtain due to low crossability and result in more variable chromosome numbers and low yield in the hybrids (Fedak 1992). This combination, however, can avoid the problem of pisilloidy in backcross progeny (Taketa et al. 1998). Backcross plants can still be difficult to obtain, but tissue culture can be used to multiply wheat x barley hybrids and produce enough plants for pollination (Molnar-Lang et al. 2000; Molnar-Lang et al. 2005).

The majority of reports of wheat x barley crosses have used varieties with high crossability in intergeneric crosses, which is controlled by parental genotype, but poor agronomic traits. In a study by Molnar-Lang et al. (2000), winter wheat x winter barley hybrids between agronomically useful varieties were produced. In this study, a six-row barley was the male parent and embryo rescue was used to produce hybrids. The hybrids showed a high degree of male and female sterility and reduced seed set. Thirteen barley cultivars tested as pollinators could not be crossed with wheat.

Aegilops

In a cross with *Aegilops crassa* (syn. *Triticum crassum*), vigorous but sterile hybrids were produced in tissue culture (Fedak & Nakamura 1981). In contrast, only subviable hybrids were obtained in the cross between barley and *Ae. squarrosa* (syn. *Triticum tauschii; Ae. triuncialis*) (Fedak 1992).

Elymus

Some species of *Hordeum* and some of *Elymus* can intercross naturally. However, hybrids between *H. vulgare* and *Elymus* species have only been produced with embryo rescue. The majority of the hybrids involved barley with tetraploid *Elymus* species (see Table 2). Viable hybrids are generally vigorous, self-sterile and difficult to backcross. There is little homology between the genomes and intergenomic pairing does not usually occur (Fedak 1992; Mujeeb-Kazi 1985).

Hybrids involving hexaploid *Elymus* species have also been produced. For example, Torabinejad & Mueller (1993) obtained sterile hybrids of the Australian hexaploid species *E. scabrus* and *E. rectisetus* with *H. vulgare* using embryo culture.

Secale

Crosses between *H. vulgare* and species of *Secale* are characterised by high seed set and a relatively high yield of embryos, but also a very high seedling necrosis from some cultivar combinations. Various progeny can be obtained using embryo rescue including haploids, hybrids with incomplete genomic numbers and hybrids. Surviving hybrids, sometimes referred to as *Hordecale*, are only reasonably vigorous and are self-sterile and often completely sterile. Most of the hybrids lack pairing between chromosomes, precluding any intergenomic gene transfer (Fedak 1992).

In crosses between cultivated rye (*Secale cereale*) and barley, prefertilisation barriers mean that rye pollen growth is retarded in the style after initiation (Heslop-Harrison 1982). Post-fertilisation barriers also exist, and *H. vulgare* and *S. cereale* crosses are incompatible because of an early abortion of the endosperm and embryo (Bajaj et al. 1980). Wojciechowska & Pudelska (1992) overcame incompatibility barriers using embryo rescue, tissue culture and colchicine treatment to produce barley x rye hybrids. The numbers of embryos obtained was low and lethality of seedlings was strong: from 62 crosses of different varieties, only 69 seedlings and 9 plants were obtained. The plants were completely sterile and chiasma frequency was very low (Wojciechowska & Pudelska 1992).

Trigeneric hybrids

Trigeneric hybrids involving *Hordeum, Triticum* and *Secale* are commonly produced. For example, a trigeneric hybrid can be obtained by crossing barley and *Triticale*, which is a commercially grown artificial hybrid of rye and wheat. The cross requires embryo rescue and the hybrids are generally sterile (Balyan & Fedak 1989; Fedak 1992).

Trigeneric hybrids can also be produced by crossing *Secale* onto *Hordeum-Triticum (Tritordeum)* hybrids, or by intercrossing *Triticale* and *Tritordeum* (for example, see Fedak & Armstrong 1980). In some combinations, the resulting hybrids can produce viable seed without embryo rescue (Fedak 1992).

Table 2: Species that can be crossed with *Hordeum vulgare* under experimental conditions.

Species	Common name	Ploidy level	Hybrids under natural conditions?	References
Hordeum vulgare ssp. *spontaneum*	Wild barley	2x	Yes	see Section 9.1
H. bulbosum	Bulbous barley	2x, 4x	No	see Section 9.2
H. arizonicum	Arizona barley	6x	No	Linde-Laursen & von Bothmer (1988)
H. bogdani	–	2x	No	Von Bothmer & Jacobsen (1986)
H. brachyantherum	Meadow barley	4x, 6x	No	Jorgensen et al. (1986)
H. brevisubulatum	–	2x, 4x, 6x	No	Jorgensen et al. (1986)
H. capense	Cape wild barley	4x	No	Jorgensen et al. (1986)
H. chilense	–	2x	No	Thomas & Pickering (1985)
H. comosum	–	2x	No	Von Bothmer & Jacobsen (1986)
H. cordobense	–	2x	No	Von Bothmer & Jacobsen (1986)
H. depressum	Dwarf barley	2x, 4x	No	Von Bothmer & Jacobsen (1986)
H. erectifolium	–	2x	No	Von Bothmer & Jacobsen (1986)
H. euclaston	Argentine barley	2x	No	Von Bothmer & Jacobsen (1986)
H. flexuosum	–	2x	No	Von Bothmer & Jacobsen (1986)
H. fuegianum	–	4x	No	Von Bothmer & Jacobsen (1986)
H. intercedens	Bobtail barley	2x	No	Von Bothmer & Jacobsen (1986)
H. jubatum	Foxtail barley	4x	No	Orton (1979) Jorgensen et al. (1986)
H. lechleri	–	6x	No	Von Bothmer et al. (1999) Jorgensen et al. (1986)
H. marinum	Sea barley	2x, 4x	No	Finch (1983)
H. murinum	Mouse barley	2x, 4x, 6x	No	Von Bothmer & Jacobsen (1986)
H. muticum	–	2x	No	Von Bothmer & Jacobsen (1986)
H. parodii	–	6x	No	Jorgensen et al. (1986)
H. patagonicum	–	2x	No	Von Bothmer & Jacobsen (1986)
H. procerum	–	6x	No	Jorgensen et al. (1986)
H. pubiflorum	Antarctic barley	2x	No	Von Bothmer & Jacobsen (1986)
H. pusillum	Little barley	2x	No	Von Bothmer & Jacobsen (1986)
H. roshevitzii	–	2x, 4x	No	Jorgensen et al. (1986)

Species	**Common name**	**Ploidy level**	**Hybrids under natural conditions?**	**References**
H. secalinum	–	4x	No	Von Bothmer & Jacobsen (1986)
H. stenostachys	Centenillo	2x	No	Von Bothmer & Jacobsen (1986)
H. tetraploidum	–	4x	No	Jorgensen et al. (1986)
Triticum aestivum	Bread wheat	6x	No	Fedak (1992) Molnar-Lang et al. (2000)
T. dicoccum	Cultivated emmer wheat	4x	No	Fedak (1992)
T. monococcum	Einkorn wheat	2x	No	Fedak (1992)
T. persicum	Persian black wheat	4x	No	Fedak (1992)
T. timopheevi	Sanduri wheat	4x	No	Fedak (1992)
T. turgidum	Rivet wheat, Poulard wheat	4x	No	Fedak (1992)
Aegilops crassa	Persian goatgrass	6x	No	Fedak & Nakamura (1981)
Ae. sqarrosa	Barbed goatgrass	2x	No	Fedak (1992)
Elymus arenarius	Blue lime grass	6x	No	Fedak (1992)
E. canadensis	Canada wild rye	4x	No	Dahleen (1999)
E. caninus	Bearded wheatgrass	4x	No	Fedak (1992)
E. elongatus	Rush wheatgrass	4x	No	Dahleen (1999) Mujeeb-Kazi (1996)
E. humidus	–	6x	No	Muramatsu et al. (1993)
E. lanceolatus	Thick spike wheatgrass	4x	No	Fedak (1992)
E. mollis	American dunegrass	4x	No	Fedak (1992)
E. patagonicus	–	6x	No	Mujeeb-Kazi (1985)
E. rectisetus	–	6x	No	Torabinejad & Mueller (1993)
E. scabrus	Common wheatgrass	6x	No	Torabinejad & Mueller (1993)
E. trachycaulus	Slender wheatgrass	4x	No	Aung (1991)
Secale cereale	Rye	2x	No	Fedak (1992)
S. africanum	Wild rye	2x	No	Fedak (1992)
S. kuprijanovii	–	2x	No	Fedak (1992)
S. montanum	Mountain rye	2x	No	Fedak (1992)
S. vavilovii	–	2x	No	Fedak (1992)
Psathyrostachys fragilis (syn. *Elymus fragilis*)	–	2x	No	Von Bothmer et al. (1984)
Thinopyrum intermedium (syn. *Elymus hispidus*)	Intermediate wheatgrass	6x	No	Fedak (1992)

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Appendix A Weed Risk Assessment of Barley

Species: *Hordeum vulgare* (barley)

Relevant land uses:

1. Intensive[11] uses (ALUM[12] 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 used in this assessment are based on the South Australian Weed Risk Management Guide (Virtue 2004). Questions 1 – 5 relate to invasiveness and questions 6 – 11 relate to impact of barley on the relevant land use areas. 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 barley has some traits associated with weeds, it is not considered as an invasive weed in Australia. Other than agricultural areas where it is cultivated, barley can occur along the sides of roads and railway lines that have acted as routes for its transportation. With the exception of WA, Groves et al. (2003) do not give barley a rank in agricultural ecosystems in any Australian state or territory, indicating it is either not a problem or does not occur in agricultural environments. In WA barley receives the rank of ‘5c’. This rank indicates it is a naturalised species known to be a major problem at four or more locations and that it is currently under active control in part of the state (Groves et al. 2003). Groves et al. (2003) categorise barley as a minor weed in natural ecosystems warranting control at four or more locations within a State or territory.

Unless cited, information in this weed assessment is taken from this document *The Biology of* Hordeum vulgare L. (*Barley*) v2 (OGTR 2017). This WRA is for **non-GM barley volunteers** and includes non-GM herbicide tolerant varieties of this crop. Reference made to barley as a cultivated crop is only to inform its assessment as a volunteer.

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[11] *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.

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

Invasiveness questions	**Barley**
1. What is barley's ability to establish amongst existing plants?	**Rating: Low in all relevant land uses** Barley is a domesticated crop that grows best under agricultural conditions. It prefers well drained soils with high fertility and responds well to limited irrigation. However, compared to other cereals, barley is better adapted to drought and salinity. Barley volunteers would mainly be derived from seed that is shed before or during harvest and can readily establish in disturbed lands of *dryland and irrigated cropping areas*, especially along the margins of fields or is subsequent crops sown on the same land where barley was grown and harvested. Seed losses can also occur in *intensive use areas* involved in the transport, storage and processing of barley; volunteers often grow along roadsides or near grain silos. Barley has limited dormancy and thus dispersed seed is likely to germinate early and die in unfavourable environmental conditions or be consumed by predators. Barley does not compete well with other vegetation.
2. What is barley's tolerance to average weed management practices in the land use?	**Rating: Low in all relevant land uses** Weed management practices (preventive, cultural and chemical) aim to reduce the presence of weeds and loss in yields due to weeds. In *dryland and irrigated cropping areas*, where barley is grown in rotation with other crops, these practices effectively control barley volunteers. Nevertheless, seeds may germinate after herbicides have been broken down and volunteers may become established. In *intensive use areas*, such as land adjacent to grain silos and along roadsides and railway tracks, weed management practices minimise the spread of volunteers. The degrees of susceptibility of the currently available barley varieties to herbicides are available in the respective grower guides for each state[13].
3. Reproductive ability of barley in the land use:	
3a. What is the time to seeding in the land uses?	**Rating: < 1 year in all relevant land uses** Barley is an annual crop that generally takes five to seven months to complete its lifecycle under standard agricultural conditions. Volunteer barley behaves in a similar way.
3b. What is the annual seed production in the land use per square metre?	**Rating: Low in all relevant land use areas (from volunteers)** As a crop in *dryland and irrigated cropping areas*, barley seed yields vary greatly with environmental

[13] Source: Grains Research and Development Corporation website; accessed 21 March 2017.

Invasiveness questions	**Barley**
	conditions and variety. In Australia the average yield for 2014/15 was 2.12 tonnes/ha or about 212 g/m^2. Assuming an average seed weight of 4.2 grams per 100 seeds or 0.042 gm/seed (Agriculture Victoria Website, accessed 12 January 2017), this is equivalent to about 5050 seeds/m^2. Barley crop loses up to and including harvest can range from 5 to 10 % (Agriculture Victoria Website, accessed 12 January 2017). An average loss of 7.5% equates to about 410 seeds/m^2 remaining on the ground post-harvest. 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 barley volunteers) through herbicide sprays, grazing or cultivation. In *intensive use areas*, seed production per unit area is likely to be considerably less than that in *dryland and irrigated cropping areas*, due to suboptimal germination and growth conditions (e.g. lack of moisture and nutrients), competition by other plants and grazing.
3c. Can barley reproduce vegetatively?	The production of rooted tillers has occasionally been described as a form of vegetative reproduction, as barley tillers separated from the main plant can grow supported by the adventitious roots only. Otherwise, barley is not capable of vegetative spread.
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)?	**Rating: Occasional in all relevant land uses** There is no evidence that flying animals play a major factor in the dispersal of barley seeds. Corellas, galahs, house sparrows, mallard ducks, pheasants, red-winged black birds and rock pigeons fed barley seeds did not excrete any intact barley seeds. Barley has special bristles on the spikelets, which allows them to adhere well to the furs of larger animals, the feathers of birds and the clothing of people, and the seeds may be dispersed in this way. Viable seed may be transported on the muddy feet/legs of birds.
4b. Are viable plant parts dispersed by land based animals?	**Rating: Unlikely to Occasional in all relevant land uses** Barley has special bristles on the spikelet, which allows them to adhere well to the furs of larger animals, the feathers of birds and the clothing of people, and the seeds may be dispersed in this way. Whole and undamaged barley seeds have been reported in the dung of cattle, suggesting there is the potential for livestock to disperse viable barley seed after consumption. Dispersal in the hooves of animals is also probable, but not well reported, thus the frequency is not

Invasiveness questions	**Barley**
	known. Rodents which hoard seeds could disperse barley seed from crop production areas (e.g. after harvest) or from volunteers.
4c. Are viable plant parts dispersed by water?	**Rating: Unlikely to Occasional in all relevant land uses** Dispersal by water is possible, but no data is available. Seed dispersed by water typically has adaptations which make it resistant to sinking (e.g. hairs or slime), provide a high surface to volume ratio (e.g. small size, unwettable), or low specific gravity (e.g. air spaces, cork, oil) (Howe & Smallwood 1982). Barley seed does not have these adaptions. Barley seed has a high specific gravity and will typically sink in water (Derr 1910). Thus barley seed is not well adapted for dispersal by water.
4d. Are viable parts dispersed by wind?	**Rating: Unlikely to Occasional in all relevant land uses** Dispersal by high winds is possible, but no data is available. Barley seeds are heavy and do not possess appendages that are designed to facilitate wind dispersal (e.g. they are not “winged”).
5. Long distance seed dispersal (more than 100 m) by human means in land uses:	
5a. How likely is deliberate spread via people	**Rating: Common in/from all relevant land uses** Barley 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 barley is present as a volunteer, it is managed like other weeds. In those instances, barley would not be spread deliberately.
5b. How likely is accidental spread via people, machinery and vehicles?	**Rating: Occasional (to common) in/from all relevant land uses** In *dryland and irrigated cropping areas*, where barley is planted as a crop, it is common for seed to be accidently 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 barley 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 barley 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 *intensive use areas*. Practices such as the mowing of weeds along roadsides could lead to occasional spread of seeds by machinery.

Invasiveness questions	Barley
5c. How likely is spread via contaminated produce?	**Rating: Occasional in/from all land use areas.** Barley farming in dryland and irrigated cropping areas is characterised by rotation with other crops, such as wheat, oats and pasture. The amount of barley seed left in the field prior to the planting of a rotation crop will depend upon the efficiency of the barley harvest, seed cleaning of machinery, and general weed management procedures. Growth of barley volunteers within a rotation crop depends on the weed management procedures of the latter crop, while the spread of this barley 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.
5d. How likely is spread via domestic/farm animals?	**Rating: Occasional in all relevant land uses** If livestock are grazed in or adjacent to a barley field, then it is possible that viable barley seeds may be spread either in their hooves, fur, wool or excrement. The separation of plant and animal farming minimises this possibility, but livestock are grazed on rotation crops such as pastures. Whole barley seed, or that which has been processed (crushed or rolled), straw, stubble and silage constitute some livestock feeds (DPI NSW 2014). As noted above (4a & b), intact barley seeds are not known to survive digestion by a number of birds, but can remain intact after digestion by cattle. Survival of whole seed through other animals is not known. In the case of processed barley (crushed or rolled), 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.

Impact Questions	Barley
6. Does barley reduce the establishment of desired plants?	**Rating: Reduces establishment by < 10% in all relevant land uses** Barley is a domesticated and cultivated plant that typically establishes where land has been disturbed, most particularly in *dryland and irrigated cropping areas*. These areas are subject to standard weed management practices that would minimise the impact of any barley volunteers on the establishment

Impact Questions	**Barley**
	of desired crop plants. In *intensive use areas*, 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, barley would be treated as a weed and managed accordingly. If left untreated, barley is not competitive and would struggle to survive and persist amongst other vegetation. Dispersed barley seed (e.g. along transport routes) is likely to germinate in unfavourable environmental conditions or be consumed by predators.
7. Does barley reduce the yield or amount of desired plants?	**Rating: Reduces yield/amount by < 10% in all relevant land uses** Barley is commonly used in rotation with other crops. The rationale behind crop rotation in *cropping areas* 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 barley volunteers) would be managed by mechanical or chemical means, thus greatly reducing the density of barley volunteers. Barley 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).
8. Does barley reduce the quality of products or services obtained from the land use?	**Rating: Low in all relevant land uses** As discussed in questions 6 and 7 above, barley (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 barley 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 barley 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 barley seeds (2 seeds per 200 g of lentils), can lower the quality of the crop (Pulse Australia 2016).

Impact Questions	**Barley**
9. What is the potential of barley to restrict the physical movement of people, animals, vehicles, machinery and/or water?	**Rating: Low in all relevant land uses** As a densely planted mature crop, barley 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 barley volunteers very low. Thus, when growing as a volunteer, the potential for barley to restrict the physical movement of people, animals or water would be low.
10. What is the potential of barley to negatively affect the health of animals and/or people?	**Rating: Low in all relevant land uses** Barley has been part of the human diet for thousands of years and there is no evidence that barley is toxic to humans. A small number of people do suffer from barley induced allergies via inhalation of barley flour, chiefly caused by proteins in the cereal trypsin/α-amylase inhibitor family. 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. The main use of barley in Australia is for animal feed. Nonetheless, elevated levels of phytic acid in barley can be a problem, chelating minerals and preventing their dietary use after digestion by animals. Similarly, the lectins found in barley grain can cause lesions in the intestinal tract and thus impair absorption of nutrients by animals. Standard management practices as well as environmental conditions would keep the density of barley volunteers very low. The proportion of volunteer barley in animal feed (e.g. hay) is unlikely to be great enough to negatively affect he health of animals. Thus the potential for barley to negatively affect the health of animals or people is considered low.

Impact Questions	Barley
11. Major positive and negative effects of barley on environmental health in each relevant land use:	
11a. Does barley provide food and/or shelter for pathogens, pests and/or diseases in the land use?	**Rating: Minor or no effect in all land uses** In crop rotation regimes, barley 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, barley is associated with a number of insect pests that infect multiple crops. It is susceptible to a range of pathogens, such as viruses, nematodes and fungi. Infected barley volunteers could act as a reservoir of these pathogens that can infect crops in subsequent years. Most of these pathogens are specific to barley or cereals in general, and do no infect plants that are more distantly related. However, the density of barley volunteers is expected to be low and thus may have only minor or no effect.
11b. Does barley change the fire regime in the land use?	**Rating: Minor or no effect in all relevant land uses** The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to affect fire regimes.
11c. Does barley change the nutrient levels in the land use?	**Rating: Minor or no effect in all relevant land uses** The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to affect nutrient levels.
11d. Does the species affect the degree of soil salinity in the land use?	**Rating: Minor or no effect in all relevant land uses** The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to affect soil salinity.
11e. Does the species affect the soil stability in the land use?	**Rating: Minor or no effect in all relevant land uses** The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to affect soil stability.
11f. Does the species affect the soil water table in the land use	**Rating: Minor or no effect in all relevant land uses** The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to affect the soil water table.
11g. Does the species alter the structure of	**Rating: Minor or no effect in all relevant land uses**

Impact Questions	**Barley**
nature conservation by adding a new strata level?	The number and density of barley volunteers is expected to be low for all relevant land uses, and would not be expected to add a new strata level.