



Australian Government

Department of Health and Ageing

Office of the Gene Technology Regulator

The Biology of *Zea mays* L. ssp *mays* (maize or corn)



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

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PREAMBLE

This document describes the biology of *Zea mays* L. subspecies (ssp.) *mays*, with particular reference to the Australian environment, cultivation and use. Information included relates to the taxonomy and origins of cultivated *Z. mays* ssp. *mays*, 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 *Z. mays* ssp. *mays* that may be released into the Australian environment.

As maize is one of the best researched and characterised plants, significant amounts of information are available for many aspects of the biology of maize, and the reader is referred to the literature provided in this document as a starting point.

In this document the terms maize and corn are used to refer to *Z. mays* ssp. *mays*. Other subspecies of *Zea mays* are referred to as teosintes.

Maize is an annual grass growing up to 4 m tall. The female inflorescences, the ears, develop in leaf axils on the stalk, which terminates in the male inflorescence, the tassel. The broad leaf sheaths are overlapping around the stalk and the leaves are arranged in two opposing rows along the stalk. Maize has a multitude of uses and is used in the preparation of food or drinks, as animal feed or for industrial purposes.

SECTION 1 TAXONOMY

The genus *Zea* belongs to the tribe Andropogoneae in the subfamily Panicoideae in the family Poaceae (reviewed in OECD 2003; USDA 2005). There are currently 86 recognised genera within the Andropogoneae tribe (USDA 2005). Currently, there are five species included in the genus *Zea*. Species of *Zea* that have been examined, largely have a chromosome number of $2n = 20$, except for *Z. perennis* (perennial teosinte with $2n = 40$) (as reviewed in Tito et al. 1991; Ellneskog-Staam et al. 2007; Table 1). The species *Z. nicaraguensis* was described by Iltis and Benz (2000); it is closely related to *Z. luxurians* but currently, the number of chromosomes and sexual compatibility with other *Zea* spp. are unknown.

Table 1 Zea species and subspecies

	Species	Chromosome number	Subspecies	Synonyms
1.	<i>Zea diploperennis</i> HH Iltis et al	2n = 20	-	-
2.	<i>Zea luxurians</i> (Durieu & Asch.) RM Bird	2n = 20	-	<i>Euchlaena luxurians</i> Durieu & Asch. <i>Zea mays</i> ssp <i>luxurians</i> (Durieu & Asch.) HH Iltis
3.	<i>Zea mays</i> L.	2n = 20	<i>Zea mays</i> ssp <i>huehuetenangensis</i> (HH Iltis & Doebley) Doebley <i>Zea mays</i> ssp <i>mays</i>	<i>Zea curagua</i> Molina <i>Zea indentata</i> Sturtev. <i>Zea indurata</i> Sturtev. <i>Zea japonica</i> Van Houtte <i>Zea mays</i> cv <i>alba</i> Alef. <i>Zea mays</i> cv <i>leucodon</i> Alef. <i>Zea mays</i> var <i>flavorubra</i> <i>Zea mays</i> var <i>indentata</i> (Sturtev.) LH Bailey <i>Zea mays</i> var <i>indurata</i> (Sturtev.) LH Bailey <i>Zea mays</i> var <i>japonica</i> (Van Houtte) Alph. Wood <i>Zea mays</i> var <i>saccharata</i> (Sturtev.) LH Bailey <i>Zea mays</i> var <i>tunicata</i> Larrañaga ex A.St.-Hil. <i>Zea mays</i> var <i>vulgate</i> Koern. & H Werner <i>Zea saccharata</i> Sturtev.
			<i>Zea mays</i> ssp <i>mexicana</i> (Schrad.) HH Iltis	<i>Euchlaena mexicana</i> Schrad. <i>Zea mexicana</i> (Schrad.) Kuntze
			<i>Zea mays</i> ssp <i>parviglumis</i> HH Iltis & Doebley	<i>Zea mays</i> var <i>parviglumis</i>
4.	<i>Zea nicaraguensis</i> HH Iltis & BF Benz	2n = ?	-	-
5.	<i>Zea perennis</i> (Hitchc.) Reeves & Mangelsd.	2n = 40	-	<i>Euchlaena perennis</i> Hitchc.

Source: (USDA 2005)

Z. mays^a ssp. *mays* is the only cultivated species; the other species and subspecies are wild grasses, referred to as teosintes.

^a The name *Zea* is from the Greek *zea* meaning cereal or grain. The specific epithet *mays* is thought to derive from the native Arawak word *maiz* or *mahiz* used in the Americas to describe the plant; the word was adopted by the Spanish crew of Columbus' first voyage who first collected the grain from the Americas and took it to Europe (Hyam & Pankhurst 1995; Desjardins & McCarthy 2004).

In addition to the basic A chromosome complement, maize plants may contain one or more supernumerary chromosomes, called B chromosomes, which do not pair with A chromosomes during meiosis (as reviewed in Jones et al. 2008).

The maize genome is large, being somewhere between 2.3 – 2.7 Gbp^b (Arumuganathan & Earle 1991), with a total gene number of between 42,000 and 56,000 genes. Considerable work has been done on characterizing the maize genome (see eg Rabinowicz & Bennetzen 2006; Messing & Dooner 2006). The maize genome is characterised by a high percentage of repetitive sequences, including transposons and retrotransposons (Hake & Walbot 1980; Liu et al. 2007). To date, the best characterised transposons are the *Activator* (Ac) and *Dissociation* (Ds) elements, first described by Barbara McClintock (reviewed in Fedoroff 2000). The presence of the autonomous Ac element is needed for transposition, whereas Ds elements are non-autonomous and trans-activated by an Ac element. Maize chloroplast and mitochondrial genes have been characterised in detail, with a focus on cytoplasmic male sterility (reviewed in OECD 2003). There is a programme initiated in 2005 to sequence the maize genome and a dedicated website describes progress of the various maize genome sequencing projects (<http://www.maizegenome.org/>).

SECTION 2 ORIGIN AND CULTIVATION

2.1 Centre of diversity and domestication

The centre of origin of maize is the Mesoamerican region, probably in the Mexican highlands, from where it spread rapidly. Archaeological records and phylogenetic analysis suggest that domestication began at least 6,000 years ago (Piperno & Flannery 2001; Matsuoka et al. 2002). Maize spread around the world after European discovery of the Americas in the 15th century, particularly in temperate zones (Paliwal 2000d; Farnham et al. 2003).

Maize is only known as a cultivated crop and its exact genealogy remains uncertain. *Zea mays* ssp. *parviglumis* is hypothesised to be the progenitor of cultivated maize. This hypothesis is supported by the close genetic compatibility and relationship between the two sub-species (reviewed in Doebley 2004). However, ribosomal internal transcribed spacer sequence data suggest that *Z. mays* ssp. *mays* diverged no later than the ssp. *mexicana* and *parviglumis* (Buckler & Holtsford 1996). The latter is supported by data on the distribution of alleles in organelles, but conflicting with isozyme data (discussed in Buckler & Holtsford 1996).

During the domestication of maize, every region in which it has been cultivated over the centuries has produced a selection of maize cultivars or landraces (refer Section 2.4). Farmers have maintained and improved these and they are adapted to local requirements and characteristics (Paliwal 2000a).

Maize can be grown in a number of environments (reviewed in Paliwal 2000b; Farnham et al. 2003) from 58° North (eg Canada and the Russian Federation) to 40° South (eg Chile). Generally, tropical maize is grown between 30° North and 30°

^b The amount of DNA in the nucleus of a eukaryotic cell is expressed as the total number of base pairs (bp) in a haploid (1C) chromosome complement.

South, subtropical maize between 30 and 34° both North or South, and temperate maize beyond 34° latitudes. It can be grown in a range of altitudes from sea level up to 3,800 metres and with growing seasons between 42 and 400 days. This ability to grow in a wide range of environments is reflected in the high diversity of morphological and physiological traits.

2.2 Commercial uses

Maize is one of the oldest cultivated grains and one of the most productive crop species with a global average yield of more than 4 tonnes per hectare (reviewed in Paliwal 2000b; Farnham et al. 2003).

It can be directly consumed as food at various developmental stages from baby corn to mature grain.

A high proportion of maize produced is used as stock feed, eg 40% in tropical areas and up to 85% in developed countries (reviewed in Paliwal 2000g; Farnham et al. 2003). It can be fed to stock as green chop, dry forage, silage or grain. Various fractions of milling processes can also be used as animal feed. Stover is the term used to describe the dried stalks and leaves of a crop used as animal fodder after the grain has been harvested.

Maize can be processed for a range of uses both as an ingredient in food or drinks, eg corn syrup in soft drinks or maize meal, or for industrial purposes. Maize is the major source of starch world wide, and is used as a food ingredient, either in its native form or chemically modified (White 1994). Corn starch can be fermented into alcohol, including fuel ethanol, while the paper industry is the biggest non-food user of maize starch. The oil and protein are often of commercial value as by-products of starch production and are used in food manufacturing (Boyer & Hannah 1994; Paliwal 2000h; Hobbs 2003; McCutcheon 2007).

2.2.1 *Maize types and their uses*

A number of maize types can be discerned on the basis of endosperm and kernel composition (Purseglove 1972; Paliwal 2000c; Darrah et al. 2003).

Flint maize kernels are characterised by their high percentage of hard endosperm (see Figure 3) around a small soft centre. Flint maize is grown predominantly in Latin America and Europe for food use.

Dent maize is the most commonly grown for grain and silage, and is the predominant type grown in the USA. Hard endosperm is present on the sides and base of the kernel. The remainder of the kernel is filled with soft starch; when the grain starts drying the soft starch at the top of the kernel contracts, producing the depression for which it is named.

Floury maize is being grown predominantly in the Andean region. Its endosperm is mainly composed of soft starch, making it easy to grind and process into foods.

Waxy maize kernels contain almost entirely amylopectin as their starch (rather than the normal 70% amylopectin and 30% amylose). Waxy maize is preferred for food in

some parts of East Asia and for some industrial uses; it produces a starch similar to tapioca.

Pop maize kernels are characterised by a high proportion of hard endosperm, which is much higher than in any other maize kernel. Pop maize is grown on a small scale compared to other types but popped kernels are consumed world-wide as a snack food. The taxonomic relationship of pop maize with other maize is still under discussion (reviewed in Ziegler 2003).

Sweet maize is grown for green ears (sweet corn). The ears are harvested at approximately 18 to 20 days post pollination when kernel moisture is approximately 70%. The developing grain of sweet maize is higher in sugar content due to one or more recessive mutations blocking conversion of sugar to starch.

2.2.2 *Processing of grain maize*

Important ways of processing grain maize include

- ♦ *Traditional processing*: Grain maize is eaten by numerous people, especially in Latin America, the USA, Africa and Asia. A vast number of recipes exist, involving whole grains, maize meal or maize flour. Maize grains may or may not be roasted before lye-cooking, lime-cooking and/or fermenting to prepare traditional foods or drinks. An important way of preparing maize grains for cooking involves lime-cooking, steeping and removal of the pericarp resulting in ‘nixtamal’, which can be used in the preparation of various soups or doughs (masa). Masa can be baked into tortillas, chips etc (reviewed in Rooney & Serna-Saldivar 2003).
- ♦ *Dry-milling*: Maize grains are either subjected to the
 - Full-Fat Milling Process resulting in maize meal in which germ and crude fibre content are highly similar to whole maize grains;
 - Bolted Milling Process by which the maize meal is sifted to exclude large particles, germ, tip cap and bran pieces. By-products of this process include maize flour and hominy grits; or
 - Tempering-Degerming Milling Process by which moisture is added in the milling process (tempering) to facilitate almost complete removal of the germ (degerming) and bran fractions. In addition to the prime grits, meals and flours obtained from the endosperm fraction of the grain, hominy feed for use in the manufacture of cattle, swine, poultry and aquatic feed can be obtained.

These descriptions are based on Duensing et al (2003).

- ♦ *Wet-milling*: During the highly complex processes of wet-milling the constituents of the maize grains – carbohydrates, proteins, oil and crude fibre – are separated and prepared for the use in food, food manufacture, animal feed and industrial uses. A series of steps involving steeping the grain, coarse and fine grinding, centrifugation, and evaporation of steep water are employed.

- The starch fraction of the maize grains has a variety of uses including: Native starch used in baby foods, snack foods, salad dressings, paper products, insulating materials, paints, tablet binders; modified starch is used in bakery products, sauces and gravies, icings and glazes, pastes and glues, ceramics, dyes and sandpaper; glucose and fructose (in corn syrup) are used in beverages, cheese spreads, desserts, fruit juices, frozen seafoods, explosives and shoe polish. The starch is also fermented to produce alcoholic beverages, flavour enhancers, industrial alcohols, engine fuel and solvents.
- The germ fraction can be separated into the oil fraction and meal fraction, the latter of which can be used as animal feed. The oil can be used as cooking oil, as a carrier for oil soluble vitamins, and as an ingredient in mayonnaise, shortenings, soups, insecticides, linoleum etc.
- Both the fibre and protein fractions can be used in animal feeds. The steep water can be used for industrial purposes, eg in the production of chemicals or yeast culture.

The above descriptions are mainly based on Johnson and May (2003).

2.2.3 World maize production

In 2000, North America accounted for nearly 50% of the world maize production. The USA produced approximately 42%, China approximately 18% and Europe approximately 10%, whereas Australia produced less than 0.1% (data reviewed in Farnham et al. 2003).

Table 2 shows the world production of maize. There are little data available on the area cultivated world wide for forage and silage. In the United States of America silage production accounts for approximately 10% of the total area planted to maize.

Table 2: World production of maize grain and green corn

		Year			
		1975	1985	1995	2006
Maize grain					
Area (ha)	World	121,444,141	130,503,715	136,461,796	144,376,477
	USA	27,366,480	30,436,000	26,389,000	28,590,000
	Australia	51,395	102,872	50,219	76,000 ^c
Yield (kg/ha)	World	2,813	3,720	3,789	4,815
	USA	5,421	7,407	7,123	9,359
	Australia	2,593	2,832	4,826	5,000
Production (t)	World	341,661,971	485,527,301	517,139,871	695,228,280
	USA	148,361,072	225,453,008	187,968,992	267,598,000
	Australia	133,300	291,430	242,370	380,000
Green corn					
Area (ha)	World	871,011	855,213	980,925	1,053,038
	USA	278,460	253,500	286,960	260,140
	Australia	3,100	4,293	5,488	4,000
Yield (kg/ha)	World	6,386	6,971	8,240	8,737
	USA	10,141	12,266	13,953	15,823
	Australia	8,497	11,469	13,494	10,000
Production (t)	World	5,562,590	5,962,206	8,083,182	9,200,824
	USA	2,824,000	3,109,600	4,004,100	4,116,260
	Australia	26,341	49,237	74,055	40,000

Source: Figures for 1975 – 1995 (incl.) were taken from information supplied at the FAOSTAT website (<http://faostat.fao.org/>) in 2006. The 2006 figures were taken from the same site in 2008.

2.3 Cultivation in Australia

It is thought that although maize had been introduced by the Portuguese to the southeast Asian archipelago in the 16th century and that there were Portuguese settlements on the island of Timor (less than 500 km from the north west coast of Australia), no agriculture was introduced to Australia by the Portuguese, Malaysians or Indonesians in the 16th or 17th centuries. It is therefore likely that maize was introduced to Australia with the first fleet in 1788, being grown initially on Norfolk Island and in Sydney (Port Jackson) (Desjardins & McCarthy 2004). In the Northern Territory it was grown by the first white settlers in 1824 (O'Gara 2007).

The first recorded systematic inbreeding of maize in Australia began in the 1920s, firstly at Grafton Experiment Farm (NSW) and later in other areas – Queensland Agricultural College (Gatton), Glen Innes and Bathurst Experiment Farms (NSW), Hawkesbury Agricultural College (NSW) (Colless 1979). The major early cultivars

^c The figure for area sown to maize in Australia is somewhat different from that supplied by ABARE (2008) and discussed in Section 2.3. The ABARE estimate for area sown in Australia in 2006/07 was 49,000 ha and in 2007/08 was 68,000 ha.

were 'Wellingrove', Funk's Yellow Dent', 'Large Red Hogan' and 'Fitzroy'. It was not until 1947 that the first commercial hybrid maize crops were produced in Australia, based on a widely-grown US Corn Belt hybrid, and not until the 1948 – 49 season that the first Australian-bred hybrids (GH96A and GH112A) were released (Colless 1979). Maize breeding in north Queensland began in 1961 and resulted in the release of the first tropical, rust-resistant cultivar (QK37).

In Australia now, maize may be grown in every State and in the Northern Territory (NT) as an irrigated or dryland crop depending on rainfall conditions (eg Price 1997; DPI&F 2006; Farrell & O'Keeffe 2007; DPIW - Tasmania 2008). It is, however, grown mostly in Queensland (Atherton Tableland, Burnett, Darling Downs) and southern New South Wales (Murrumbidgee, Murray and Lachlan River Valleys) (Birch et al. 2003). All maize crops in southern NSW and Victoria are irrigated compared to approximately half of the crops in northern NSW and Queensland (Robinson & Kirkby 2002). Characteristics of some representative maize growing areas in Australia are given in Tables 3 & 4.

Table 3: Characteristics of some of the current maize growing regions in NSW

Representative site (within area)	Quirindi – Liverpool Plains (Northern Inland)	Leeton (Southern Inland))	Inverell (Northern Tablelands)	Casino (North Coast)
Average daily max/min temperature °C (Oct - Mar)**	29.6/13.5	28.6/14.5	28/12.3	28.8/16.9
Average daily max/min temperature °C (Apr - Sept)**	19.5/4.3	17.5/6.2	19.8/2.5	16.9/9.3
Average monthly rainfall mm (Oct - Mar)**	67.4	33.8	93.7	112.6
Average monthly rainfall mm (Apr - Sept)**	46.3	38.2	40	50.4
Growing season*	August – October	September – November	September – November	August – January
Example of arable soil type	Black vertosol***	****Transitional red- brown earth	Black earth (loam)*****	Red friable loam

Sources: * Farrell and O'Keeffe (2007); ** <<http://www.bom.gov.au>>; *** Scott et al. (2004);

**** Mosier et al (1986); ***** NSW Government (2008); *****

<<http://www.environment.nsw.gov.au/bioregions/NorthCoast-Landform.htm>>

Table 4: Characteristics of some of the current maize growing regions in QLD

Representative site (within area)	Kingaroy (South Burnett)	Dalby (Darling Downs)	Gatton (Moreton)	Atherton (Atherton Tableland)
Average daily max/min temperature °C (Oct - Mar)**	28.2/15.5	30.7/16.6	30.2/17.1	28/17.8
Average daily max/min temperature °C (Apr - Sept)**	21.2/7.1	23/7.3	23.4/8.9	23.2/12.9
Average monthly rainfall mm (Oct - Mar)****	90.1	75	88.7	172.7
Average monthly rainfall mm (Apr - Sept)**	39.2	27.6	39.4	52.4
Ideal planting time*	October - January	December	August - January	November - January
Example of arable soil type***	ferrosol	vertosol	vertosol	ferrosol

Sources: * Hughes (2006d); ** <<http://www.bom.gov.au>>; *** Birch et al. (2003)

The area sown to maize in Australia was greatest in 1910 – 1911 (168,040 ha) (Colless 1979) and, apart from a transient increase in 1940 – 41 (147,000 ha), gradually declined to around 50,000 ha between the mid 1970s – 2005. There is some indication that the area is increasing again with the 2008 – 09 forecast being 71,000 ha (ABARE 2008). An indication of the demographics and farm size/yield associated with maize growing in Australia is given in Robinson & Kirkby (2002). In particular, the average area grown to maize per farm is 250 ha in Southern NSW and 100 ha in northern NSW and southern Queensland. Average yield ranges from 10 t/ha in southern NSW to 7.5 t/ha in northern NSW and 5.2 t/ha in southern Queensland. It is suggested that the differences between the regions reflects different degrees of irrigation between the regions. Maize is generally grown in rotation with other crops (Robinson & Kirkby 2002).

Cultivars, covering all end uses, fall into two major categories (Colless 1979):

- ♦ Early/quick-maturing hybrids (as low as 95 days CRM^d) that are short (approximately 250 cm), used mainly in inland areas and do not grow well in humid conditions, have loose husks, and tend to be susceptible to Northern Leaf Blight (*Drechslera turcica*).
- ♦ Late/slow-maturing hybrids (up to approximately 135 days CRM) that are tall-growing (up to 400 cm), adapted to sub-tropical and tropical humid coastal

^d CRM = Comparative Relative Maturity. It is a measure of the time from planting to the stage when grain moisture content is suitable for harvest (Birch et al. 2003; Farrell & O'Keefe 2007). It indicates the rate of maturity relative to a 'standard' hybrid and is used to determine where a hybrid should be grown.

regions, have ears with well-covered husks, and are generally resistant to *D. turcica*.

However, there is a continuum of differently maturing cultivars within these two extremes (Hughes 2006d; Farrell & O'Keeffe 2007).

Although *Z. mays* subsp. *mays* is an important grain crop internationally (see Section 2.2.3), its significance in Australia is limited. For example, in 2008, only 387,000 t of grain maize were produced in Australia (as compared to 13,039,000 t of wheat grain); approximately 12,000 t were exported as compared to 6,617,000 t of wheat (ABARE 2008).

Detailed information on maize cultivation practices in Australia is covered in publications by the Departments of Primary Industries of every State and the NT as well as in journal articles, books and conference proceedings (eg Colless 1979; Price 1997; Birch et al. 2003; DPI&F 2006; Farrell & O'Keeffe 2007; DPIW - Tasmania 2008; Birch et al. 2008). The more important points are considered below.

2.3.1 Commercial propagation

Maize is an annual plant and reproduces exclusively by seed, ie vegetative reproduction under natural condition does not occur. This is in contrast to other *Zea* spp. and the related *Tripsacum* spp., which may be perennial and reproduce not only by seed but also vegetatively by way of rhizomes (Paliwal 2000f). Seed size varies from 4,400 seeds/kg to 2,500 seeds/kg (Hughes 2006d). Seed for planting is usually treated with protective insecticides and fungicides (Colless 1992) (see also Section 7). In developed countries, including Australia, hybrid maize is usually grown.

Important considerations regarding which cultivars/hybrids should be planted (Colless 1992; Birch et al. 2008) include:

- ♦ maturity: length of growing season (water availability, temperature etc)
- ♦ end use (grain vs silage vs sweet corn etc)
- ♦ yield
- ♦ lodging resistance
- ♦ disease resistance

Maize is an outcrossing plant species. In order to be able to conduct directed crosses, two requirements must be observed:

- ♦ The female parent must be either male sterile or de-tasseled^e before pollen reaches maturity. In maize, three types of cytoplasmic male sterility are known: T, C and S male sterility. Before 1970, Texas-male sterile lines were used extensively. However, Texas-male sterile lines are susceptible to southern corn leaf blight (*Helminthosporium maydis* Nisikado and Miyake), race T, which caused great losses to corn producers in the USA. Although C and S male sterile lines were discovered later (and they are not susceptible to southern corn leaf blight), they are not important as growers have lost trust in male sterility (reviewed in Darrah et

^e Tassel is the term used to refer to the male inflorescence (see Sections 3 & 4)

al. 2003; Sleper & Poehlman 2006). Currently, detasseling is the preferred method to achieve controlled crosses.

- ◆ Seed breeding must be conducted in isolation from other maize plants:
 - Feil and Schmid (2002) reviewed the isolation distances required or recommended by various organisations for seed breeding. Isolation distances of up to 5,000 metres (USSR, seed of inbred lines) are listed, with the majority in the 200 – 300 metre range.
 - The OECD requires 200 m isolation distance for the production of Basic and Certified Seed for all maize varieties, with purities of at least 99.5 and 99.0%, respectively. For the production of Basic Seed of parental lines and single cross hybrids, purities must be 99.9%. The production of Certified Seed of hybrid varieties requires that the minimum varietal purity of both parents must be 99.8% (OECD 2008).
 - In the USA, an isolation distance of 201 m is required for production of seed of 99% or higher purity. One option for reducing this distance is the planting of male border rows, whereby one border row equals 5 m distance. However, even under those circumstances, plantings for maize seed must be isolated by at least 134 m from other maize. Predominant winds and storms in the seed breeding area are also to be considered (Darrah et al. 2003).

All recommended cultivars in Australia are hybrids and originate from government or public breeding centres and private seed companies (Colless 1979). They are mostly produced under a voluntary seed certification scheme that ensures a minimum standard for purity, seed germination and seed-borne disease. Certified seed is classed according to its generation along the pedigree. Breeders seed is used to produce Pre-basic, which is then used to produce Basic, which in turn is used to produce First Generation or C1 certified seed. Most certified seed is C1 class grown from Basic seed (Smith & Baxter 2002).

Market access to many countries, including the European Union, requires Australian seed to be produced in accordance with the OECD (Organisation for Economic Co-operation and Development) Seed Schemes. The Australian Seeds Authority Limited oversees seed certification in Australia and is licensed to administer the OECD Seed Schemes (Australian Seeds Authority Ltd. 2006; Australian Seeds Authority Ltd. 2007a).

The figures for *Z. mays* certified seed production in Australia under the OECD Seed Schemes are given in Table 5.

Table 5. *Zea mays* certified seed produced in Australia under the OECD Seed Schemes between 2000 and 2004*

Year	Seed produced (kg) in the 12 months ending 30 June
2000	9,950
2001	10,288
2002	9,901
2003	5,386
2004	3,783

* data taken from Australian Seeds Authority Ltd. (2007b)

2.3.2 *Scale of cultivation*

Z. mays ssp. *mays* is grown as a grain crop for stockfeed, food processing (eg for breakfast cereals, corn chips, grits, flour), industrial starch and popcorn (Farrell & O'Keefe 2007). Green chop and ensiled maize may be used as supplementary feed in the dairy industry and also as feed for other animals, including goats and horses (Roche & Dalley 1996; Moran 2006; Pearson 2007; McGregor 2007). Sweet corn shows increasing domestic and international popularity in human consumption as a fresh, canned or frozen vegetable (Beckingham 2007). Maize plays a subordinate role in ethanol production in Australia, eg the major feedstocks for bioethanol production in Victoria are wheat, sorghum and molasses (McCutcheon 2007).

Commercial GM maize in Australia

Currently, no GM maize is authorised for release in Australia (<http://www.ogtr.gov.au/>).

Grain maize

More than 95% of the grain maize produced is used domestically, and the remainder for export. QLD and NSW account for most of the grain maize produced. ABARE (2008) estimated that in the 2007/08 growing season approximately 68,000 ha were used for maize production.

Silage and green chop maize

The size of areas used for silage and green chop maize production could not be obtained, presumably because the planting areas per farm are not significant and most of the product is fed to animals on-farm.

Sweet corn

In 2002, approximately 5434 ha were used in sweet corn production in Australia. Approximately 90% of this production area was located in NSW, QLD and VIC (Beckingham 2007).

2.3.3 *Cultivation practices*

Z. mays ssp. *mays* may be grown as a dryland or irrigated crop (Birch et al. 2003; Farrell & O'Keefe 2007). In Australia, maize is generally produced as a summer crop

(QLD: DPI&F 2006; NSW: Farrell & O'Keeffe 2007). Maize is suitable for mechanical cultivation during its entire development, including harvesting.

Planting should commence when soil temperatures at planting depth reach 12°C or higher at 9.00 am, with an upward trend (Farrell & O'Keeffe 2007); for sweet corn planting at 14 – 16°C is recommended (Beckingham 2007). Planting may also occur through to summer. However, planting times which will lead to flowering during the hottest period of summer should be avoided as pollen blasting (damage to pollen) and consequently poor seed set may result. Planting times should also try to avoid maturation during cool/cold weather as diseases and pests may cause poorer quality and/or lower yields. Frost should be avoided during the entire life cycle of maize as should water stress, the latter especially between two weeks to pollen shed and silking where it could cause disproportional yield losses. Generally, maize is less water stress tolerant than other crops, including sorghum (Farrell & O'Keeffe 2007; Beckingham 2007).

Maize plants grow best in well-draining, nutrient-rich soils with a pH (CaCl₂) between 5.5 and 7.0. Maize is not very tolerant of saline soils. The nutrient status of the soil is important for the productivity of maize and substantial amounts of nutrients are removed from the soil by harvesting maize cobs or plants. Therefore, soil tests for various nutrients should be carried out to inform the grower before planting. Nutrient availability varies with soil type. Nitrogen is yield limiting in maize production. The amount of nitrogen that needs to be added to the soil depends on various factors, including cropping history and yield target. Phosphorus, potassium, zinc and molybdenum application may also be necessary. Banded application of nitrogen and phosphorous may be carried out at sowing to reduce the chance of damage to the seedling by fertiliser burn and to make those nutrients available during the early stages of development, when they are of greatest importance (Farrell & O'Keeffe 2007).

In NSW, maize was grown mainly in the Northern and Southern inland, the North Coast and the Tablelands in the 2006/07 season (Farrell & O'Keeffe 2007). In QLD, maize can be grown in North QLD, Central QLD, South Burnett, the Darling Downs and Moreton (Hughes 2006d). Lists of hybrids that can be grown in those areas are provided by the above authors. A list of sweet corn hybrids for QLD is provided in Beckingham (2007).

In Victoria, maize production may be followed by green bean (*Phaseolus vulgaris* L.) plantings (Dimsey 1994). Sweet corn may be grown in rotation with *Brassica* crops, including canola and lettuce, or in rotation with lucerne (*Medicago sativa* L. ssp *sativa*) and other vegetable crops, in which case it may be followed by grazing oats (Beckingham 2007).

Grain maize

Grain maize usually takes approximately 130 to 150 days from planting to harvest. Crop density for irrigated maize grain crops is typically around 60,000 – 80,000 plants per hectare. For dryland crops density mainly depends on rainfall, varying from approximately 20,000 – 30,000 per hectare for dryer inland area up to approximately 45,000 – 55,000 per hectare for coastal or other high rainfall areas. Seeds are planted at depths of 3 – 5 cm in rows with spacing varying between 75 and 110 cm. In dryland

production systems, single or double row skipping on 100 cm rows may increase yields.

Irrigated maize may be irrigated pre- or post-plant, depending on soil characteristics. Dryland maize should be planted into soil that is wet to a depth of at least one metre. Maize has low tolerance to water stress, and high yielding hybrids may use up to 850 mm of water during the growing season. Crops require continued water supply, from irrigation or rain, throughout their growth.

When physiological maturity is reached, the moisture content of the kernels is usually 28 – 34%. Grain storage is best if grain moisture is approximately 12%. Therefore, dry down is required. Dry down of grains on the plant can continue as long as conditions are not too cool, which could result in infection with mycotoxin producing fungi. Harvest usually commences at a moisture content of 18% and further artificial drying is required. Typical grain yields, depending on the region, are approximately 2 – 8 t/ha for dryland maize crops and approximately 5 – 13 t/ha for irrigated crops.

Information in this section is based on Farrell & O'Keeffe (2007).

Silage and forage maize

Silage and forage maize is grown similarly to grain maize, except that planting density should be increased to 50,000 – 60,000 plants per hectare for dryland cultivation and 70,000 – 100,000 plants per hectare for irrigated cultivation to obtain optimum yields. Later maturing hybrids can be grown as maize with ears at the dough stage of grain development is best for fodder and silage production. Silage is a moist preserved fodder, in which anaerobic fermentation improves digestibility and preserves most of the nutrient content of the ensiled material. Therefore, silage and forage maize are ideally harvested when the dry matter content is between 30 and 35% (Colless 1992). Maize silage production requires chopping, compaction and careful packing of the plant material so as to exclude air. Yield for silage is about six to ten times that for grain (Colless 1992).

The information in this section is based on Farrell & O'Keeffe (2007), except where indicated otherwise.

Sweet corn

Sweet corn differs from other forms of maize as the kernels have high sugar content at the milk and early dough stage of grain development due to mutation/s in the starch synthesis pathway, eg the *sugary1* or *shrunk2* allele is present in the sweet corn line. Cultivation is similar to that for grain maize, although low seedling vigour, due to reduced seed starch, requires more precise early season management. Crop density ranges from approximately 35,000 plants/ha under marginal conditions to 70,000 plants/ha for well managed irrigated crops.

Cobs are ready to harvest when the kernels reach the milk or very early dough stage. This occurs approximately 75 – 105 days after planting (21 – 28 days after silk emergence), depending on variety, climate and soil moisture. Harvesting may be by hand or machine. Alternatively, the crop may be harvested for baby corn, usually by hand within two days of silks emerging, when ears are 4 – 10 cm long. The early

harvest of sweet corn (ie prior to kernels reaching physiological maturity) allows two crops per season in warmer areas.

Sweet corn is preferred to field maize for production of green ears for fresh consumption in Australia and other developed countries. Approximately 80% of sweet corn produced in Australia is processed (canned or frozen), with the remainder going to the fresh food market. In 2002, approximately 50% of the national production, ie 40,000 t, was in NSW, followed by Victoria producing 30,000 t and QLD producing 7,000 t. Average yield of sweet corn is approximately 17 t/ha in NSW and QLD.

The information in this section is based on Beckingham (2007).

2.4 Crop Improvement

The fact that maize has high commercial value and is the main staple in the diet of millions of people in sub-Saharan Africa and Latin America means that there is much to be gained from improvement programmes. A number of international organizations and networks are involved in coordinating the improvement of maize growing in poorly developed countries. Significant among these are:

- ♦ CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo) – which was established in Mexico and now has regional offices in many countries. One of the aims of the Global Maize Program is to use ‘maize genetic resources to provide diverse, high-yielding varieties that withstand infertile soils, drought, insect pests, and diseases’ (http://www.cimmyt.org/english/wpp/afr_liveli/index.cfm). Major projects include ‘Insect Resistant Maize for Africa’; ‘Drought Tolerant Maize for Africa Initiative’; ‘Water Efficient Maize for Africa’.
- ♦ FAO Crop & Grassland Service (AGPC) - supports maize production improvement through FAO Field Programme projects in many countries, including Afghanistan, Bangladesh, China and Eritrea (<http://www.fao.org/ag/AGP/AGPC/doc/crops/4a-2.html>).
- ♦ The Tropical Asian Maize Network (TAMNET) – which was established in 1993 by AGPC to strengthen collaboration between national institutions in maize research and development and to increase maize production and productivity, particularly through hybrids. In 1998 CIMMYT's regional office in Bangkok took responsibility for coordinating technical activities, including hybrid trials.
- ♦ The Asian Maize Biotechnology Network (AMBIONET) – which was established in 1998 as a collaborative research, training, and information network, aiming to help maize programmes in China, India, Indonesia, Philippines, Thailand and Vietnam (George et al. 2004).

Extensive genetic and cytogenetic studies have contributed to an understanding of maize and are important tools in maize improvement.

In 2005, several years after launching the concept of the Maize Genome Sequencing Project (Chandler & Brendel 2002), the US Department of Agriculture, Department of Energy, and National Science Foundation announced a joint US\$32 million programme for sequencing the maize genome (also see online information at <http://www.maizegenome.org/>). Considerable work laying a foundation for this project had already been completed (see reviews in Haberer et al. 2005; Rabinowicz & Bennetzen 2006; Messing & Dooner 2006).

The Maize Genetics Cooperation (<http://maizecoop.cropsci.uiuc.edu/>) operated by the US Department of Agriculture Agricultural Research Service collects, maintains and

distributes seeds of maize genetic stocks and provides information through the Maize Genetics and Genomics Database (<http://www.maizegdb.org/>).

A large number of maize mutants have been identified and allow the identification of genes that are important in controlling maize plant development (for example, maize morphogenesis mutants - Sheridan 1988).

2.4.1 Breeding

A wealth of information regarding the improvement of maize is available (see Paliwal et al. 2000; Sleper & Poehlman 2006; Lee & Tollenaar 2007). The sections below indicate important trends in maize breeding.

Conventional breeding

Maize is predominantly outcrossing (cross-fertilising), which has its advantages and disadvantages for plant breeders and growers. For example, outcrossing species are characterised by a wider genetic base and are quick to adapt to changes in the environment, whereas predominantly inbreeding species have the advantage of consistency and relative genetic uniformity within a given cultivar.

Maize possesses diverse morphological and physiological traits resulting from a wide genetic base available for selection and, therefore, is adapted to a wide range of conditions (Paliwal 2000a). It has been selected for desirable traits by farmer breeders for more than 6,000 years, and by professional breeders for approximately 150 years (Paliwal 2000a; Piperno & Flannery 2001; Matsuoka et al. 2002). Its long history of domestication has led to the (co)existence of a wide variety of primitive (largely unimproved) races, land races (local varieties adapted for local conditions), cultivars improved and maintained by farmers, and highly-improved professionally-bred open pollinated varieties (Paliwal 2000a). Currently, the highest yielding maize cultivars are various types of maize hybrids.

Breeding has been, and is being, used to improve or alter traits such as plant height, ear number, yield, maturity, kernel properties, and disease and pest resistance (reviewed in Paliwal et al. 2000; Sleper & Poehlman 2006). In addition, plant breeding is also aimed at increased nutrient content in cultivated field maize varieties (reviewed in Zhu et al. 2007). Speciality maize varieties are also being bred for sweet corn, high-oil content, high-quality protein, popcorn and silage. In developing countries, farmers select and maintain maize varieties adapted to specific local uses and conditions (Paliwal 2000a).

In the 1940s, local maize varieties were collected in countries of Central and South America by scientists from the USA and Mexico, and those with similar morphological characteristics were grouped into land races. This classification allowed breeders to easily access maize germplasm with a particular trait of interest. However, many of these collections have been lost and new collections have been made. Currently, over 13,000 germplasm accessions are stored at CIMMYT in Mexico, with duplicate storage elsewhere (reviewed in Darrah et al. 2003; Sleper & Poehlman 2006).

Open-pollinated cultivars

Open pollinated cultivars result from random pollination of ovules without pollen control. As each ear is pollinated by a random mixture of pollen, it is possible that each resulting seed will grow into a plant that is genotypically and phenotypically different to the plants developing from the other seeds on the same cob. Therefore, open pollinated cultivars are characterised by their heterozygosity and high genetic variability. Open pollination and mass selection of maize has been and is being used by farmer-breeders to improve important visible plant characteristics, such as maturity, seed characteristics and plant height. Plants derived from open-pollination are generally not uniform and one of the aims in breeding projects was to control the pollen source to increase plant uniformity (reviewed in Darrah et al. 2003; Sleper & Poehlman 2006).

Improved maize breeding using open pollination includes ear-to-row breeding and variety hybridisation. In ear-to-row breeding, seeds are harvested, labelled and stored separately from each ear. Some seeds from each ear are planted in individual rows; remaining seed is stored. Each row is evaluated for improved characteristics and combined remnant seed from superior performing rows is planted in a single plot in the next growing season allowing for open pollination to occur. Ear-to-row selection is repeated over a number of generations. Variety hybridisation includes planting of two different varieties of open-pollinated maize in one plot, whereby the plants from one variety are detasselled. This breeding method results in improved yields in the following generation. However, it was never widely used in maize breeding (reviewed in Darrah et al. 2003; Sleper & Poehlman 2006).

Hybrid breeding

Hybrid breeding was first used in the early 1900's by professional breeders in the USA (see discussion in Lee & Tollenaar 2007). An important requirement for hybrid breeding was that the source of pollen in crosses could be controlled by the breeder. This was achieved by either detasseling of the female parent or by the use of cytoplasmic male sterile lines as the female parent in combination with a male fertility restorer line.

Initially, the main goal of plant breeders was the selection for genotypes that would survive the inbreeding process that is followed by hybrid seed production, as inbreeding generally leads to an accumulation of deleterious alleles within a given population. An important consideration in hybrid breeding is the combining ability of individual inbred lines as generally few combinations results in superior hybrids.

In single crosses, two inbred lines are used in the production of hybrid seed (line A x line B = A x B); the plants derived from the hybrid seed show increased vigour and yield (heterosis). As inbred lines generally showed low vigour and yield, single crosses were substituted by double crosses, in which four unrelated inbred lines are used in the production of the two parent lines. The two parent lines are then crossed resulting in double cross hybrid seed ((A x B) x (C x D)). An alternative to the double cross is the modified single cross involving the recombination of two related inbred lines in the generation of the female parent, which is then crossed to another inbred line resulting in the hybrid seed ((A' x A'') x B). Three-way crosses are similar to modified single crosses, with the exception that three unrelated inbred lines are used

in the generation of hybrid seed ((A x B) x C). As inbred lines were improved over time, single cross hybrids are now used widely in maize breeding.

A major difficulty in the evaluation of plant material is the separation of genetic and environmental effects on some (especially polygenic) traits. This difficulty was overcome by conducting test crosses over a number of seasons in a range of environments (reviewed in Darrah et al. 2003; Sleper & Poehlman 2006). Currently, maize hybrids play an important role in the maize production in developed countries. The entire process from initial hybrid cross to commercial release takes approximately 5 years (Duvick & Cassman 1999).

The most important selection criteria used by commercial maize breeders in developed countries such as the United States are yield and yield stability and the relatively short time that hybrids remain on the commercial market (less than 10 years on average) is due to their replacement by more high-yielding hybrids rather than any problems with disease or insect susceptibility (Duvick & Cassman 1999). Several maize traits have changed significantly in association with the selection efforts for increased yield and include increased grain starch: protein ratio, decreased tassel size, reduction in barrenness at high density, and reduced rate of leaf senescence during grain filling (Duvick & Cassman 1999).

Mutation breeding

Mutation breeding in maize encompasses a number of approaches, including spontaneous mutation, cell- or tissue-culture induced mutation (also referred to as somaclonal variation), chemical mutagenesis, transposon mutagenesis and irradiation mutagenesis. Spontaneous mutations occurring within plant cells may lead to new and useful characteristics, which are employed in crop breeding. In maize, spontaneous mutations have been exploited commercially. For example, all the major types of maize, including dent, flint, flour and pop maize as well as sweet corn were available to Native Americans by the time Columbus arrived in the Americas (reviewed in Boyer & Hannah 1994). Mutagenesis has also been used to increase the range of characters available for selective breeding. For example, somaclonal variation has been used successfully in the development of commercially available imidazolinone-tolerant maize varieties (Anderson & Georgeson 1989; Newhouse et al. 1991; reviewed in Tan et al. 2005) (see also Section 7.1).

2.4.2 Genetic modification

The most important advances in maize improvement via genetic modification are discussed below. Singletary (2003) has provided a detailed review on this subject.

Monocot plants such as maize are generally more difficult to transform than dicot species. However, both efficient transient and stable transformation protocols for maize have been developed and improved over time, including *Agrobacterium*-mediated transformation, transformation through protoplast fusion, particle bombardment and silicon carbide whiskers (eg Gordon-Kamm et al. 1990; Gould et al. 1991; Frame et al. 1994; Ishida et al. 1996; Wright et al. 2001; Frame et al. 2002).

The latest advances of genetic modification in maize include the development of circular maize minichromosomes (MMCs), which can facilitate autonomous

replication of the introduced DNA. Advantages of this type of genetic modification include that the likelihood of position effects may be much lower than when using gene insertion methods and that larger DNA fragments can be delivered and expressed (Carlson et al. 2007).

The major focus in the production of GM plants has been on resistance to insects and tolerance to herbicides. For example, resistance to corn rootworm has been achieved by using *cry*-genes from *Bacillus thuringiensis* and tolerance to the herbicides glufosinate ammonium and glyphosate using the *pat*-gene from *Streptomyces viridochromogenes* and the *cp4epsps*-gene from *Agrobacterium* spp., respectively.

Another focus in early maize research was to increase lysine levels in maize, which was achieved by transformation with the *cordapA* gene from *Corynebacterium glutamicum* encoding lysine-insensitive dihydrodipicolinate synthase. These examples are approved for commercial release overseas and for use in human food in Australia and overseas (FSANZ 2002; APHIS/USDA 2002; APHIS/USDA 2005; APHIS/USDA 2006a; APHIS/USDA 2006b; APHIS/USDA 2007).

Maize grains, like those of other cereals, do not contain the amino acids lysine, tryptophan and methionine at levels that are sufficient in the diet of humans and other monogastric animals (as reviewed in Lai & Messing 2002) (see also discussion in Section 5.1.2). Current molecular studies are aimed at addressing those deficiencies.

SECTION 3 MORPHOLOGY

The following descriptions are adapted from Paliwal (2000f) and Farnham et al (2003).

3.1 Plant morphology

The typical maize plant is a tall (1 – 4 m) annual grass (monocot) which forms a seasonal root system bearing a single erect stem (culm) made up of nodes and internodes, although some cultivars may develop elongated lateral branches (tillers). Many temperate cultivars are shorter than tropical (and subtropical) cultivars.

Nodes gradually taper to the top of the plant. Leaves are broad and a single leaf develops at each node in two opposite ranks – the leaf arrangement maize is distichous (reviewed in Esau 1977b). Each leaf consists of a sheath surrounding the stalk and an expanded blade connected to the sheath by the blade joint, or collar. The mature plant can have up to approximately 30 leaves, with considerable variation in leaf number, size and orientation between maize races. Generally, tropical maize plants develop more leaves than temperate cultivars.

The epidermis is the outermost layer that can be discerned in cross-sections of the stalk. Several layers of sclerenchyma tissue are underneath it and increase the strength of the stalk. The arrangement of vascular bundles is complex and they appear scattered throughout the parenchyma tissue that constitutes the remainder of the cross-section, although they are arranged more loosely towards the middle (reviewed in Esau 1977b).

Maize – like many plants that evolved under tropical conditions – is a C₄ plant and, therefore, is more efficient at utilising carbon dioxide than C₃ plants. These physiological characteristics are reflected in leaf morphology down to the microscopic level. For example, bundle sheath cells are richer in chloroplasts than mesophyll cells. The chloroplasts are also larger than those of mesophyll cells (reviewed in Esau 1977a).

3.2 Reproductive morphology

Maize is a monoecious plant: one or more lateral branches, the shanks, develop in the leaf axis of the plant. They terminate in a female inflorescence, an ear (see Figure 1). The male inflorescence, the tassel, forms at the top of the stem.

Usually one or two lateral shoots in the upper part of the plant develop into female inflorescences. The shank consists of nodes and short internodes, the lengths of which vary between maize races. The ears arise from axillary bud apices. The ear is covered in a number of leaves called husks. Those leaves differ in appearance when compared to those on the stalk: they surround and protect the developing ear. Where maize is left to dry in the fields, more husks are generally desired to protect the grains from birds and insects. Where maize is harvested earlier, it is often desirable for a cultivar to have a lower number of thin husks.

The ear does not usually show any lateral branching. The thick axis of the ear, the cob, bears an even number of rows (between 4 and 30) of ovaries, each containing a single ovule. The number of ovules that will develop into kernels ranges from 300 – 1,000 and is dependant on the cultivar/variety as well as factors occurring later in development (Purseglove 1972). The silks of the maize ear are the styler canals of the mature ovaries.

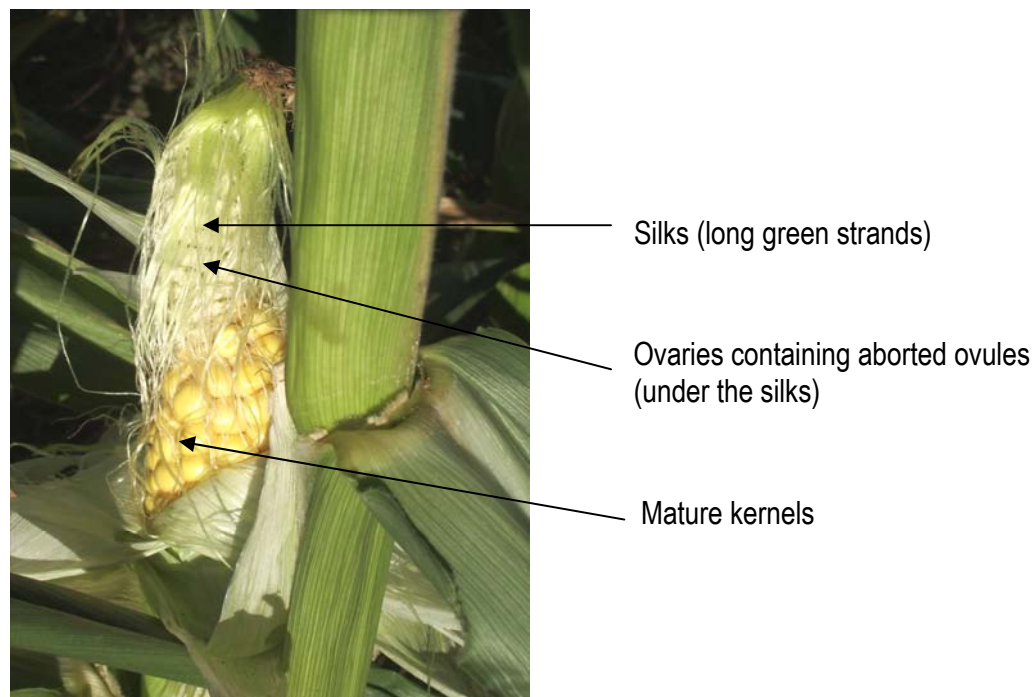


Figure 1. Mature female inflorescence of a sweet corn cultivar (the husks have been removed to expose the cob).

The apical meristem of the stem develops into the tassel, a prominent branched structure at the top of the plant consisting of a central spike and a variable number of lateral branches (up to approximately 40) bearing the male flowers. The peduncle of the tassel grows vigorously, pushing the tassel out of the top of the plant.

SECTION 4 DEVELOPMENT

4.1 Reproduction

4.1.1 *Asexual reproduction*

Under natural conditions maize reproduces only through seed.

4.1.2 *Sexual reproduction*

Maize is a quantitative short-day plant but some cultivars have low or no sensitivity to daylength (Kiniry et al. 1983). In those cultivars that are photoperiod sensitive (mainly those that are late-maturing), flowering may be delayed when the photoperiod is greater than a critical threshold value ranging from 10 – 13.5 h (Kiniry et al. 1983). Those adapted to the tropics may show delayed maturity if grown in more temperate areas with longer days (Birch et al. 2003) (see also Section 4.5).

Unless stated otherwise, the following description is adapted from Paliwal (2000f).

Initially male and female inflorescences have primordia of bisexual flowers. However, during their development, primordia of stamens abort in the axillary inflorescences, and primordia of gynoecia abort in the apical inflorescence.

The apical meristem elongates once the leaf primordia are initiated. It is transformed into a reproductive meristem that develops into the tassel. Pollen is shed from the tassel continuously for a week or more as upper and lower florets in the male spikelets show developmental differences and the spikes mature asynchronously.

The female inflorescences (ears) arise from axillary buds and bear flowers in rows along the cob. Development of the flowers and the ovules on the ear proceeds from the base upwards (acropetal). From each flower a style begins to elongate towards the tip of the cob, forming long threads, or silks. Silk development begins from the flowers near the base of the ear and proceeds towards the tip over several days. Receptive silks emerge over the husks over a period of three to five days and can grow to more than 30.5 cm length, extending beyond the end of the husks. The silks have short hairs, trichomes, which form an angle to the stylar canals and help harbouring pollen grains. Receptive silks are moist and sticky.

Maize is often considered as protandrous (anthers reaching maturity before the gynoecium), as anthers on the spikelets on the upper part of the central spike protrude out of the florets and start shedding pollen one or two days (under optimal growth conditions) before the silks emerge above the husks. However, the gynoecium matures and the silks become receptive before they appear above the husk tips. Under any stress (especially water stress – see Section 6.3), the interval between pollen release and silk emergence increases. Selective breeding is aimed at producing many maize varieties with a reduced interval, to ensure good seed set.

4.2 Pollen dispersal, pollination and outcrossing rates

4.2.1 Pollen

Maize pollen is relatively large when compared to other grass pollen. For example, Baltazar et al (2005) reported pollen diameters of 94 to 103 μm . Maize pollen is surrounded by a double layer consisting of exine and intine, and is, therefore, well protected (reviewed in Cheng & Pareddy 1994). However, temperatures above 35°C at pollen release may result in pollen blasting, a major problem in some maize growing areas in Australia that may result in poor seed set (barrenness; Farrell & O'Keefe 2007). A single plant may produce up to 2×10^6 pollen grains per day (Jarosz et al. 2003) and between $6 \times 10^6 - 25 \times 10^6$ in total, depending on the variety (Bannert & Stamp 2007). At eight plants per square metre (at the high end for crop density), this would equate to approximately 200 million pollen grains released per square metre.

Luna et al. (2001) reported that pollen viability as measured by the ability to produce seed decreased to 0% after atmospheric exposure for 2 hrs near San Jose de Valle in Mexico. In that study, 80% of pollen lost viability within 1 hr. Similar results were obtained in a study by Baltazar et al (2005) that was conducted in Tapachula in Mexico: 68% to 84% of pollen was dehydrated after 1 hr of atmospheric exposure. The study by Luna et al (2001) also showed that high humidity prevented loss of viability: at high relative humidity, pollen viability declined by 58% within 1 hr, whereas it declined by 96% within 1 hr under lower atmospheric humidity. Aylor (2004) carried out *in-vitro* germination tests to investigate pollen viability under a number of environmental conditions in New Haven in the USA. It was found that pollen viability was relatively insensitive to solar radiation and decreased most with loss of moisture. A decrease of pollen viability to 50% was observed between 60 min and 4 hrs, depending on environmental conditions. Feil and Schmid (2002) mentioned reports of maize pollen being viable between 20 min and 24 hrs.

Various authors have reported that visible characteristics can be used as an indication of pollen viability: fresh pollen appears spherical in shape and white, whereas non-viable pollen is collapsed and yellow (eg Luna et al. 2001).

4.2.2 Pollen dispersal and pollination

Maize is normally outcrossing and the rate of self pollination is approximately 5% (reviewed in Sleper & Poehlman 2006). During normal cross-pollination, the pollen is shed mainly during mid-morning (Luna et al. 2001). Pollen is shed continuously for a week or more from each plant, starting approximately 1 to 3 days before silk emergence (reviewed in Paliwal 2000f; Sleper & Poehlman 2006), with a crop as a whole producing pollen over a 14 day period. Despite the short viability period of individual pollen grains, the temporal spread in both pollen shed and silking of individual plants within a field means that, on a whole field basis, cross pollination between a donor field and a receptor field could occur over a 7 day period (Bannert & Stamp 2007).

The horizontal settling speed of maize pollen is in the range of 21 – 32 cm/s, depending on how much dehydration of the pollen has occurred (Aylor 2002). In plants where the tassels are at a height of about 2.5 m and the silks are at a height of

about 1 m, a settling distance of approximately 1.5 m is required for pollination between adjacent plants and could take 5 s under ideal conditions (Bannert & Stamp 2007). The vertical movement of pollen in thermals and air turbulence could extend dispersal distances but only in those areas where conditions do not favour horizontal dispersal (Bannert & Stamp 2007).

Insect pollination in maize has not been reported, although Feil and Schmid (2002) mention reports of maize tassels being visited by honey bees. However, as honey bees have not been observed on female inflorescences, pollination of maize by honey bees has been ruled out.

4.2.3 *Outcrossing rates and isolation distances*

Feil and Schmid (2002), Brookes et al. (2004) and Sanvido et al. (2008) have recently reviewed literature on maize pollen dispersal and outcrossing rates. These reviews as well as a number of other publications (Ingram 2000; Luna et al. 2001; Stevens et al. 2004; Halsey et al. 2005; Ireland et al. 2006; Messeguer et al. 2006; Bannert & Stamp 2007) point out a number of biotic and abiotic factors that can influence outcrossing rates in maize, including

- ♦ synchrony in flowering time in pollen donor and receptor
- ♦ ambient temperature at pollen shed
- ♦ relative ambient humidity at pollen shed
- ♦ wind speeds (and turbulences) and direction of prevailing winds
- ♦ topography of the terrain in question
- ♦ distance between pollen donor and pollen receptor
- ♦ competition between foreign pollen and pollen shed on the receptor plot (the scale of pollen emission from the donor relative to the size of the pollen receptor plot as well as the absolute size of the receptor plot – the larger the receptor plot, the more the foreign presence is diluted and therefore the lower the average outcrossing rate per plot (ACRE 2003) ie outcrossing is highest at plot margins than at the plot midpoint)
- ♦ experimental design, eg physical arrangements between pollen donor and receptor (eg, are pollen donor and receptor arranged in a concentric fashion, neighbouring or distant from each other?), method of determining outcrossing rates (Is pollen collected or are resulting seeds sampled?)
- ♦ agronomic practices such as detasseling, use of border rows, cytoplasmic male sterility

The dependence of outcrossing rates on a large number of factors may explain the range of results obtained in the scientific literature and the range of isolation distances recommended by various organisations with regard to seed production and food/feed production. (eg see discussion in Sections 2.3.1 and 9.1). As an indication of cross-pollination rates, a recent Swiss study (Bannert & Stamp 2007) found that at distances of 50 – 4,500 m between pollen donor and receptor fields, the cross pollination rate in a field was never more than 0.02%. In 89% of cases, cross-pollination was represented by a single fertilization event in an ear.

In Australia, the following isolation distances for the production of speciality maize currently are recommended:

- ♦ In QLD, the production of sweet corn requires either a 400 m isolation distance from all other maize or staggering maize plantings so that there are at least 14 – 21 days between pollination times to all other maize (Beckingham 2007).
- ♦ In NSW, the production of speciality maize, eg waxy, white and popcorn varieties, requires either 800 m isolation distance or staggering maize plantings at least six week so as to avoid cross pollination (Farrell & O'Keeffe 2007).

As reviewed in Feil and Schmid (2002), isolation distances of 300 metres (Germany; sugar maize for consumption) to 1,600 metres (Canada; sugar maize for consumption) were recommended.

Isolation distances recommended for seed breeding are covered in Section 2.3.1.

4.3 Embryogenesis, fruit/seed development and seed dispersal

Pollen grains germinate immediately after settling on the silk. The pollen tube takes between 12 and 24 hours to reach and fertilise the ovule (reviewed in Sleper & Poehlman 2006). Upon completion of fertilisation the silk detaches from the ovary and dries out.

4.3.1 Embryogenesis

The following information is adapted from Sass (1977) and Sheridan and Clark (1994).

In the first phase of embryogenesis, irregular cell divisions result in a proembryo consisting of approximately 12 – 24 cells within 100 hrs after fertilisation. The initial basal cell divides into a number of large, vacuolated suspensor cells. By the same time, the initial apical cell has given rise to 9 – 18 small cells that are densely filled with cytoplasm.

Starting approximately 8 – 9 days after fertilisation, the second phase of embryogenesis commences, which leads to the establishment of meristems and the embryonic axis by approximately 13 days after fertilisation (transition embryo). Approximately 14 – 15 days after fertilisation, the coleoptilar embryo is established, characterised by the differentiation and growth of scutellum^f, coleoptile^g, coleorhiza^h and root and shoot apical meristem (see Figure 3). By approximately 16 days after fertilisation, the first leaf primordium arises. After this time, the embryo is referred to as stage 1 embryo. It is now approximately 1 mm long and weighs approximately 1 mg.

During the last stage of embryogenesis (during 30 – 40 days after the first leaf primordium appears), embryo growth continues, more leaf primordia and a primary and one or more secondary root primordia develop, and the whole embryo is enveloped by the expanding scutellum. Storage products also accumulate within the embryo during the final phase of embryogenesis, especially in the scutellum. At

^f The scutellum is the name given to the cotyledon of grasses (Raven et al. 1999). It functions in the absorption of food by the embryo from the endosperm (see Section 5.1.3)

^g The coleoptile is a leaflike sheath that protects the shoot meristem

^h The coleorhiza is a sheath that protects the root meristem

kernel maturity the embryo may have a fresh weight of approximately 50 mg (Sheridan 1988).

4.3.2 *Fruit/seed development*

The fruit of maize is a caryopsis, a dry indehiscent single-seeded fruit (Figure 2).



Figure 2. Mature maize caryopses [photo credit: Steve Hurst @ USDA-NRCS PLANTS Database, Provided by [ARS Systematic Botany and Mycology Laboratory](http://plants.usda.gov/java/profile?symbol=ZEMA). Bolivia, Cochabamba. (<http://plants.usda.gov/java/profile?symbol=ZEMA>)]

The pericarp (ovary wall) and testa (seed coat) are fused to form the fruit wall and because of this tight adhesion between fruit and seed, the two structures actually appear to be a single structure. This structure is commonly referred to by a number of interchangeable terms – fruit, kernel, grain and seed. The kernels are composed of three main parts - the embryo, the endosperm and the fruit wall (see Figure 3). The number of kernels per ear and the number of ears that develop is established at, or shortly after, pollination (Duncan 1975).

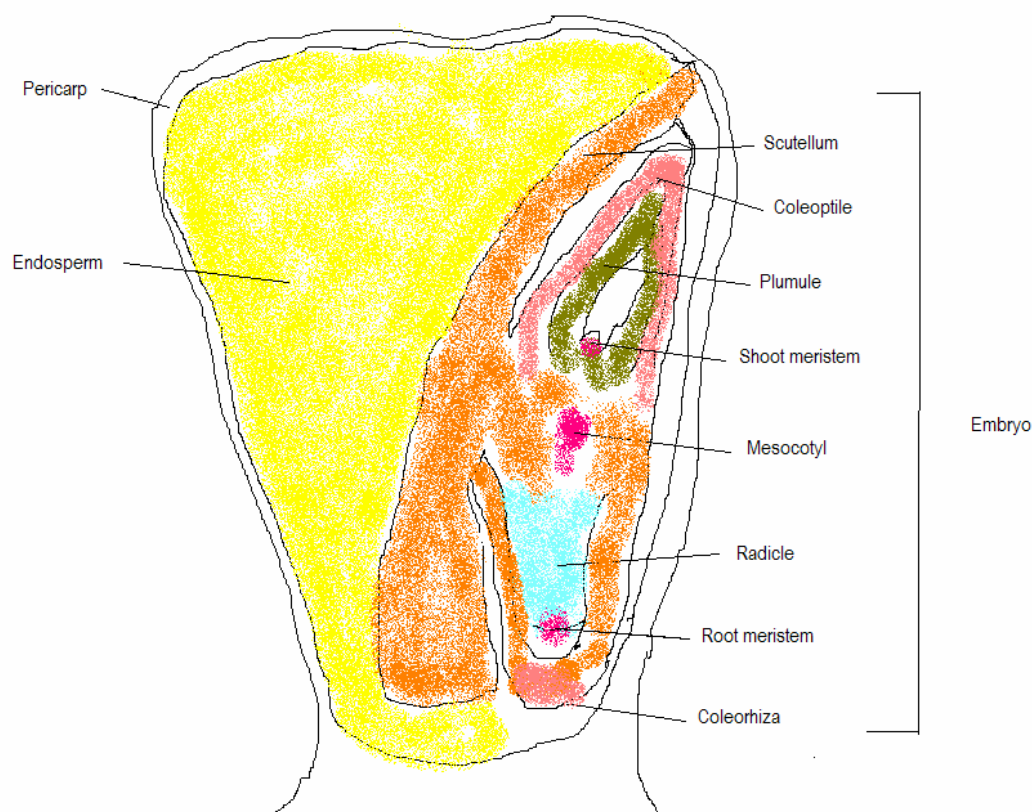


Figure 3. Diagrammatic representation of a longitudinal section through a mature maize kernel (Raven et al. 1999). Refer to text for definitions of the various parts.

The rate of cob development is dependant on environmental factors, such as climate (particularly temperature) and genetic factors, such as cultivar (see discussion in Norman et al. 1995; Sleper & Poehlman 2006).

The grain filling period in maize is approximately 8 weeks in length (Lee & Tollenaar 2007). As reviewed by Farnham et al. (2003), the following stages can be discerned during kernel development: blister stage, milk stage, dough stage, (dent stage in dent maize varieties) and physiological maturity. Physiological maturity is generally reached approximately 55 – 65 days after silking.

- ♦ For the first 10 – 14 days after fertilisation, the husks, cob and shank develop rapidly and soon after, nutrients are accumulated in the developing kernels (Farrell & O'Keeffe 2007). The small blister-shaped kernels are filled with a clear fluid.
- ♦ The milk stage is characterised by the presence in the kernels of a white fluid with high sugar content.
- ♦ During dough stage, the kernels are filled with a white paste and, starting at the tip of the kernel opposite the embryo, starch is deposited. This starch deposition is visible, as a 'milk line' develops (soon after denting in dent maize varieties) between hard (starch-filled) and soft (paste-filled) phases of the endosperm. A milk line of 0 indicates that no starch deposition has occurred, whereas a milk line

of 5 indicates that starch deposition is completed. Monitoring the progress of the milk line towards the base of the kernels allows estimating the time to physiological maturity.

- ♦ Physiological maturity is reached once maximum dry matter has been accumulated in the kernels and their moisture content is approximately 30 – 38%. A ‘black layer’ is formed underneath the tip of the kernel that is attached to the cob. It seals off the kernel from the remainder of the plant.

Information on harvesting and post-harvest can be found in a number of sources (see Colless 1992; Lafitte 2000b; Farnham et al. 2003). The moisture content of the grain at physiological maturity is usually above 30%. After physiological maturity is reached, kernels continue to lose moisture and in moist tropical environments, harvest should not proceed until moisture content has been reduced to approximately 25% (Paliwal 2000e). Usually, mechanical harvesters perform best at a kernel moisture content of approximately 18 – 24%. After harvest, maize grains must be dried artificially to no more than 14% moisture in order to minimise infestation with pests and development of diseases during storage. Artificial drying should be carried out at temperatures below 49°C.

The rate of development of maize is linked to temperature (over 24 hours) rather than to photosynthesis which is governed by temperature only during daylight hours (Duncan 1975). The concept of thermal time (expressed in units of day degrees) can be used to categorise maize cultivars into early- and late-maturing (see also discussion in Section 2.3). Basically, thermal time is a measure of accumulated temperature that is required for a phenological character (such as flowering) to take place. Lafitte (2000b) and Norman et al. (1995) note that tropical maize cultivars have a lower yield than temperate cultivars because, while temperatures are higher in the tropics, the plants have a much shorter time to maturity.

Xenia

Pollen can have an immediate effect on kernel characteristics, a phenomenon that is known under the name ‘Xenia’ (reviewed in Sleper & Poehlman 2006). The underlying cause for it is the fertilisation of the diploid polar nucleus by the haploid vegetative sperm nucleus, resulting in triploid endosperm cells. As the endosperm comprises approximately 80% of the mature maize grain (reviewed in Boyer & Hannah 1994), kernel characteristics depend on the genotypes of both female and male parent. Endosperm characteristics that exhibit Xenia include endosperm colour (eg yellow vs white), waxy vs non-waxy endosperm, aleurone colour (purple vs colourless), starchy vs sugary endosperm and non-shrunken vs shrunken endosperm.

4.3.3 *Seed dispersal*

The maize cob lacks any abscission layers between its basic units and therefore the cob remains intact at maturity (Doebley et al. 1990). Thus the tightly held grains are unable to be dispersed and confer a low survival rate to the maize plant in nature (Fedoroff 2003). The cob itself usually remains on the plant until harvested but if left on the plant or if damaged by insects or disease will eventually fall to the ground. This means that there may be localized dispersal of grains around the base of the plant. Harvesting activities and grain transport result in more widespread grain dispersal (see

Section 8.1 for a discussion of volunteerism). Indications from the scientific literature would not suggest that dispersal of maize grain by animals, including birds is significant although there is the possibility that intact grain may be spread as the result of the activities of vertebrate pests (see Section 7.2.2).

4.4 Seed dormancy and germination

Dormancy is not associated with modern maize cultivars although it does occur in other *Zea* spp. (Simpson 1990). Seeds from one maize crop can survive over winter and germinate in warmer weather. However, there is no or little inhibition of germination and mature seed can begin to germinate immediately under favourable conditions, even if still attached to the cob (Duncan 1975).

The plant hormone abscisic acid (ABA) has been shown to be important in the regulation of the onset and maintenance of dormancy in seed (see discussion in Bewley 1997). Some maize plants show germination before seed maturity (Mangelsdorf 1930). There is evidence that a balance between ABA and another natural hormone, gibberellin, determines whether precocious germination before maturation (known as vivipary) occurs (White & Rivin 2000; White et al. 2000). Several mutants known as *viviparous* (*vp*), have been identified in maize and, as a result of deficiencies in the ABA biosynthetic pathway, do not show dormancy.

Maize germination requires good soil moisture and a minimum soil temperature of about 12°C, and does not occur in soil temperatures below 10°C (AGBIOS 2005; Farrell & O'Keeffe 2007). The rate of germination is dependent to some extent on temperature and, for example, tropical maize may start germination within 2 – 3 days under high temperatures (such as during tropical summer conditions) while it could take 6 – 8 days under lower temperatures (such as during winter or at high altitudes) (Paliwal 2000f). There is some evidence that the pigment phytochrome may be involved in the control of germination in maize, particularly under conditions of osmotic stress (Thanos & Mitrakos 2004).

Maize seed is usually planted to a depth of 2 – 10 cm if adequate moisture is available but can be planted down to 20 cm in arid regions (Purseglove 1972). The maximum depth from which a seedling can emerge is limited by the maximum potential for elongation of the specialized meristematic area (known as the mesocotyl) just below the coleoptile node (Duncan 1975) (see Figure 3).

Maize germination follows a similar pattern to that of many grasses except for differences in scale that occur as a result of the large endosperm and embryo in the maize seed. The cytohistology of germination has been described by Sass (1977). Basically, it is an ordered process that follows imbibition of water through the pericarp. Mitosis and cell elongation start in the radicle (root) approximately 24 hours after imbibition and then begin in other areas along the embryonic axis.

Seedling emergence is described in Section 4.5 below.

4.5 Vegetative growth

Hanway (1963) proposed eleven stages of growth of maize, with stage 0 being germination and emergence and stages 6 – 10 occurring after silking. In terms of crop

management it is more usual to condense the number of stages to six, with stage 6 incorporating dry-down and grain harvesting (Colless 1992). The vegetative stages of growth, together with their characteristics, can broadly be described as follows (Hanway 1963; Purseglove 1972; Duncan 1975; Colless 1992; Paliwal 2000f):

Stage 1: Germination and Emergence (approx. 0 – 14 days after planting) – timing is dependent on factors such as soil temperature and moisture, depth of sowing, and surface hardness. The coleorhiza and radicle (root) emerge and 1-2 days later the coleoptile and plumule (first foliage leaves) break through the seed coat (refer to Figure 3). Plants develop primary (seminal) roots, a temporary root system, until about the three-leaf stage of the seedling. Six to 10 days after planting the coleoptile emerges from the soil, splitting at the tip to allow the growth of the first foliage leaves. The shoot meristem itself remains just below the soil surface.

Stage 2: Early Vegetative (approx. 14 – 42 days after planting) – during this stage, secondary (adventitious) roots develop from the first node below the soil surface and from each successive node up to between seven and ten nodes, all below the soil surface. These develop into a thick, permanent fibrous root system reaching down typically to 1 – 2 m. Some adventitious roots may also emerge from nodes above ground, and are termed brace roots. Maize races show marked differences in the mass, branching and spread of lateral roots. The number of leaves that will develop on the plant (up to about 30) is determined (Irish & Jegla 1997) and the tassel begins to differentiate when about 5 leaves have emerged. The shoot meristem and the tassel primordium emerge above the soil surface by the six-leaf stage and when eight leaves have fully emerged the shoot meristem is approximately 15 cm above the soil. Lower leaves may start to senesce by the end of Stage 2.

Stage 3: Late Vegetative (approx. 42 – 60 days after planting) – this is the stage of rapid growth (linear dry matter accumulation) of both roots and leaves. During development there is a basic repeating unit structure comprising leaf blade, leaf sheath, node and internode that makes up the entire vegetative shoot. Internode elongation produces a new leaf every three to four days. Eventually, the elongation of the lower internodes contributes to the formation of a stalk-like structure that rises up through the leaf sheaths. By the end of Stage 3 the 16th leaf will have started to emerge, the tassel will have reached full size although will not have fully emerged and the ears within the husks will be a few centimetres long. The first 5 – 6 lower leaves may senesce and cease to be functional. Aerial or brace roots usually emerge from the lower, above-ground nodes. The extent of aerial root production is cultivar dependent as well as being influenced by rate of planting and nutrition. Tillering (development of stalks from axillary buds) is cultivar dependent, with some cultivars forming few if any tillers under any conditions, and some forming numerous tillers under all conditions.

There is a correlation between the final number of leaves produced on a plant and the time between sowing and silking. The duration of vegetative development is linked to the thermal interval between the appearance of successive leaf tips (called the phyllocron) and differs according to the temperature found in latitudinal zones, being higher in tropical than temperate areas (Tojo Soler et al. 2005) (see also corresponding discussion in Section 4.3.2).

In terms of crop performance, growth refers to biomass accumulation and is measured by parameters such as leaf area, shoot/root weights and plant height. Techniques used to quantify growth are known as growth analysis and comprise a number of indexes such as Crop Growth Rate, Relative Growth Rate, Net Assimilation Rate, Leaf Area Ratio, and Leaf Area Index (LAI) (for a detailed discussion see Fageria et al. 2006). Improvements in maize grain yields over time have been associated with delayed leaf senescence in newer hybrids leading to higher LAIs just after silking when the grain is filling (Valentinuz & Tollenaar 2004; Lee & Tollenaar 2007). The major contribution to ear development and final grain yield are made by the earleaf and all leaves below the earleaf (Subedi & Ma 2005).

Maize has a C4 photosynthetic pathway, which allows a continued response to increasing radiation up to full sunlight coupled with low levels of photorespiration. The maximum level of leaf photosynthesis per unit area occurs between full leaf expansion and silking (Lee & Tollenaar 2007). The growth of grain is dependent on total photosynthetic production only after flowering and is discussed in Section 4.3.2 (see also discussion in Norman et al. 1995; Lafitte 2000b; Lee & Tollenaar 2007). Thus, vegetative dry matter continues to accumulate in maize after flowering (Fageria et al. 2006; Lee & Tollenaar 2007). If flowering is inhibited, vegetative growth is significantly increased; tropical maize types that are grown in the long summer days of temperate regions such as the Midwest of the USA have delayed flowering and consequently produce more vegetative growth, manifested as taller plants with high sugar levels in the stems (University of Illinois 2007). In a mature temperate maize plant approximately 50% of the total dry matter is allocated to the grain and 50% to the stover (crop residue following harvest) – as shown by the HI of approx. 0.5 (see Section 4.3.2). Compared with other crops, maize has a disproportionately high amount of stover (over 50% of which is stalk) and it has been proposed that this could be utilised in the biofuels industry (Dhugga 2007).

SECTION 5 BIOCHEMISTRY

5.1 Nutrient components of the maize kernel

The typical mature kernel as a whole is composed of 70 – 75% starch, 8 – 10% protein and 4 - 5% oil (Boyer & Hannah 1994). However, there are large differences in the relative concentrations of these components between different parts of the kernel (see Table 6). The two major structures of the kernel are the endosperm and the germ (embryo), constituting about 80% and 10% of the mature kernel dry weight, respectively. The endosperm is largely starch (approximately 90%) while the germ contains high levels of fat (approximately 33%) and protein (approximately 18%). These differences become a significant consideration when maize is processed for consumption.

Table 6. Relative content (%) of nutrient components in parts of the maize kernel*

	Pericarp (seed coat)	Endosperm	Germ (embryo)
Protein	3.7	8.0	18.4
Crude fibre	86.7	2.7	8.8
Crude fat	1.0	0.8	33.2
Starch	7.3	87.6	8.3
Sugar	0.34	0.62	10.8

* Data taken from FAO (1992)

Table 7 provides a more detailed breakdown of the nutrients that can be found in the whole kernel of sweet corn. Pellagra is a nutritional disease caused by a deficiency in niacin, and may be associated with maize-based diets in the Americas and Africa. While niacin is present in maize, it exists in a bound form that is not biologically available to monogastric (single-stomach) animals (Okoruwa & Kling 1996).

Table 7. Nutrient content of sweet corn, fresh, boiled (FSANZ 2006)

Nutrient	Value per 100 g	
Proximates		
Energy	438	kJ
Moisture	74.0	g
Nitrogen	0.67	g
Protein	4.2	g
Fat	2.8	g
Ash	1.0	g
Fructose	0.3	g
Glucose	0.4	g
Sucrose	4.6	g
Sugars, total	5.3	g
Starch	7.5	g
Available Carbohydrate	12.8	g
Total Dietary Fibre	4.8	g
Minerals		
Calcium	3	mg
Copper	0.060	mg
Iron	0.6	mg
Magnesium	41	mg
Manganese	0.340	mg
Phosphorus	110	mg
Potassium	258	mg
Sodium	105	mg
Zinc	0.7	mg
Vitamins		
Thiamin	0.15	mg
Riboflavin	0.06	mg
Niacin	2.0	mg
Niacin derived from Tryptophan or Protein	0.6	mg
Niacin Equivalents	2.6	mg
Folate	31	µg
Dietary Folate Equivalents	31	µg
Vitamin C	4	mg
Alpha Carotene	12	µg
Beta Carotene	6	µg
Beta Carotene equivalents	12	µg
Retinol Equivalents	2	µg
Lipids		
C16:0	0.25	g
C18:0	0.04	g
C20:0	0.01	g
Total Saturated Fatty Acids	0.3	g
C18:1	0.64	g
C20:1	0.01	g
Total Monounsaturated Fatty Acids	0.6	g
C18:2 (undifferentiated)	1.27	g
C18:3 (undifferentiated)	0.02	g
Total Polyunsaturated Fatty Acids	1.3	g
Total Long Chain Omega 3 Polyunsaturates	0	
Cholesterol	0	
Amino Acids		
Alanine	335	mg
Arginine	159	mg
Aspartic Acid	257	mg
Cystine + Cysteine	95	mg
Glutamic Acid	713	mg
Glycine	145	mg
Histidine	124	mg
Isoleucine	155	mg
Leucine	467	mg
Lysine	135	mg
Methionine	105	mg
Phenylalanine	192	mg
Proline	325	mg
Serine	198	mg
Threonine	199	mg
Tryptophan	32	mg
Tyrosine	155	mg
Valine	224	mg
Organic Acids		
Citric Acid	1.0	g
Malic Acid	0.2	g

5.1.1 Starch

Starch synthesis has been reviewed in a number of articles (Boyer & Hannah 1994; Nelson & Pan 1995; Boyer 1996; James et al. 2003).

Starch is synthesised as part of a mega-molecular assembly, the starch granule, within the amyloplasts of maize endosperm cells and, in most cases, contains two major types of glucose homopolymers, amylose and amylopectin. In amylose, the glucose residues are mainly linked via α -1,4 linkages, which results in a linear chain of glucose units. In amylopectin, the majority of linkages are α -1,4 linkages, with α -1,6 linkages providing branching. Highly branched regions alternate with regions devoid of branching. The latter regions make it possible for other linear glucose chains to align in the form of parallel helices in the gaps, giving starch its semicrystalline structure. The primary source of the carbon skeletons for starch synthesis is sucrose translocated to the endosperm. The starch synthesis pathway in cereal endosperm requires enzyme isoforms that are not present in other cereal tissues or non-cereal plants.

As endosperm cells mature, the starch granules increase in size and in the proportion of amylose so that the mature cell typically contains the ratio 3: 1 amylopectin: amylose. Within an endosperm cell type, all mature starch granules are of a similar size. A mature granule may contain as many as 10^9 amylose and 10^7 amylopectin molecules. These molecules are arranged regularly, giving the granule stability and crystalline properties.

The maize mutants *waxy* (*wx*) and *amylose extender* (*ae*) are grown extensively for their unique starches (see discussion in Ferguson 2000). In the *waxy* mutant, the starch is composed almost entirely of amylopectin and the mature kernel has an opaque phenotype. Mutations at the *ae* locus result in an increase in the amylose content of the endosperm relative to its amylopectin content; such starch can be used to produce tough, edible or biodegradable films and gels (Robertson & Stinard 1988).

5.1.2 Protein

Discussion of maize kernel proteins can be found in a number of articles (Boyer & Hannah 1994; Woo et al. 2001; Monjardino et al. 2005; Monjardino et al. 2006). Storage protein (a 7S globulin) is found in the embryo and in the endosperm. The relative amount of protein is highest in the embryo (see Table 5) but, because the endosperm occupies a greater part of the kernel, it contributes the greatest total amount of protein (FAO 1992). The endosperm proteins can be divided into prolamins, collectively referred to as zeins, and comprising about 52% of kernel nitrogen; glutelins (*ca* 25% of kernel nitrogen); albumins (*ca* 7%); and globulins (*ca* 5%).

Zeins, which accumulate in the rough endoplasmic reticulum of endosperm cells, contain large amounts of the amino acids glutamine, proline, leucine and alanine but are very low in the essential amino acids lysine and tryptophan. Embryo proteins provide higher levels of tryptophan and lysine (FAO 1992). A number of different molecular weight zeins have been identified by SDS-PAGE and have been further classified, based on their solubility and structural relationships, into α - (22 and 19 kD), β - (15 kD), γ - (27, 16 and 50 kD) and δ - (10 and 18 kD) zeins. The α -zeins are

the most abundant at *ca* 80% of total zeins and are encoded by a large family of genes, while the other classes of zeins are encoded by only one or two genes each.

The *opaque2* locus (*o2*) in maize regulates the expression of many members of the zein multigene family and maize plants carrying an *o2* mutation have seeds with an opaque appearance that is attributable to a dramatic reduction in the zein storage proteins and concomitant increase in lysine (Mertz et al. 1964) and tryptophan (Misra et al. 1972). Apart from the desirable high lysine and tryptophan content, these mutants have agronomically inferior characteristics including reduced yield and soft floury grain endosperm that increases disease and insect susceptibility and makes food processing difficult (see review in Ufaz & Galili 2008). Breeding at the International Maize and Wheat Improvement Center in Mexico in the early 1990s saw the development of *opaque2* - derived QPM (Quality Protein Maize) lines with better performance and nutritional values. These have now been adapted for use in many countries (Ufaz & Galili 2008). QPM varieties with high levels of the amino acid tryptophan may also compensate to some extent for the lack of available niacin in maize (see Section 5.1).

5.1.3 Lipids

Lipids (oil) are found mainly in the embryo, specifically in the scutellum. They comprise 40% of the dry weight of the scutellum and are used for gluconeogenesis to support the developing embryo following germination (Oaks & Beevers 1964). The embryo contains approximately 33% oil (see Table 5) while a typical whole kernel contains approximately 4% oil (see Table 7). However, the amount and composition of oil in the kernel is under genetic control and, for example, selection in one line (Illinois High Oil) after 106 generations, over more than 100 years, has continuously increased the percentage of kernel oil to over 20% (Dudley 2007).

Fatty acids in corn oil nearly always occur esterified to the hydroxyl groups of glycerol, thus forming triacylglycerides. These triacylglycerides contain a mixture of saturated and unsaturated fatty acids distributed approximately as follows (Boyer & Hannah 1994):

- ♦ Saturated: 12% palmitic acid (16:0), 2% stearic acid (18:0),
- ♦ Unsaturated: 25% oleic acid (18:1), 60% linoleic acid (18:2), and 1% linolenic acid (18:3).

Maize oil is generally accepted as high quality, as determined by the high linoleic acid and low linolenic acid content. There is a suggestion that the breakdown of esterified linolenic acid to the free form in stored maize meal may be associated with predisposition to carcinogenesis of the oesophagus (Sammon & Iputo 2006).

The genetics of lipid content in maize oil is complex, probably controlled by multigenic inheritance of a large number of genes (Boyer & Hannah 1994).

5.2 Toxins

Toxic reactions after feeding livestock with maize (especially green chop) or allowing animals to graze on maize may result from nitrate or nitrite poisoning. Nitrite and nitrogen dioxide are produced by bacteria associated with maize plants causing toxicity in humans and animals. Also, mycotoxins produced by fungi, which may

infect maize plants and/or grain, may be present in maize. Since those toxins are produced by plant-associated microorganisms rather than the plant itself, they are discussed in Section 7.2.4.

5.2.1 Nitrate poisoning

Nitrate is taken up and used in the biosynthesis of proteins and other nitrogen containing components by plants (eg reviewed in Pavelchak 1999). Under certain environmental conditions, eg after a drought breaks, some plant species can accumulate relatively high levels of nitrate as it may be present at relatively high levels in the soil. Maize, particularly the lowermost parts of the stalk (< 20 cm), may accumulate nitrate to levels that can be toxic to stock (Everist 1981). Ruminants are less susceptible to nitrate poisoning, if their diet includes sufficient amounts of carbohydrates while they are fed nitrate-rich feed. Microorganisms in the rumen convert nitrate to nitrite, which is then converted to ammonia by other rumen-inhabiting microorganisms. Symptoms of nitrate poisoning in stock are mainly abdominal pain, diarrhoea and salivation (Halpin & Hides 2002).

5.3 Allergens

Although maize is not considered highly allergenic, some allergic reactions have been reported in the scientific literature: maize can cause both food and inhalation allergies. For example, pollen and maize dust may cause allergies, such as hay-fever and baker's asthma. The International Union of Immunological Societies currently lists four maize allergens on its website (<http://www.allergen.org/Allergen.aspx>): Zea m 1, Zea m 12, Zea m 14 and Zea m 25. Information on maize allergens is given below.

Pollen allergens include the Zea m1 protein, also named EXPB, a β -expansin with a molecular weight of approximately 27 kD. Zea m 1 is a homolog of the Lol p 1 allergen in ryegrass (*Lolium perenne*) (Broadwater et al. 1993). The expansin is present in maize pollen in four isoforms, the most abundant one being EXPB1 (reviewed in Yennawar et al. 2006).

The allergen Zea m 12 is a profilin with the molecular weight of approximately 14 kDa. In maize, profilins are encoded by a multi-gene family (Staiger et al. 1993). Profilins have also been described in a number of plant species, including alder (*Alnus glutinosa*), hazel (*Corylus avellana*), timothy grass (*Phleum pratense*) and rye (*Secale cereale*), and a profilin from birch (*Betula verrucosa*) was characterised in a study by Valenta et al. (1991) as a major pollen allergen.

In one study, Pastorello et al (2000) identified a major food allergen of maize as a 9 kD lipid transfer protein (LTP, Swiss Prot Data Bank, accession number P19656) that shows homology to LTPs from rice, peach and apricot. It is also known as the Zea m 14 cereal allergen. Pre-incubation of immune sera from patients allergic to maize with either rice or peach extracts abolished antibody binding in immunoblots meaning that cross-reaction of the Zea m 14 allergen with rice or peach allergens occurs.

The second most important food allergen in maize found in that study was a 16 kD inhibitor of trypsin/activated Hageman factor (XIIA; Swiss Prot Data Bank, accession number P01088). It has been shown that members of this trypsin and α -amylase

inhibitor protein family present in other cereals can cause Baker's asthma. Pre-incubation of immune sera of allergic patients with Timothy grass pollen, wheat, rice or barley extract completely inhibited binding of antibodies to the 16 kD allergen as well as other, minor maize seed allergens.

In addition to the previously described allergenic β -expansins, profilins and LTPs, Weichel et al. (2006) also found thioredoxins, such as Zea m 25 in enriched repertoires of IgE-binding sequences of maize.

Pasini et al (2002) also identified a 50 kDa protein as a major allergen, which is both heat stable and resistant to peptic/pancreatic digestion. Lee et al (2005) described a 50 kDa γ -zein from maize with strong *in-vitro* cross-reactivity with the almond major protein (AMP), a major allergen in almonds (*Prunus amygdalus*). It is currently not clear if the two 50 kDa proteins correspond to the same allergen in maize.

5.4 Other undesirable phytochemicals

Maize contains low levels of some anti-nutrients, chemicals that block the normal uptake or utilisation of nutrients:

Phosphorous is mainly stored in plants in the form of phytic acid, or phytate, which is not easily accessible to humans and other animals. This has a number of consequences: humans may need to obtain phosphate from different sources, animal feed needs to be fortified with phosphate and, as a consequence of the latter, phosphate is excreted at high levels leading to environmental problems. Phytate also acts as an anti-nutrient as it chelates metal ions, including iron, and prevents those from being accessible to humans and other animals at sufficiently high levels (reviewed in Hurrell 2003). Recently, progress has been made in genetically engineering maize expressing phytase (eg Drakakaki et al. 2005; Chen et al. 2007).

Another anti-nutrient that is present in maize is the sugar raffinose. Raffinose is non-digestible, and is considered an anti-nutrient due to gas production and resulting flatulence. It can be removed from food and feed by soaking, cooking, and irradiation or by enzyme or solvent treatment (OECD 2002).

Both trypsin and chymotrypsin inhibitors are present at low levels in maize (OECD 2002). They are not considered important for human or animal nutrition.

5.5 Beneficial phytochemicals

Maize is considered an important food crop for humans and a high-energy feed for animals (FAO 1992). In the human diet it is a good source of vitamin B1, vitamin B5, folate, dietary fibre, vitamin C, phosphorus and manganese (see Table 6) and as a staple it compares favourably with root and tuber crops and is similar in energy to dried legumes (Okoruwa & Kling 1996). The average nutritional content of various forms of maize is given in Table 8. Processing reduces the concentration of proteins, lipids and fibre (FAO 1992).

Table 8. Ranges for proximate analysis of maize grain, sweet corn kernels and silage

		Maize grain	Sweet corn	Maize silage
Moisture	% fresh weight	7 - 23	74.7 - 84	62 - 78
Protein	% dry weight	6 - 12	11.3 - 15.6	4.7 - 9.2
Lipid (total)	% dry weight	3.1 - 5.8	4.86 - 8.75	
Ash	% dry weight	1.1 - 3.9	2.58 - 3.86	2.9 - 5.7
Carbohydrate	% dry weight	82.2 - 82.9	72.5 - 79.18	
Fibre	% dry weight	8.3 - 11.9 (total dietary fibre)	11.2 - 15.6 (total dietary fibre)	40 - 48.2 (neutral detergent fibre)

Source: OECD (2002)

SECTION 6 ABIOTIC INTERACTIONS

Maize shows a wide genetic base for abiotic stress tolerance, which is mirrored by its ability to grow in a variety of environments, although it is essentially a crop of warm climates with adequate moisture (Purseglove 1972) and is therefore not suited to semi-arid or wet tropical climates.

It is argued that all of the genetic improvement in maize yield over the past 70 years is the result of changes to physiological attributes that, in turn, have imparted enhanced abiotic stress tolerance (Lee & Tollenaar 2007) ie selection of hybrids for high density planting has been accompanied by increased resistance to stresses such as drought and has permitted consistent performance across a range of variable environments (Duvick & Cassman 1999; Dhugga 2007). One way that abiotic stress affects the maize plant is by moving the source-sink balance (Lee & Tollenaar 2007). Classic symptoms of excess source capacity are purpling of leaves, sheath tissues and stalks during grainfilling while symptoms of excess sink capacity are premature senescence of leaves and stalks during grainfilling (Lee & Tollenaar 2007).

6.1 Nutrient requirements

Maize grown commercially, whether for grain or silage, has a high demand for nutrients, especially nitrogen (N), phosphorus (P) and potassium (K) (Birch et al. 2003). As an example, Table 9 gives some figures for nutrient removal by a sweet corn crop.

Table 9. N, P & K removal by a 28 t/ha crop of sweet corn (Beckingham 2007).

	Nitrogen (kg/ha)	Phosphorus (kg/ha)	Potassium (kg/ha)
Removal by cobs	110	16	60
Removal by vegetative parts	200	24	150
Total removal	310	40	210

The micronutrients zinc and molybdenum may, depending on soil type, also be important to apply to maize crops to prevent deficiency symptoms.

Seedlings do not tolerate high levels of fertilizer and therefore starter fertilizer should be drilled at least 5 cm to the side of the seed during sowing (Hughes 2006c).

In the maize-growing areas of the tropics, acid soils are widespread and plant growth is constrained by the associated aluminium toxicities that lead to stunting and impairment of root growth and subsequent inability of plants to take up moisture from the soil (Lafitte 2000a).

Nitrogen

If water and temperature conditions are ideal productivity of maize is mainly limited by availability of nitrogen (Purseglove 1972; Lafitte 2000a; Birch et al. 2003). It has been suggested that in irrigated maize, nitrogen deficiency caused by denitrification in irrigated soils that are slowly permeable to water may be the principal cause for low yield. However, in a study done in the Murrumbidgee Irrigation area of southern NSW it was concluded that poor transport of nitrogen associated with anoxic conditions in the root zone of water-logged plants may also play a significant role (Mosier et al. 1986).

Nitrogen is a component of a number of compounds (eg proteins, nucleic acids, chlorophylls) and has an important role in many plant physiological processes (Raven et al. 1999). In particular, it is important in the efficient capture and use of solar radiation and therefore affects yield (Lafitte 2000a; Birch et al. 2003). Maize begins to rapidly take up nitrogen (and other nutrients) during the middle vegetative growth period with the maximum rate of nitrogen uptake occurring near silk (Hanway 1963). Nitrogen deficiency is indicated by leaf yellowing (first in the lowest leaves) that starts at the tip and then extends along the mid-rib, stunted plants, delayed flowering and short, poorly filled ears (Colless 1992; Hughes 2006c).

Maize can utilise nitrogen in both the ammonium and nitrate forms but, because of the ready conversion of ammonium to nitrate by soil microbes, most nitrogen is taken up as nitrate (Colless 1992; Farnham et al. 2003). If nitrogen is supplied via irrigation water, urea is the best source (Birch et al. 2003).

Phosphorus

Phosphorus is a component of energy-carrying phosphate compounds such as ATP and ADP (Raven et al. 1999). Phosphorus deficiency reduces the leaf area index (LAI) of maize, thus reducing the amount of photosynthetically active radiation absorbed by the canopy and leading ultimately to lower biomass accumulation (Pellerin et al. 2000). The negative effect of phosphorus deficiency on LAI also adversely affects adventitious root emergence and therefore may further exacerbate phosphorus uptake (Pellerin et al. 2000). Symptoms of phosphorus deficiency are slow growth, late maturity, a reddening of leaves, poorly developed root systems and small ear size (Colless 1992; Lafitte 2000a; Hughes 2006c).

In the Murrumbidgee and Coleambally irrigation areas of southern New South Wales where maize was grown in rotation with flooded rice crops, it was noted that growth of the maize crop was significantly reduced because of phosphorus unavailability associated with increased iron oxides that immobilized the phosphorus (Willett et al. 1978). For this reason maize is now rarely grown in rotation with flooded rice. Some

maize growing soils in Australia (eg the vertosols of the Darling Downs, Lockyer Valley and Liverpool Plains) have inherently high phosphorus status (Birch et al. 2003).

Potassium

The potassium requirement of maize, particularly if it is used for silage, is high (Birch et al. 2003). Potassium has a crucial role in a number of plant physiological responses, such as stomatal opening and closing, driven by osmosis and ionic balance. It is also an activator of many enzymes (Raven et al. 1999) and influences photosynthesis, nutrient and assimilate transport and enzyme activation for protein synthesis (see discussion and references in Jordan-Meille & Pellerin 2004). Potassium deficiency causes a reduction in LAI probably through altered plant-water relationships that reduce leaf elongation rate (Jordan-Meille & Pellerin 2004). Deficiency symptoms include yellowing and death of leaf margins particularly in the lower leaves, the tendency of the crop to lodge and development of small ears that fail to fill at the tip (Colless 1992; Hughes 2006c).

Zinc

Maize grown on alkaline soils such as the vertosols can show severe zinc deficiency symptoms (Colless 1992; Birch et al. 2003). These symptoms include light streaking of leaves in from the leaf margins (leaf edges, midrib and tip remain green), and stunted growth of the crop (Colless 1992; Hughes 2006c).

Molybdenum

Acid soils, particularly in high rainfall coastal regions of Australia, can be deficient in molybdenum. Deficiency symptoms include yellowing and eventual death of leaf tips, and stunting and sometimes death of plants (Colless 1992; Hughes 2006c).

6.2 Temperature requirements and tolerances

Maize is a summer-growing crop requiring warm daytime temperatures of between 25° C - 30° C and cool nights (Colless 1992). Temperatures below 8° C (or 0° C after silking) or above approximately 40° C usually cause cessation of development (Birch et al. 2003). Different maize cultivars have different optimal temperature requirements and, for example, tropical cultivars derived from 'highland' maize are better able to grow and develop at lower temperatures than those adapted to 'lowland' or 'mid-altitude' areas. Temperatures that are outside the range of adaptation of a cultivar may impact negatively on factors such as photosynthesis, translocation, and pollen viability (see discussion in Lafitte 2000a, summarised in Table 10). In particular, high temperatures have a negative impact on kernel growth, kernel mass and protein accumulation (Jones et al. 1984; Jones et al. 1985; Monjardino et al. 2005; Monjardino et al. 2006).

Table 10. Effects of temperature on key processes in maize (summarised from Lafitte 2000)

	Process	Effect
High Temperature	Photosynthesis	Reduced above 40° C due to membrane damage; irreversible damage above 45° C
	Root hormone production (Abscisic acid and cytokinin)	Reduced hormone production restricts chloroplast development and photosynthetic activity
	Pollination	Pollen viability reduced above 35° C especially if there is low humidity. May reduce grain set.
	Grain yield	Grainfilling duration is reduced; grainfilling rate is increased. Overall yield is usually reduced. Exacerbated by water stress.
Low Temperature	Photosynthesis	Reduced due to reduced enzyme function and membrane damage
	Leaf extension	Reduced due to reduced enzyme function and membrane damage
	Water & nutrient uptake	Reduced due to reduced enzyme function and membrane damage in roots
	Grain yield	Reduced, especially in tropical lowland cultivars at less than 15° C
	Translocation	Reduced, especially in tropical lowland cultivars at less than 10° C;

Maize varieties grown in Australia are mostly adapted to tropical, sub-tropical and warm temperate regions and are therefore not grown in areas where frost may limit early development. Prior to emergence plants may survive frosts for as long as their growing point is below the soil surface, ie at least until four-leaf stage (Farnham et al. 2003). Yields in areas with high temperatures (such as Katherine and Kununurra) are generally lower than in areas with more moderate climates (such as Gatton and the Riverina) (discussed in Birch et al. 2003). The high temperatures affect yield by both shortening the time to maturity (thus limiting grain filling) and exacerbating water stress (Birch et al. 2003) (see also discussion in Section 4.3.2).

6.3 Water

Water deficiency

Worldwide, the average yield losses in maize crops due to drought can be high, particularly in the tropics (Srinivasan et al. 2004). Rainfall is a limiting factor to dryland production of commercial maize crops and irrigation is essential in areas with a winter dominant rainfall pattern or where the amount of summer dominant rain is highly variable (Birch et al. 2003). Maize is particularly susceptible to water stress at the flowering stage when yield potential is being set (Colless 1992; Birch et al. 2003; Srinivasan et al. 2004) especially as this coincides with the high evapotranspiration

rates of mid-summer (Farnham et al. 2003). Stress at this time can reduce grain yield by 6 – 8% for each day of stress (Colless 1992). Grant et al. (1989) did a study to determine the timing of sensitivity of maize yield components to water stress and concluded that kernel number was sensitive to water stress between 2 – 22 d after silking and kernel weight was most sensitive 12 – 16 d after silking. The reduction in kernel number has been proposed to be due to a number of factors including lack of pollination, abortion of ovules prior to fertilization and abortion of fertilized kernels (see discussion in Grant et al. (1989); Bassetti et al. (1993); Srinivasan et al. (2004)). The latter is the most probable and is likely to be due to decreased assimilate flow to the developing grain (Grant et al. 1989; Zinselmeier et al. 1995).

Waterlogging

In the major maize growing areas of Asia and America, significant annual losses can occur because of waterlogging (Suszkiw 1994; Srinivasan et al. 2004). Plants growing for prolonged periods in waterlogged soils show stomatal closure, reduced leaf area growth, chlorosis, reduced root growth, root death and ultimately plant mortality (Lafitte 2000a; Srinivasan et al. 2004). Damage to roots is due mainly to the accumulation of toxic products (such as lactic acid) as a result of anaerobic respiration. Tropical and sub-tropical cultivars are most susceptible to waterlogging at the early vegetative stage and at ‘knee-high’ stage, ie prior to tasseling (Srinivasan et al. 2004).

Molecular and cellular changes to maize seedlings under short-term waterlogging has been widely studied as maize typically shows an ‘anaerobic response’ in which some 20 proteins, mostly associated with glycolysis or sugar-phosphate metabolism, are synthesized (Sachs et al. 1996; Subbaiah & Sachs 2003). Root porosity, that facilitates oxygen diffusion from the above ground parts to the submerged roots, is increased by the selective death of root cortical cells and helps to prolong the survival of plants (Subbaiah & Sachs 2003). Root tip death, also characteristic of response to anoxia, may enhance survival and subsequent recovery, when waterlogging is removed, by eliminating an area of metabolically active tissue (Subbaiah & Sachs 2003). Development of adventitious roots on the soil surface is also important in conferring flooding tolerance (Mano et al. 2005).

6.4 Other abiotic stresses

Salinity

Salinity is regarded more as a problem of irrigated rather than dryland crops. Maize is classed as a salt-sensitive or moderately salt-tolerant plant (Kaddah & Ghowail 1964; Lafitte 2000a) although there is wide variation between cultivars in response to salinity (Rao & McNeilly 1999). It is a ‘salt excluder’ rather than a ‘salt accumulator’ and therefore shows rapid productivity decline with increasing salinity (Yensen & Biel 2006); salt excluders, because they cause salt to accumulate around the roots, find themselves in an increasingly toxic environment. For maize growing in a moderate to slow draining soil in an inland NSW climate it is estimated that a 10% reduction in yield would occur if the crop were irrigated with water of electrical conductivity 1.7 dS/m compared to water of 1.1 dS/m (Evans 2006).

Kaddah & Ghowail (1964), in a study of maize grown in Egypt, noted the following with regard to the effect of salinity (up to 9,000 ppm of a mixture of NaCl and CaCl₂) at various stages of growth:

- ♦ Salinity delayed germination but had no effect on final emergence.
- ♦ Salinity applied at seeding time resulted in reduced vegetative growth, delayed tasseling and silking, smaller cobs and fewer developed kernels (i.e. reduced yield).
- ♦ Salinity applied 21 days after seeding had less deleterious effects
- ♦ Plants in which salinity was applied at the commencement of visible tasselling did not show any specific sensitivity to the salt concentrations that were tested.

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

Although maize is a vigorous and tall-growing plant, it is susceptible to competition from summer weeds, particularly at the early stages of crop growth and particularly because the wide spacing between rows provides opportunity for weed establishment (Pritchard 1995; James et al. 2000; Farrell & O'Keeffe 2007; Morris 2008). Weeds may directly lead to yield reduction by competing with the maize plants for nutrients and water and need to be controlled within 3 weeks of crop emergence (James et al. 2000). Minimising weeds through to crop maturity is also important in terms of ease of harvest and reducing grain contamination. The latter is a significant consideration for maize grain imported into Australia (Pheloung et al. 1999a).

A range of annual grasses (eg barnyard grass – *Echinochloa colona*; crowsfoot grass – *Eleusine indica*; *Pennisetum* spp.; *Digitaria* spp.; *Brachiaria* spp.) and broadleaf weeds (eg caltrop – *Tribulus terrestris*; senna – *Senna obtusifolia*; nutgrass – *Cyperus rotundus*; pigweed – *Potrtulaca* spp.) occur in maize crops (see eg Hughes 2006e; O'Gara 2007). Some weeds such as Hardheads (*Acroptilon repens*) and Witchweed (*Striga* spp.) are of concern because they occur generally in cereal growing areas and are difficult to eradicate (DPI Vic 2007; Johnson 2008).

Weed management can take a number of forms with an integrated approach being recommended (Farrell & O'Keeffe 2007) and including crop rotations, planting into weed-free seedbeds, pre-plant cultivation, inter-row cultivation, use of pre-plant/pre-emergence/post-emergence herbicides and use of conventionally bred imidazolinone tolerant maize hybrids (Hughes 2006e; Farrell & O'Keeffe 2007; O'Gara 2007).

A range of herbicides offer flexible options for weed control and often two herbicides can be used in combination to give a broader spectrum of control (O'Gara 2007). Commonly used herbicides include atrazine, flumetulam, dicamba, metolachlor, fluroxypyr, pendimethalin, propachlor, tribenuron methyl and triclopyr (Storrie et al. 2005; Farrell & O'Keeffe 2007; O'Gara 2007). The Clearfield® production system provides weed management through the use of two imidazolinone-tolerant maize varieties and imidazolinone herbicides such as imazethpyr + imazapyr (O'Gara 2007; Agricentre 2008). A similar system using resistant maize seed dressed with imazypyr + pyrithiobac has been developed by CIMMYT for use in subsistence farming areas where *Striga* spp. cause significant losses (Kanampiu et al. 2001).

7.2 Pests and diseases

7.2.1 *Insects and other invertebrate pests*

Maize is most susceptible to damage by insects during the establishment phase when soil insects can cause up to 30% losses and necessitate replanting of the crop, and from tasselling to harvest (Goodyer 1985; Farrell & O'Keeffe 2007; O'Gara 2007).

Invertebrate pests of establishing crops damage germinating seeds and seedlings and include (Table 11) black field earwigs, wireworms, false wireworms, cutworms, maize stem borer, and beetles such as the African black beetle. The recent development of insecticidal seed treatments (eg imidicloroprid and thiamethoxam) has helped to control soil pests and some above-ground insects (O'Gara 2007) while more traditional methods such as in-furrow spraying and agronomic practices at sowing are also effective (Hughes 2006b).

Invertebrate pests of developing and maturing crops include (Table 11) common armyworm, corn earworm, maize leafhopper, redshouldered leaf beetle, corn aphid, two-spotted spider mite, green vegetable bug, maize weevil and thrips. Insect pests multiply and develop faster in the tropical north of Australia than in southern environments and can represent a significant problem there (O'Gara 2007). Specific pesticides have been developed for control of specific pests (see Hertel & Roberts 2007). In irrigated maize, 'chemigation' (application of pesticides through irrigation water) is an option (O'Gara 2007).

The cereals are susceptible to insect attack during grain storage and maize weevil (*Sitophilus zeamais*) is a particularly serious pest of stored maize as well as infesting maturing cobs (Goodyer 1985; Collins 1998).

Table 11. Common invertebrate pests of maize in Australia

Classification	Taxonomic name	Common name	Impact
Arachnid			
Acarina:			
Tetranychidae	<i>Tetranychus urticae</i>	Two spotted spider mite	May cause excessive leaf damage and hence reduction in yield.
Insect			
Coleoptera:			
Tenebrionidae	<i>Gonocephalum spp.</i> ; <i>Pterohelaeus spp.</i>	False wireworm	Feeds on germinating seeds and shoots. In dry conditions can feed on dry seed.
Elateridae	Elateridae family	Wireworm	Feeds on seed, but more usually attack underground stems.
Scarabaeidae	<i>Heteronychus arator</i>	African black beetle	Chews into the stems of young plants, killing the growing point.
Chrysomelidae	<i>Monolepta australis</i>	Redshouldered leaf beetle	Feeds on foliage, tassels, silks and the husks of the cob. Injury to the silks

Classification	Taxonomic name	Common name	Impact
			may impair seed set.
Curculionidae	<i>Sitophilus zeamais</i>	Maize weevil	Lays eggs in or on maturing grains and the immature stages then feed on the grains. Infestation continues into grain storage.
Dermaptera:			
Labiduridae	<i>Nala lividipes</i>	Black field earwig	Feeds on shoots, roots and stems.
Hemiptera:			
Cicadellidae	<i>Cicadulina bimaculata</i>	Maize leafhopper	Apart from feeding, the leafhopper injects a toxin while feeding which causes 'wallaby ear'.
Pentatomidae	<i>Nezara viridula</i>	Green vegetable bug	Feeds on the bases of cobs causing grain damage.
Homoptera:			
Aphididae	<i>Rhopalosiphum maidis</i>	Corn aphid	Transmits transmit maize dwarf mosaic virus, but is considered a problem in fresh exports.
Lepidoptera:			
Noctuidae	<i>Agrotis spp.</i>	Cutworm	Feeds on young leaves and stems.
	<i>Batytricha truncata</i>	Maize stem borer	Tunnels into stems of young plants causing the central leaves to wither.
	<i>Helicoverpa armigera</i>	Corn earworm	Can cause serious damage during tasseling and silking by reducing pollination and seed set. Insect damage facilitates entry of fungal diseases.
	<i>Mythimna convecta</i>	Common armyworm	Feeds on leaves and may cause severe defoliation at silking that reduces seed yield.
Thysanoptera:			
Thripidae	<i>Frankliniella williamsi</i>	Maize thrip	Most commonly found in whorls, tassels, ears, or on the underside of leaves. Sucks fluid from cells. At ear formation, thrip injury provides entry for infection by <i>Fusarium</i> spp.

Sources: (Goodyer 1985; Heinrichs et al. 2000; Hughes 2006b; Farrell & O'Keeffe 2007; O'Gara 2007; Hertel & Roberts 2007)

7.2.2 Vertebrate pests

Damage to crops can be caused by a variety of birds and animals.

- ♦ Australian native parrots such as Sulphur-crested cockatoos (*Cacatua galerita*); Galahs (*Elophus roseicapilla* syn. *Cacatua roseicapilla*); Little corellas (*Cacatua sanguinea*); and Scaly-breasted lorikeets (*Trichoglossus chlorolepidotus*) can all cause damage to germinating grain and will also pull back husks of cobs on mature plants to remove the grains (Temby & Marshall 2003; Price 1997; Tracey et al. 2007; O'Gara 2007).
- ♦ Native crows and ravens (*Corvus* spp.) commonly consume grain during sowing (Tracey et al. 2007).
- ♦ Pigs reduce yields in grain crops by consuming grain or trampling plants to form bedding or to gain access to the centre of the crop (Choquenot et al. 1996; Price 1997; O'Gara 2007).
- ♦ Rodents such as mice (*Mus domesticus*) and long-haired rats (*Rattus villosissimus*) will chew on the stems of young plants to feed on sap (Animal Control Technologies 2004) or will eat newly sown grain (Staples et al. 2003). Long-haired rats caused significant damage to maize in the Ord River Valley in 1983 (WA Government 2007). Zinc phosphide can be used to control rodent infestations in maize crops in Australia (Staples et al. 2003).

7.2.3 Diseases

A list of the more common diseases of maize in Australia is given in Table 12. To some extent the impact of a disease is related to geographical/climatic factors that may favour the growth and spread of the causal agents, eg *Gibberella zeae* is common in the Atherton Tablelands of Queensland but much less serious in southern Queensland (Hughes 2006a); wallaby ear virus can be a significant problem in the Northern Territory because of the abundance of leafhoppers (O'Gara 2007). Hybrids have now been bred that show degrees of resistance to a variety of diseases (see Farrell & O'Keefe 2007 for a listing of cultivars used in NSW). While chemicals are available for control of fungal pathogens, disease management is mainly through hygienic practices such as regular crop inspection; washing down equipment; controlling weeds and volunteers that may spread the disease; controlling insects that may be associated with disease spread or cause damage that increases plant susceptibility to disease; post infection practices such as paddock quarantine, burning of infected plants/stubble; and agronomic practices such as seed treatment, crop rotation, avoiding moisture stress in plants, minimising damage to plants during cultural operations, harvesting before kernels start to split (Stovold 1984; Beckingham 2006; Farrell & O'Keefe 2007).

Table 12. Common diseases of maize in Australia

Pathogen classification	Pathogen name	Disease	Impact of disease
Bacterium			
Enterobacteriales	<i>Erwinia</i> spp.	Soft rot	Upper stalks rot and fall over.
Fungus			
Hypocreales	<i>Fusarium verticillioides</i> (formerly <i>F. moniliforme</i>) <i>F. proliferatum</i> ; <i>F. subglutinans</i>	Fusarium cob rot and stalk rot	Poor seedling root development. Mature plants with rotted stalk tissues, lodge easily. White fungal growth

Pathogen classification	Pathogen name	Disease	Impact of disease
			covers kernels or the entire cob causing yield reduction. Toxins produced by the fungus may be problematic (see Section 5.1.2).
	<i>Gibberella zeae</i> (asexual state = <i>Fusarium graminearum</i>)	Gibberella stalk rot or Gibberella ear rot or pink ear rot	Can occur as seedling blight. Plants may die prematurely. Stalks rot and break easily. Ear rot causes grain yield loss. Can produce a toxin (Zearalenone) harmful to livestock.
Microbotryales	<i>Sphacelotheca reiliana</i>	Head smut	Black masses of spores replace the ears and/or tassels.
Pleosporales	<i>Cochliobolus heterostrophus</i> (<i>Bipolaris maydis</i>)	Maydis leaf blight or Southern leaf blight	Brown spots on leaves, may also cause rot of the kernels on the ear.
	<i>Setosphaeria turcica</i> (<i>Exserohilum turcicum</i>)	Turcica/Turcicum leaf blight or northern leaf blight	Greyish-green, water-soaked spots which may cover most of leaf and reduce photosynthetic area.
Sclerosporales	<i>Sclerophthora macrospora</i>	Downy mildew	Stunted, yellow, thickened leaves; tassels usually do not develop or show abnormal development.
Uredinales	<i>Puccinia sorghi</i>	Common rust	Pustules form on leaves, mass of red-brown powdery spores. More serious on sweet corn.
	<i>Puccinia polysora</i>	Polysora rust or tropical rust or southern corn rust	Pustules evenly spread over leaf surface. May cause defoliation starting from the base.
Ustilaginales	<i>Ustilago maydis</i>	Boil smut	Attacks any above-ground growing part of the plant to form blisters or galls containing black spores. Can survive in the soil for many years.
Oomycete			
Pythiales	<i>Pythium spp.</i>	Pythium	Seedling disease. Seedling may not emerge or may yellow and die after emergence.
Virus			
		Maize dwarf mosaic/ Johnson grass mosaic	Light and dark green mosaic, ring-spot or yellowing of leaves causing yield reduction. Spread by aphids. Sweet

Pathogen classification	Pathogen name	Disease	Impact of disease
			corn varieties, especially supersweets, are most susceptible.
		Wallaby Ear	Leaves have erect growth and roll upwards and inwards; there are numerous galls on the leaf veins.

Sources: (Stovold 1984; Nyall 1999; Beckingham 2006; Hughes 2006a; Farrell & O'Keeffe 2007; Watson 2007)

7.2.4 *Other adverse associations with maize*

Nitrite poisoning

Nitrite can be generated by microbial organisms from nitrate and may be taken up by animals through their feed, such as mouldy hay, or, in ruminants, it may result from the conversion of nitrate. If, in ruminants, microbes cannot convert nitrite to ammonium, it may accumulate. Non-ruminants have no mechanism to detoxify nitrite, so they are generally susceptible to nitrite poisoning. Nitrite is absorbed into the blood, leading to a reduction in its ability to transport oxygen (oxygen starvation). Symptoms of nitrite poisoning are breathing difficulties in staggering/weak animals. In severe cases, the animal may convulse and die, in less severe cases, cows may abort their foetus (Halpin & Hides 2002).

Silo filler's disease

Gaseous oxides of nitrogen, including nitrogen dioxide (NO₂), are released from maize after the conversion of nitrates through microorganisms after ensiling (reviewed in Brightwell 1972; Everist 1981; Maw et al. 2002; Leavey et al. 2004). The World Health Organization has developed guidelines that recommend not exceeding an annual mean of 40 µg/m³ (ie 0.02 ppm) and 200 µg/m³ (ie 0.1 ppm) for short term exposure (World Health Organisation 2005). However, in the USA, measurements of over 100,000 ppm have been documented in maize silos (reviewed in Everist 1981). Both humans and stock may be affected by those oxides, which may lead to dyspnea, pulmonary oedema and death within a few days in severe cases (Everist 1981; Leavey et al. 2004). In other (human) cases, respiratory distress over a period of 2 – 3 weeks may be followed by chills, breathing difficulty, cyanosis and death within six weeks after exposure (Everist 1981).

Mycotoxins

Mycotoxins are low-molecular-weight natural products produced as secondary metabolites by filamentous fungi and are toxic to vertebrates and other animal groups in low concentration (Bennett & Klich 2003). The fungi that produce them typically grow on agricultural products (eg cereal grains, rice and cottonseed meal, groundnuts and other legumes) before or after harvest or during transportation or storage (FAO 1998). Maize has one of the most serious mycotoxin problems of all crops (Munkvold 2003).

Mycotoxins are stable compounds that are not destroyed by processing and may also be present in the meat, milk or eggs of animals that have ingested them. In most

instances the main source of mycotoxins for humans is contaminated cereals and legumes rather than animal products (FAO 1998). The occurrence of mycotoxins in grain harvested and stored in Australia is generally not significant because the moisture content at harvest is below that permitting fungal growth (Webley & Jackson 1998). Many nations have maximum tolerated levels of mycotoxins in food and feed and mycotoxin contamination can lead to rejection of maize imports. Common mycotoxins occurring in maize are given in Table 13.

Table 13. Mycotoxins associated with maize grains

Mycotoxin Category	Produced by	Comment
Aflatoxin	<i>Aspergillus flavus</i> ; <i>A. parasiticus</i>	The fungi also cause cob rot. Aflatoxins can occur on maize preharvest (favoured by high temperature and high humidity at grain maturation and/or by stress) but are usually associated with mould growth in storage.
Ochratoxin A	<i>Aspergillus ochraceus</i> ; <i>A. niger</i>	Occurrence in Australia is much less common than that of aflatoxin. Occurs in Queensland occasionally.
Fumonisin	<i>Fusarium verticillioides</i>	Fumonisin production occurs preharvest when plant defences are weakened by stress. Development of fumisinis in stored grain is unlikely because of the high moisture requirements of <i>Fusarium</i> spp.
Tricothecenes	<i>F. graminearum</i>	Of the 150 toxins in this group, deoxynivalenol (DON) and nivalenol are the most significant in Australia. The latter occurs on maize grown on parts of the Atherton Tableland. DON has occurred in the Liverpool Plains region of NSW associated with cool, moist conditions during grain maturation.
Zearalenone	<i>F. graminearum</i>	Fungus grows on the grain before harvest. Particularly found in maize grown in cool, wet upland regions such as the Atherton Tableland.

Sources: (Webley & Jackson 1998; Koenning 1999; Blaney 2004; Farrell & O'Keeffe 2007)

High or abnormal fluctuations in temperature and drought stress predispose pre-harvest maize to fungal growth and subsequent mycotoxin accumulation. Insect infestation is also considered to facilitate mycotoxin contamination because insects act as vectors for fungal spores and insect damage leads to wounds in the plant through which fungal colonization can occur (Munkvold 2003). Evidence would suggest that, in areas where there are insect pests, maize lines genetically modified with the gene coding for the *Bacillus thuringiensis* (Bt) toxin, that protects plants from insect pests, have lower levels of mycotoxins than non-GM lines (Wu 2008).

7.3 Other biotic interactions

Mycorrhizae

Arbuscular mycorrhizal fungi (AMF) colonize the roots of most crop species and maize is a mycorrhizal host (Mozafar et al. 2000; Jansa et al. 2003; Grigera et al. 2006). In general, it is considered that colonization of roots by AMF improves crop productivity for a variety of reasons (see discussion and references in Sylvia et al. 1993). Data on the significance or otherwise of mycorrhizal associations with maize

are not always clear and, at times, are conflicting. There would appear to be some interaction between mycorrhizal effect and nutrient (particularly phosphorus) and water status and there is an obvious requirement for further research in this area. In trials using artificially inoculated plants it has been shown that AMF improve plant growth and yield of maize by improving uptake of phosphorus and copper particularly under conditions of water stress (Sylvia et al. 1993). There is uncertainty about the specific effects of mycorrhizae on root development with Kothari et al. (1990) noting a decrease in root length per plant and Osonubi (1994) finding an increase. Inoculated plants show higher transpiration rates than non-inoculated plants possibly due to the total greater leaf area of inoculated plants (Kothari et al. 1990). Under optimal growing conditions carbon may be reallocated to the fungi from the plant, a factor that potentially may reduce grain yield in the crop, but there is evidence that this is offset by increased uptake of phosphorus by the crop as a result of mycorrhizal contribution (Grigera et al. 2006). Soil tillage affects the relative prevalence of different genera of mycorrhizal fungi in the maize rhizosphere (Mozafar et al. 2000).

SECTION 8 WEEDINESS

8.1 Weediness status on a global scale

Weeds are plants that spread and persist outside their natural geographic range or intended growing areas such as farms or gardens. Weediness in Australia is often correlated with weediness of the plant, or a close relative, elsewhere in the world (Panetta 1993; Pheloung et al. 1999b). The likelihood of weediness is increased by repeated intentional introductions of plants outside their natural geographic range that increase the opportunity for plants to establish and spread into new environments, eg escapes of commonly used garden plants (Groves et al. 2005).

Characteristics in plants that are generally associated with weediness include prolonged seed dormancy, long persistence of seeds in the soil, germination under a broad range of environmental conditions, rapid vegetative growth, short lifecycle, very high seed output, high seed dispersal and long-distance seed dispersal (Keeler 1989; Keeler et al. 1996).

During development of the maize plant the main vegetative growing meristem is transformed into a reproductive meristem which is then removed at harvesting. Coupled with the fact that maize does not resprout or reproduce vegetatively (see Section 4.1), this means that harvesting effectively destroys the plant. There is, however, a significant mass of plant material (stover) that is left in the ground following harvest and this may be removed, retained as is for oversowing with another crop, incorporated into the soil after tilling or sometimes burnt (Robinson & Kirkby 2002; Dhugga 2007).

As discussed in Section 4.3.3, corn seeds generally remain tightly attached to the cob and are collected during harvest or may be transferred to the ground if the ear becomes detached prior to harvest (eg as a result of insect or disease damage). In the latter instance, the hundreds of maize kernels inside can germinate in the following season but, because of competition for light and soil, very few are able to reach maturity (Doebley 2004).

Volunteer plants [self sown plants derived from seed of a previous crop (Brookes et al. 2004)] can also occur as a result of harvesting or transport. Although maize volunteer plants occur consistently, they are not regarded as a serious weed problem except perhaps when grown in rotation with soybean (Andersen et al. 1982; CFIA 1994; Eastham & Sweet 2002; Owen 2005). Harvest grain losses can be as great as 206 kg/ha of maize grain and occur when, for example, harvest machinery does not efficiently gather ears or shell the grain from the cob, or when weeds plug grain sieves (AGBIOS 2005). Volunteerism is a greater problem in no/low tillage systems when the dropped seeds remain near the soil surface. It is suggested that volunteer plants rarely produce viable seed for the next growing season (EC 2000a). In areas with cold winters, frosts will normally kill volunteers (EC 2000b) and feral populations of maize have not been observed in Europe (COGEM 2008). With the recent adoption of genetically modified (GM) herbicide resistant (glufosinate ammonium; glyphosate) maize cultivars (see Section 2.4.2) there has been concern with management of potential GM maize volunteer plants.

The fact that *Zea mays* ssp. *mays* has no vegetative means of spreading combined with its complete dependence on humans for survival, means that it represents a minimal weed risk. However, some of its relatives may have some weed potential eg:

- ♦ Balsas teosinte (*Zea mays* ssp. *parviglumis*) can invade fields in Mexico and is therefore considered weedy in places (reviewed in Doebley 2004).
- ♦ In central Mexico, *Zea mays* ssp. *mexicana* is a troublesome weed of maize fields where, until flowering, the plant can be difficult to distinguish from domesticated maize (reviewed in Desjardins & McCarthy 2004).
- ♦ Randall (2002) notes that *Z. mays* ssp. *mexicana* and *Z. mays* ssp. *parviglumis* are listed as naturalised weeds in the USA; *Z. luxurians* is a cultivation escape in Guyana; *Tripsacum andersoni* is a weed in Guyana and Peru; *T. latifolium* is a cultivation escape in Puerto Rica; and *T. laxacum* is a cultivation escape in several countries.

8.2 Weediness status in Australia

Groves et al (2003) assigned a rating of '1' to *Zea mays* ssp. *mays* and *Zea mays* ssp. *mexicana* in natural ecosystems indicating that they are "naturalised and may be a minor problem but not considered important enough to warrant control at any location". In agricultural ecosystems, the two species are also not considered a problem (Groves et al. 2003). *Z. mays* ssp. *mexicana* can be found in north Queensland and Western Australia (Pheloung et al. 1999a) and is also cited in Randall (2002) as being naturalised in Australia. *Tripsacum dactyloides* has been collected in Australia (Australia's Virtual Herbarium, <http://www.cpbr.gov.au/avh.html>) and is listed by Randall (2002) as a naturalised weed there.

8.5 Control measures

While maize is not a weed problem as such, it may be necessary to remove volunteer plants that arise in a subsequent non-maize crop following a rotation. Farmers have traditionally used herbicides (eg glyphosate or graminicides such as diclofop (Andersen et al. 1982)) and tillage to control volunteers. With the increase in the use

of glyphosate-tolerant maize cultivars (especially in rotation with glyphosate-tolerant soybeans) herbicides such as sethoxydim, clethodium, fenoxaprop-p-ethyl, fluazifop-p-butyl and quizalofop-p-ethyl can also be used to control volunteer maize (Beckie & Gill 2005; Soltani et al. 2005).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

Vertical gene transfer is the transfer of genetic material from parent to offspring by reproduction. This type of gene transfer can occur by sexual or asexual reproduction. This section deals with gene transfer to other plants of the same species or closely related species by sexual reproduction.

Successful gene transfer requires that three criteria are satisfied. The plant populations must: 1) overlap spatially (sympatry); 2) overlap temporally (including flowering duration within a year and flowering time within a day); and 3) be sufficiently close biologically that the resulting hybrids are fertile, facilitating introgression into a new population (den Nijs et al. 2004).

As discussed in Section 1, *Z. mays* ssp. *mays* is the only cultivated species within the genus *Zea* and the other species and subspecies [originally classified as races (Wilkes 1977)] are wild grasses, referred to as teosintes. Three of the annual teosintes are subspecies of *Z. mays*, namely ssp. *mexicana* (central Mexico), ssp. *parviglumis* (southern and western Mexico) and ssp. *huehuetenangensis* (western highlands of Guatemala) (Doebley 1990). Other species of teosinte are *Z. diploperennis* (a diploid perennial), *Z. perennis* (a tetraploid perennial) and *Z. luxurians* (an annual). As many publications tend to discuss crossing between teosintes and maize generally, it is sometimes difficult to be able to distinguish between intraspecific and interspecific crosses within the genus, so these have been considered together.

9.1 Natural intraspecific and interspecific crossing

All the various types of *Z. mays* ssp. *mays* freely cross-pollinate and form fertile hybrids (Purseglove 1972). Since maize is predominantly outcrossing, intraspecific crosses are highly likely between nearby plants if flowering time overlaps and other factors (see Section 4.2.3) are favourable. Volunteers are not likely agents of gene transfer in maize since their occurrence is minimized by the fact that the maize cob cannot shed seed naturally (see Section 4.3).

Outcrossing has been discussed in Sections 2.3.1 and 4.2.3. Wind pollination can occur between maize crops over hundreds of metres but the relatively large weight and diameter of the pollen grains favours most pollen deposition within approximately 60 m of the source plant (Raynor et al. 1972; Luna et al. 2001; Aylor 2002; Jarosz et al. 2003) and there is little or no cross pollination at 300 m (Luna et al. 2001). Halsey et al. (2005) have considered both time and distance components of pollen-mediated gene flow in maize and concluded that, under their experimental conditions, 200 m was sufficient to reduce outcrossing to < 0.1%. Also of significance in considering the likelihood of cross-pollination in maize is pollen competition. The fact that a single plant can produce millions of pollen grains (see Section 4.2.1) means that, even if there is long distance spread of pollen from a plant, the pollen will be greatly outnumbered by 'local' pollen (Bannert & Stamp 2007). Ironically, measures to reduce pollen production such as detasseling or cytoplasmic male sterility may

actually increase the likelihood of long distance cross pollination because they reduce pollen competition (Bannert & Stamp 2007).

The international seed certification standards provide a guide to the physical separation of crops to minimise gene flow (see Section 2.3.1), and a separation distance of less than or equal to 300 m is standard worldwide for production of certified seed while basic seed has a higher requirement (eg 400 m in France (Messean et al. 2006)).

Separation distances have also been discussed in considerations of gene flow between genetically modified (GM) and non-GM maize crops (Henry et al. 2003; Eastham & Sweet 2002; Stevens et al. 2004; Goggi et al. 2006; Messeguer et al. 2006; Sanvido et al. 2008). The variation in results reflects the range of factors that can be taken into account when defining the distances (eg see discussion in Section 4.2.3), and especially the level of gene flow that might be tolerated, but it would appear that for gene flow rates of < 0.1%, recommended distances are similar to those used in non-GM certified seed production (Henry et al. 2003; Goggi et al. 2006). A comprehensive discussion of the factors to be considered in gene flow between GM and non-GM maize is given by Messean et al. (2006). Of importance in restricting gene flow between GM and non-GM corn is surrounding the GM corn with non-GM corn so as to reduce the density of any GM pollen (Goggi et al. 2006).

Various incompatibilities exist both between and within subspecies of *Z. mays* and are thought to have evolved to prevent indiscriminate hybridization (Kermicle 1997). One system that has been particularly studied is concerned with pollen-pistil incompatibility affected by six or more alleles at the *gametophyte-1* (*gal*) locus and involves the arrest or retardation of *gal* pollen tubes within *Gal-s/-* silks resulting in a prezygotic barrier to crossing (Schwartz 1950; Kermicle 1997).

The teosintes were formerly placed in the genus *Euchlaena* (Collins 1925; Mangelsdorf & Reeves 1931). Maize and all of the teosintes (except *Z. perennis*) are sexually compatible, and it is known that they naturally produce fertile hybrids in Mexico and Guatemala where they share a common distribution (Wilkes 1977; Doebley 1990). In particular spontaneous hybridization occurs between *Z. mays* ssp. *mays* and both *mexicana* teosinte and *parviglumis* teosinte (Ellstrand et al. 2007) with introgression being most common with ssp. *mexicana* (Fukunaga et al. 2005). Hybrids of ssp. *mays* x ssp. *mexicana* crosses have statistically significant heterosis compared to the wild teosinte but not when compared to the cultivated parent (Guadagnuolo et al. 2006). Despite the ease of crossing, gene flow occurs at low frequency and all the subspecies still co-exist as genetically separate entities (Baltazar et al. 2005; Fukunaga et al. 2005). Unusually, the flow of genes has occurred in both directions (reciprocal introgression) (Wilkes 1977; Doebley 1990) although a number of factors tend to favour gene flow from teosinte to maize rather than from maize to teosinte (Baltazar et al. 2005). There is also evidence of a restriction to crossability in some populations of *Z. mays* teosintes when teosinte is the female and maize the male parent and this has been linked to a teosinte gene or gene cluster known as *Teosinte crossing barrier1* (*Tcb1*) (Evans & Kermicle 2001; Kermicle 2006). The *Tcb1* locus occurs within the chromosome-4 cluster of teosinte known as Teosinte Incompatibility Complex and represents a barrier to crossing that occurs before fertilization. It is loosely linked to the *Gal* locus. Evans & Kermicle (2001) have

suggested that the transfer of *Tcb1* into maize may be useful in avoiding contamination of one commercial variety with another.

The likelihood of intraspecific or interspecific crossing occurring naturally in Australia is remote. *Z. mays* ssp. *mexicana* imported from South America can now be found in North Queensland and Western Australia (Pheloung et al. 1999a) but there have not been any reports of introgression with commercial maize cultivars.

9.2 Crossing under experimental conditions

These crosses, while possible under controlled conditions, do not occur naturally and therefore are of significance only in the context of broadening an understanding of unaided gene transfer (OECD 2006).

9.2.1 Interspecific crosses

Crosses between *Z. mays* ($2n=20$) and *Z. perennis* ($2n=40$) may normally yield only 0.1 – 1% viable seed because of endosperm collapse after approximately 21 days post pollination. However, hybrids (with $2n=30$) have been obtained following embryo rescue (del Carmen Molina & Garcia 1999). *Z. perennis* is not found in Australia.

9.2.2 Intergeneric crosses

There has been considerable speculation on the evolution of cultivated maize, including suggestion that intergeneric introgression between *Zea* and *Tripsacum* (that are both members of the sub-family Panicoidea, tribe Maydeae) may have played a role [see e.g. discussion in de Wet & Harlan (1974); Eubanks (1997)]. Consequently there have been a number of attempts to hybridize *Zea mays* and *Tripsacum* spp. although all of these have been under controlled conditions and there is no suggestion that hybridization occurs naturally. The *Tripsacum* genus comprises rhizomatous perennial grasses distributed from northern USA to Paraguay in South America. The base chromosome number is $x=18$ (Eubanks 1997) compared to the base chromosome of maize ($x=10$) and therefore the cytogenetic interactions in the hybrids have been of interest. *Tripsacum dactyloides* has been collected in Australia (Australia's Virtual Herbarium, <http://www.cpbr.gov.au/avh.html>) and is listed by Randall (2002) as a naturalised weed.

Tripsacum with a basic chromosome number of $2n=18$ is the genus most closely related to *Zea* and crosses between these two genera are possible. *T. dactyloides* and *T. andersonii* are used as fodder plants in the tropics (Cook et al. 2005a; Cook et al. 2005b). *T. dactyloides* (Eastern gamagrass) has been collected in Australia (Australia's Virtual Herbarium, <http://www.cpbr.gov.au/avh.html>). Current research addresses the value of *Tripsacum* grasses and their hybrids as fodder plants in Australia (eg maize x *T. dactyloides* hybrids as in Shavrukov et al. 2006).

Early crosses (using *Tripsacum* as the pollen donor) (Mangelsdorf & Reeves 1931) showed that some degree of successful fertilization could be obtained only if the distance the *Tripsacum* pollen tube had to grow was reduced (eg by shortening the maize styles). It appears that genetic transfer from *Tripsacum* (e.g. *T. floridanum*, *T. dactyloides*, *T. pilosum*, *T. lanceolatum*) to *Zea mays* is complex and that, depending on the choice of *Tripsacum* parent and the events occurring in early backcross generations, at least 54 chromosome combinations can be obtained (Harlan

& de Wet 1977). The hybrids are sterile or somewhat female fertile and repeated backcrosses to maize eliminate the *Tripsacum* chromosomes. Polyploids in the genus *Tripsacum* show diplosporous apomictic reproductionⁱ (Grimanelli et al. 1998) and this has been exploited commercially in maize/*Tripsacum* hybrids to introgress diplosporous apomictic reproduction into a maize background; this would eventually allow the establishment of immortalized commercial lines of apomictic maize (Kindiger & Sokolov 1998). Other traits that have been obtained in maize/*Tripsacum* hybrids include high silage biomass (Shavrukov et al. 2006).

Crosses between *Tripsacum* and *Z. mays* teosintes have not been successful but fully fertile hybrids ($2n = 20$) have been achieved between *Z. diploperennis* and *T. dactyloides* using *Tripsacum* as the female parent (Eubanks 1995; Eubanks 1997). These hybrids, referred to as Tripsacorn (Eubanks 1992) can be crossed with cultivated maize and offer a pathway for the transfer of useful genetic material into commercial maize varieties (Eubanks 2003).

The tribe Maydeae also includes five Asiatic genera (*Coix*, *Sclerachne*, *Polytoca*, *Chionachne* and *Trilobachne*) (Watson & Dallwitz 1992) but of these there has only been a report of *Z. mays* being crossed with *Coix lachryma-jobi* (Harada et al. 1954). In this instance, hybrid seed was obtained in about 6% of crosses but only when *Coix* was used as the female parent. A number of *Coix* spp. are permitted imports to Australia (AQIS 2008). *C. gasteenii* is considered a threatened species in the Cape York Peninsula area (North Australian Land Manager 2008).

Maize has also been crossed with another member of the Panicoideae sub-family. A single intergeneric hybrid has been obtained between sugarcane (*Saccharum officinarum* – tribe Andropogonae) with $2n = 80$ and *Z. mays* with two additional B chromosomes, using maize as the pollen parent (Janaki Ammal et al. 1972). The individual, whose cells contained chromosome numbers varying from 52 – 58, survived 30 years through clonal propagation and was induced to open its inflorescence by application of gibberellic acid.

Other intergeneric crosses involving maize have all been with members of the sub-family Pooideae. Available information (see eg Kynast et al. 2001) suggests that when Panicoideae are crossed with Pooideae, chromosomes of the Panicoideae are eliminated soon after fertilization. Examples include:

- ♦ Maize (pollen donor) crosses readily with hexaploid ($2n = 42$) wheat (*Triticum aestivum*) although double fertilization is rare and development of the embryo proceeds without the formation of endosperm (Zhang et al. 1996). The embryo will therefore abort, unless cultured *in vitro*, because of a lack of nutrition normally supplied by the endosperm. The maize chromosomes are eliminated during early embryogenesis resulting in the formation of a wheat haploid (Laurie & Bennett 1988). This occurs because of a failure of the kinetochores of the maize

ⁱ Apomixis is a genetically controlled mechanism in which an embryo is formed without union of male and female gametes. Diplospory is a form of apomixis in which the embryo develops from a diploid egg that has derived from an unreduced megaspore mother cell. The resulting individual is therefore genetically identical to the maternal parent (Kindiger & Sokolov 1998).

chromosomes to attach to spindle microtubules of the metaphase plate during cell division (Mochida et al. 2004).

- ♦ In controlled crosses of hexaploid ($2n = 42$) oat (*Avena sativa*) with maize, a proportion (approximately 31%) of the embryos may contain 1 – 4 maize chromosomes in addition to a full complement of oat chromosomes and are therefore referred to as partial hybrids (Riera-Lizarazu et al. 1996; Kynast et al. 2001). Oat/maize hybrids represent useful material for mapping the maize genome (Ananiev et al. 1997; Kynast et al. 2004). The hybrid plants can only be grown following embryo rescue.
- ♦ Zenkteler & Nitzsche (1984) made a number of crosses within the cereals, including barley (*Hordeum vulgare*; $2n = 14$) and rye (*Secale cereale*; $2n = 14$) as female parents with *Zea mays* as the pollen donor. The crosses were made on *in vivo* -grown plants and no attempt was made at embryo rescue. No embryos developed in the *H. vulgare* x *Z. mays* cross but globular embryos formed in some of the *S. cereale* x *Z. mays* crosses although these degenerated after 6 - 10 days presumably because of poor or no endosperm development.
- ♦ Development of embryos from barley florets pollinated with maize has been obtained following embryo rescue (Chen et al. 1991). Plants grown on from the embryos were largely sterile haploids ($2n = 7$) and there was no cytological evidence of retention of entire maize chromosomes.

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