



Australian Government

**Department of Health and Ageing
Office of the Gene Technology Regulator**

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



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

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TABLE OF CONTENTS

PREAMBLE	1
SECTION 1	TAXONOMY	1
SECTION 2	ORIGINS AND CULTIVATION	2
2.1	CENTRE OF DIVERSITY AND DOMESTICATION	2
2.2	COMMERCIAL USES	3
2.3	CULTIVATION IN AUSTRALIA	5
	2.3.1 <i>Commercial propagation</i>	5
	2.3.2 <i>Scale of cultivation</i>	5
	2.3.3 <i>Cultivation practices</i>	5
2.4	CROP IMPROVEMENT	6
	2.4.1 <i>Breeding</i>	6
	2.4.2 <i>Genetic modification</i>	7
SECTION 3	MORPHOLOGY	8
3.1	PLANT MORPHOLOGY	8
3.2	REPRODUCTIVE MORPHOLOGY	8
SECTION 4	DEVELOPMENT	9
4.1	REPRODUCTION	9
	4.1.1 <i>Asexual reproduction</i>	9
	4.1.2 <i>Sexual reproduction</i>	9
4.2	POLLINATION AND POLLEN DISPERSAL	10
4.3	FRUIT/SEED DEVELOPMENT AND SEED DISPERSAL	12
4.4	SEED DORMANCY AND GERMINATION	12
4.5	VEGETATIVE GROWTH	14
SECTION 5	BIOCHEMISTRY	16
5.1	TOXINS	16
5.2	ALLERGENS	16
5.3	OTHER UNDESIRABLE PHYTOCHEMICALS	17
5.4	BENEFICIAL PHYTOCHEMICALS	18
SECTION 6	ABIOTIC INTERACTIONS	19
6.1	ABIOTIC STRESSES LIMITING GROWTH	19
	6.1.1 <i>Nutrient stress</i>	19
	6.1.2 <i>Temperature stress</i>	19
	6.1.3 <i>Water stress</i>	19
	6.1.4 <i>Other stresses</i>	20
6.2	ABIOTIC TOLERANCES	20
SECTION 7	BIOTIC INTERACTIONS	20
7.1	WEEDS	20
7.2	PESTS AND PATHOGENS	20
7.3	OTHER BIOTIC INTERACTIONS	23
SECTION 8	WEEDINESS	23
8.1	WEEDINESS STATUS ON A GLOBAL SCALE	23
8.2	WEEDINESS STATUS IN AUSTRALIA	24
8.3	WEEDINESS IN AGRICULTURAL ECOSYSTEMS	24
8.4	WEEDINESS IN NATURAL ECOSYSTEMS	24
8.5	CONTROL MEASURES	24
SECTION 9	POTENTIAL FOR VERTICAL GENE TRANSFER	24
9.1	INTRASPECIFIC CROSSING (PRIMARY GENEPOOL)	25
9.2	INTERSPECIFIC AND INTERGENERIC CROSSING	25
	9.2.1 <i>Interspecific</i>	25
	9.2.2 <i>Intergeneric</i>	25
9.3	CROSSING UNDER EXPERIMENTAL CONDITIONS	25
REFERENCES	30

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).

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

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 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

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

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 136 million tonnes of barley is produced annually on about 56 million hectares. Countries producing the most barley in 2005–06 are summarised in Table 1. Leading exporters of barley include Australia, Ukraine, EU, Canada and Russian Federation (see Table 1), while the principal markets for importing barley are Saudi Arabia, Japan and China³.

Table 1: Barley production, area and export, 2005–06³

Country	Production ('000 tonnes)	Area harvested ('000 hectares)	Trade Year Exports ('000 tonnes)
European Union	54,752	13,790	2,587
Russian Federation	15,800	9,150	1,397
Canada	11,678	3,634	1,876
Australia	9,563	4,447	5,231
Ukraine	9,000	4,350	4,926
Turkey	7,600	3,600	550
United States	4,613	1,323	357
Peoples Republic of China	3,400	850	3
World	136,628	55,654	17,428

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 the production of 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 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 (Akar et al. 2004; OECD 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

³ USDA Foreign Agricultural Service's Production, Supply and Distribution (PSD) online database <<http://www.fas.usda.gov/psdonline/>>, queried 20 December 2007.

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 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 and Victoria, 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 (US Grains Council 2007). 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 \$1.2 billion in 2004–05 (Australian Bureau of Statistics 2006). It is grown in wheat production areas in New South Wales, Victoria, Queensland, Western Australia and South Australia. A small amount of barley is also grown in Tasmania. The area sown to barley in Australia is forecast to increase by around 10% to 4.4 million hectares in 2007–08. Australian barley production is also forecast to increase in 2007–08, to over 9 million tonnes, after severe drought conditions resulted in a drop in production in 2006–07 (ABARE 2007).

While Australia only produces about 7% of the world's barley, it provides about 30% of world barley exports, due to a relatively small domestic market (ABARE 2006). ABARE forecasts for 2007–08 predict that, of Australia's barley crop, 68% is will be exported, primarily for use as animal feed (60%) and malting barley (28%), with a small amount being used as malt (11%). The remaining 32% of barley produced in Australia is predicted to be used domestically, primarily as animal feed (88%) with smaller amounts being used as seed (7%) and for malt and other human use (6%) (ABARE 2007).

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.

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). Harvest of barley crops in Australia

usually occurs mid-November to mid-December, with harvest as early as October possible in northern regions.

Barley is typically sown at a depth of 2–3 cm and a plant density of 100–150 plants/m². Densities of less than 80 plants/m² can result in reduced yield, and above 150 plants/m² can lead to a reduction in seed weight (Western Australian Department of Agriculture and Food 2006c). 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 (eg 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. 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 (Western Australian Department of Agriculture and Food 2006d).

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 combination with this, stubble can be retained (left standing or cut and spread for mulch), or removed, for example by grazing, burning or cultivation.

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 18% for malting barley) and then aerated or dried. 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 2007a).

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). 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 (Thomas 2003; Pickering & Johnston 2005). An extensive catalogue of genetic stocks, such as aneuploid lines, deletion stocks and translocation lines, is now available for barley (Varshney et al. 2007). High density molecular genetic maps have also become available in recent years, and are being used in marker assisted selection 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 diseases resistance genes, with malting quality representing another important target (Varshney et al. 2007). A particular effort to use marker assisted selection in wheat and barley breeding programs is underway in Australia, and several new Australian varieties have been developed using this technology (Varshney et al. 2007). 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 (Wan & Lemaux 1994; Tingay et al. 1997; Travella et al. 2005; Hensel et al. 2007). Other barley transformation methods are based on androgenetic pollen cultures or isolated ovules as gene transfer targets (Hensel et al. 2007). Although transformation techniques have been developed for a range of barley cultivars (Chang et al. 2003; Hensel et al. 2007), 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).

There are no commercial genetically modified (GM) barley varieties available to date (von Wettstein 2007; Dahleen & Manoharan 2007). Nevertheless, GM barley plants aimed at commercial applications have been produced (for review, see Dahleen & Manoharan 2007). For example, a wheat gene associated with malate efflux has been introduced into barley and shown to confer aluminium tolerance to the resulting GM barley plants (Delhaize et al. 2004). Genes conferring resistance to diseases including stem rust (Horvath et al. 2003), barley yellow dwarf virus (Wan & Lemaux 1994; Wang et al. 2000; Wang et al. 2001), cereal yellow dwarf virus (Wang et al. 2001) and fungal infection (Leckband & Lorz 1998; Tobias et al. 2007) have also been introduced into barley plants.

Several genes for improved malting quality, nutrient content and feed quality have been introduced into barley. GM barley plants containing the gene encoding an engineered heat-stable (1,3;1,4)- β -glucanase for improved feed and malt have been generated and shown to be stable over many generations (Jensen et al. 1996; Horvath et al. 2001). A thermostable β -

amylase gene has also been expressed in barley plants for improved malting quality (Kihara et al. 2000).

Genes introduced into barley for improved food and feed nutrition include feed-back insensitive enzymes from the aspartate family pathway, resulting in elevated levels of lysine and methionine (Brinch-Pedersen et al. 1996), and a hybrid cellulase gene for the high level production of cellulase (Xue et al. 2003).

Barley is also considered promising for the production of pharmaceutical compounds (Dahleen & Manoharan 2007).

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 throws out 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 1). 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).

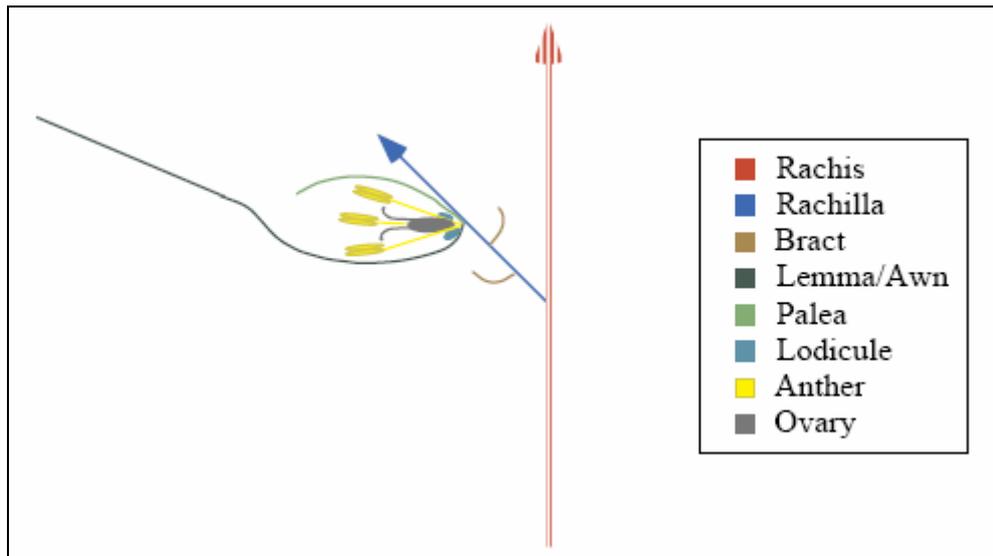


Figure 1: Depiction of the barley spikelet (Williams-Carrier et al. 1997). Reproduced with permission of the Company of Biologists.

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. Many winter barley varieties are open-flowering whereas spring barley varieties are usually closed-flowering (Nelson et al. 2001). 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 (Pope 1944; Bennett et al. 1973). 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 hours 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%) (Wagner & Allard 1991; Von Bothmer 1992; Ellstrand 2003), 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 (Chaudhary et al. 1980; Parzies et al. 2000; Abdel-Ghani et al. 2004; Gatford et al. 2006), 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). 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% (Nevo 1992). 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 (Parzies et al. 2000; Abdel-Ghani et al. 2004). 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, with the difference likely to be a result of exposure to colder temperatures. In 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 measure beyond this distance and therefore the true rate 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 South Australia, 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 (California Crop Improvement Association 2003; Canadian Seed Growers' Association 2005).

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 (Nelson et al. 2001).

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 apparatus 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 get dispersed in this way (Von Bothmer 1992; Von Bothmer et al. 1995).

Although a search of the literature did not identify any reports of barley seeds being dispersed by endozoochory, it is possible that barley seeds could germinate after passage through the digestive system of some birds or mammals. For example, viable seed from *Avena sativa*, a grass from the same subfamily as barley (Pooideae), was detected in emu droppings (Calvino-Cancela et al. 2006). Also, 15% of barley grain fed to cattle is excreted whole and undamaged (Kaiser 1999), suggesting there is the potential for livestock to disperse viable barley seed after consumption.

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 than 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 delay the disappearance of 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, a small proportion (1% and 0.02%, respectively) of barley seeds sown at depths of up to 30 cm were recovered after 15 months. In the same study it was found that burying entire spikes rather than seeds did not influence seed survival (Rauber 1988). In a Scottish survey, volunteer winter barley was reported to persist for up to five seasons 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).

In a Scottish study, some winter barley lines emerged successfully in the next season after burial at a depth of 200 mm, but no plants emerged in the second or third season after burial at depths of 50–200 mm. No data as to the viability of the buried barley seeds in this trial were provided (Davies & Wilson 1993).

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 1).

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 Queensland, barley plants take between 105 and 157 days to reach maturity (Thomas & Fukai 1995).

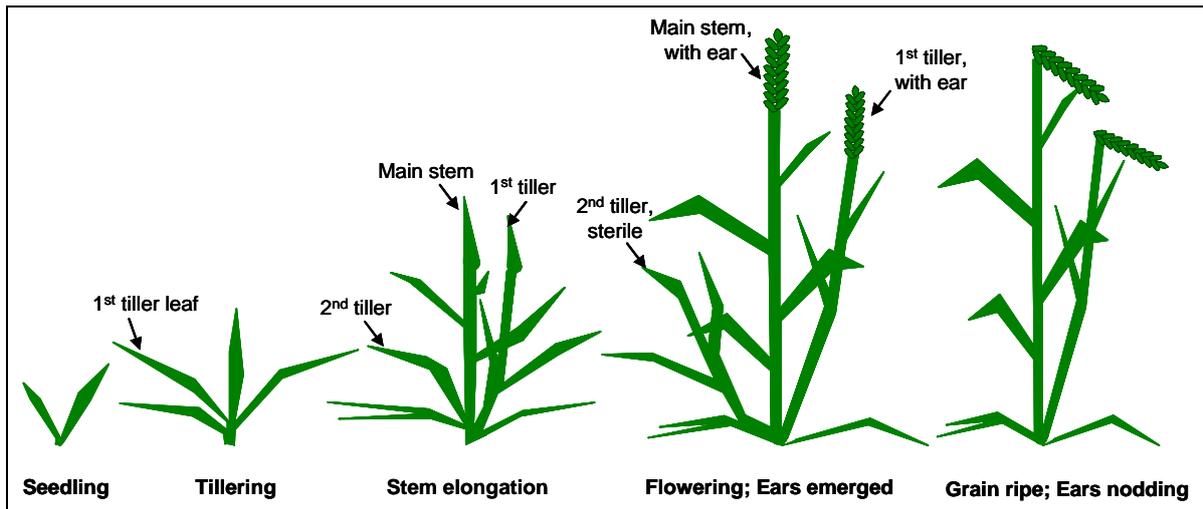


Figure 1: Schematic diagram of barley plants at successive stages of development.

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).

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 1). 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 anaphylaxis 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 transcripts show cross reactivity with known allergen transcripts and therefore the pollen may also represent a potential source of aeroallergenic proteins for individuals near agricultural sites (Astwood et al. 1995).

Coeliac disease

Coeliac disease (gluten-sensitive enteropathy) is a disorder caused by intolerance to the ingestion of gluten from wheat, barley, rye and triticale (Fraser & Nowak 1988). Gluten is a complex of two major storage proteins in cereals, namely prolamin and glutelin. The sensitivity response is triggered by the prolamin fraction of the storage proteins, which are hordeins in barley and gliadins in wheat (OECD 2004).

Inheritance of coeliac disease is multigenic and is strongly associated with European populations (Kasarda 2004). However, the disease does affect people from all ethnic groups. Fraser and Ciclitira (Fraser & Ciclitira 2001) noted that the prevalence of coeliac disease was thought to be 1 in 1500 in western countries although recent screenings of blood donors has shown a higher prevalence of 1 in 250 in Sweden and the USA. Simmonds (Simmonds 1989) had previously reported that 1 in 2000–3000 individuals in the US suffer from the coeliac condition. In Australia the prevalence of coeliac disease in children is thought to be approximately 1 in 2000 while in adults it is 1 in 3000 with female sufferers outnumbering male sufferers 2 to 1 (Australian Gastroenterology Institute 1993).

For sufferers of coeliac disease, the consumption of gluten can result in diarrhoea, malabsorption, fat in the stool, and nutritional and vitamin deficiencies. Some sufferers may have only minimal changes in the epithelium and no obvious symptoms, yet others may have severe damage to the lining of the intestine. The lesions may also affect the ileum and even stomach and rectum, and villi may be absent (Australian Gastroenterology Institute 1993).

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

5.3 Other undesirable phytochemicals

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).

Low phytic acid mutants, with reduced phytic acid accumulation and increased inorganic phosphorous, have been identified in barley (Larson et al. 1998). However, this trait has not yet been used in agricultural production.

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). Proanthocyanidin-free barley has been produced and released commercially, although it has not been used as a malting barley (von Wettstein 2007).

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 β -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 β -glucan, for example, can lower both post-prandial blood glucose levels and blood cholesterol (McIntosh et al. 1991; OECD 2004). In contrast, arabinoxylans and β -glucans can have a deleterious effect on digestion in monogastrics (OECD 2004). In addition, β -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).

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic stresses limiting growth

6.1.1 *Nutrient stress*

The main nutrients required for successful production of a barley crop are nitrogen, potassium and phosphorus, and to a lesser extent manganese, copper and zinc (Western Australian Department of Agriculture and Food 2007b). Low sulphur levels can also be a problem in areas with a long history of cultivation (Queensland Department of Primary Industries and Fisheries 2007).

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 at sowing or up to 10 weeks after sowing (Western Australian Department of Agriculture and Food 2007b). In malting barley, the requirement for nitrogen must be balanced to maximise yield without increasing the protein level in the grain (Queensland Department of Primary Industries and Fisheries 2007).

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. The timing of potassium fertiliser application also depends on rainfall, as well as measured soil potassium levels (Western Australian Department of Agriculture and Food 2007b).

Phosphorus is essential for the rapid early development of barley roots and seedlings and for seed formation. Potassium deficiency can reduce head and grain number. Phosphate fertiliser is generally applied with the seed during sowing as it is required early in development (Western Australian Department of Agriculture and Food 2007b).

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 Western Australia (WA), the climate tends to more extreme Mediterranean and crop growth is highly dependent upon winter rains (Simmonds 1989). The winter-dominant rainfall of WA

differs from the generally higher and evenly distributed rainfall of Victoria and southern New South Wales (NSW), and the summer-dominant rainfall of the northern wheat growing areas (Cramb et al. 2000).

Barley consumes less water per unit weight of dry matter produced than other cereals, and can be grown on limited irrigation (Queensland Department of Primary Industries and Fisheries 2007). 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). Like other cereals, barley is particularly susceptible to waterlogging between germination and emergence (Western Australian Department of Agriculture and Food 2006a).

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).

Weeds that can be a problem in barley crops include the broad-leaved weeds capeweed, doublegee and wild radish, and the grass weeds annual ryegrass and wild oats. Capeweed seeds are easily wind dispersed between fields and its occurrence is widespread in pastures. Seed dormancy and the staggered germination displayed by both doublegee and wild radish make these weeds hard to control. Annual ryegrass and wild oats also exhibit staggered germination, and are two of the most competitive weeds of cereal crops (Western Australian Department of Agriculture and Food 2006d).

7.2 Pests and pathogens

Damage to cereal crops by birds has been noted in Australia and around the world (Brodie 1980; Coleman & Spurr 2001; Bomford & Sinclair 2002). In Australia, the main bird pests of winter wheat, barley, oats and pulse crops are the galah, little corella, long-billed corella, cockatiel and sulphur-crested cockatoo (Bomford & Sinclair 2002). A summary of birds reported to cause damage to cereal crops in Australia is provided in Table 2.

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).

Table 2: Bird pests of cereal crops in Australia

Bird pest	Reference
emu	Davies 1978
cockatiels	Jones 1987
parakeets	Western Australian Department of Agriculture and Food 2005
sulphur-crested cockatoos	Temby & Marshall 2003; Massam 2001
little corellas	Bomford & Sinclair 2002
long-billed corellas	Temby & Marshall 2003
galahs	Temby & Marshall 2003; Jarman & McKenzie 1983
tree sparrows	Massam 2000
house sparrows	Massam 2000; Western Australian Department of Agriculture and Food 2005

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

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

Damage from field insects is not generally a major factor for barley crops, although significant damage can occur if conditions favouring the build up of insect populations occur. Potential insect pests of barley in Australia include aphids, armyworm, Australian plague locust, mites, cockchafer, cutworm, desiantha weevil, lucerne flea and webworm. 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 and snails can also cause damage

to barley crops, especially in the early seedling stage (Western Australian Department of Agriculture and Food 2006b).

Pathogens, particularly fungi, viruses and nematodes, can reduce grain yield and quality in barley. Disease management strategies include using resistant varieties and rotation with non-host crops. The main foliar diseases of barley are leaf spots, rusts and powdery mildew. A summary of diseases that affect barley in Australia is provided in Table 3.

Table 3: Diseases of barley in Australia⁴

Disease name	Causal organism	Area of occurrence on the plant
Viruses		
Barley yellow dwarf virus	Barley yellow dwarf luteoviruses, transmitted by aphids	Foliage, head
Wheat streak mosaic virus	Tritimovirus	Foliage
Cereal yellow dwarf virus	Cereal yellow dwarf luteoviruses, transmitted by aphids	Foliage, head
Nematode diseases		
Root lesion nematode	<i>Pratylenchus</i> sp.	Roots
Cereal cyst nematode	<i>Heterodera avenae</i>	Roots
Bacterial diseases		
Black chaff (bacterial streak)	<i>Xanthomonas translucens</i>	Foliage, head
Fungal diseases		
Dwarf bunt	<i>Tilletia controversa</i>	Grain, whole plant
Fusarium head blight	<i>Fusarium graminearum</i>	Head
Covered and loose smut	<i>Ustilago segetum</i> var. <i>hordei</i> ; <i>Ustilago tritici</i>	Head
Black point	Unknown	Grain
Leaf rust	<i>Puccinia hordei</i>	Foliage
Barley grass stripe rust	<i>Puccinia striiformis</i>	Foliage
Net-type and spot-type net blotch	<i>Pyrenophora teres</i> f. <i>teres</i> ; <i>Pyrenophora teres</i> f. <i>maculata</i>	Foliage
Powdery mildew	<i>Blumeria graminis</i> f.s.p. <i>hordei</i>	Foliage
Scald	<i>Rhynchosporium secalis</i>	Foliage
Stem rust	<i>Puccinia graminis</i>	Stem
Crown rot	<i>Fusarium pseudograminearum</i>	Crown, lower stem
Common root rot	<i>Bipolaris sorokiniana</i>	Roots
Take-all	<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	Roots
Rhizoctonia bare patch	<i>Rhizoctonia solani</i>	Roots
Pythium root rot	<i>Pythium</i> sp.	Roots

⁴ <http://www.agric.wa.gov.au/content/FCP/CER/BAR/PW/barley_dise_gener.htm>

<http://www.dpi.qld.gov.au/cps/rde/xchg/dpi/hs.xsl/26_3528_ENA_HTML.htm>

<<http://www.dpi.vic.gov.au/dpi/nreninf.nsf/LinkView/I9BEB5ECB3BFD81BCA256BC70082428C>>

7.3 Other biotic interactions

Endophytic actinobacteria, belonging to the genera *Streptomyces*, *Microbispora*, *Micromonospora* and *Nocardioideis*, have been isolated from surface sterilized 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 (Bertholdsson 2004; Belz 2007).

8.1 Weediness status on a global scale

An important element in predicting weediness is taxonomic relationships, considering weediness within a taxon, including its history of weediness in any part of the world (Panetta 1993; Bergelson et al. 1998; 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, Nth America, Sth 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 Australia⁵. 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 (Harden 1993; Walsh & Entwisle 1994; Eastham & Sweet 2002). 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 Western Australia 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 (eg glyphosate) will kill volunteer plants (Ogg & Parker 2000).

During the growing season, volunteer barley contaminating noncereal 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

⁵ < <http://www.anbg.gov.au/avh/>>, accessed 21 December 2007

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

9.1 Intraspecific crossing (primary gene pool)

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

H. vulgare is a diploid species which lacks the buffering capacity of multiple genomes and, therefore, can not tolerate much genetic manipulation (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 4). 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 4). 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).

H. bulbosum (secondary gene pool)

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).

Other interspecific hybrids (tertiary genepool)

H. vulgare has been crossed to numerous other *Hordeum* species using tissue culture and embryo rescue techniques (see Table 4). 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 4) (Fedak 1992), but only with extensive intervention such as hormone applications, chemical treatment and embryo rescue (Koba et al. 1991; Molnar-Lang & Sutka 1994; Molnar-Lang et al. 2000). 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 pistilloidy 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 4). 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 (Mujeeb-Kazi 1985; Fedak 1992).

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 4: Species that can be crossed with *Hordeum vulgare*.

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

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

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