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Revised Consensus Document on the Biology of Wheat (Triticum aestivum L.)

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No. 76

Revised Consensus Document on the Biology of Wheat (*Triticum aestivum* L.)

Environment Directorate

ORGANISATION FOR ECONOMIC CO-OPERATION AND DEVELOPMENT

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or contact:

OECD Environment Directorate,
Environment, Health and Safety Division
2 rue André-Pascal
75775 Paris Cedex 16
France

E-mail: ehscont@oecd.org

OECD Environment, Health and Safety Publication

FOREWORD

The consensus documents prepared by the OECD Working Party on the Harmonisation of Regulatory Oversight in Biotechnology (WP-HROB) contain information for use during the regulatory assessment of the environmental safety (or 'biosafety') of a particular product. In the area of plants, these are being published on information on the biology of certain species of crops and trees, selected traits that may be introduced into plant species, and biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of wheat (*Triticum aestivum* L.).

Australia and the United States served as the co-leads in the preparation of this document, and the draft has been revised based on the input from other member countries and stakeholders.

The WP-HROB endorsed this document, which is published under the responsibility of the Chemicals and Biotechnology Committee of the OECD.

When reading these documents, it is recommended to consult the following OECD documents with a broader scope which describe core principles for biotechnology risk assessments.

OECD (2023), OECD Consensus Document on Environmental Considerations for the Release of Transgenic Plants, https://doi.org/10.1787/62ed0e04-en.

OECD (2022), "Revised points to consider on plant biology consensus documents", in Safety Assessment of Transgenic Organisms in the Environment, Volume 9 https://doi.org/10.1787/e49bd2e8-en

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SECTION 1. Species or taxonomic group

1.1. Classification and nomenclature

Triticum aestivum L., bread wheat, is one of the top two cereal crops grown in the world for human consumption, along with rice (FAO, 2014). It is an annual grass that belongs to the family Poaceae, subfamily Pooideae and tribe Triticeae (Clayton et al., 2015). Recommended texts for a comprehensive overview of wheat breeding are The World Wheat Book: A History of Wheat Breeding, Volumes 1 and 2 (Angus et al., 2011; Bonjean and Angus, 2001).

Common names for *T. aestivum* are wheat, cultivated wheat and bread wheat. It is of note that the word 'wheat' is also used in the literature to refer to a number of species that are related to *T. aestivum*. Some of these species exist only in the wild but others have wild and domesticated forms that are currently cultivated or were cultivated in the past. In this document, either the scientific name or the term 'bread wheat' will be used to refer to *T. aestivum.*

1.1.1. The tribe Triticeae Dumort

The tribe Triticeae is a group of plants that is vital to human subsistence and was key in the advent of agriculture in the Fertile Crescent of the Near East (Kilian et al., 2009). It includes the cereal crops wheat (*Triticum* sp.), barley (*Hordeum* sp.), rye (*Secale* sp.) and triticale (*Triticosecale* sp.) that account for one third of the cereal production of the world (Feuillet, Langridge and Waugh, 2008). The tribe Triticeae contains 32 genera and over 500 species, of which approximately 100 are annual and 400 are perennial grasses (Feldman and Levy, 2015; Liu et al., 2016; Wang and Lu, 2014).

Hybridisation has played an important role in Triticeae speciation and evolution (Liu et al., 2016). The Triticeae polyploid[1] species originated by an unknown mechanism, though is likely to be a result of multiple rounds of homoploid and polyploid hybrid speciation (Marcussen et al., 2014).

The basic chromosome number[2] in Triticeae is seven ($x = 7$; Heslop-Harrison, 1992). Triticeae species have ploidy levels ranging from 2x to 12x (Liu et al., 2016). Cultivated species are diploid[3] ($2n = 2x = 14$; barley and rye), tetraploid[4] ($2n = 4x = 28$; durum or pasta wheat), or hexaploid[5] ($2n = 6x = 42$; bread wheat, spelt and triticale[6]) (Feuillet, Langridge and Waugh, 2008). Every diploid species has its own genome and the polyploid species contain the genomes of their diploid progenitors. The genomes are represented

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The statistical data for Israel are supplied by and under the responsibility of the relevant Israeli authorities. The use of such data by the OECD is without prejudice to the status of the Golan Heights, East Jerusalem and Israeli settlements in the West Bank under the terms of international law.

[1] Polyploid: organism containing more than two homologous sets of chromosomes.

[2] Basic chromosome number: the number of chromosomes in each set of chromosomes, which is constant for any one species of plant or animal. It is represented by the letter x. The number of chromosomes in each somatic cell is 2n.

[3] Diploid: organism containing two sets of chromosomes (2x in somatic cells).

[4] Tetraploid: organism containing four sets of chromosomes (4x in somatic cells).

[5] Hexaploid: organism containing six sets of chromosomes (6x in somatic cells).

[6] Tetraploid to octaploid variants also exist, but cultivated versions are primarily hexaploid (Bernard and Bernard, 1987)

by the symbols A to W, Ta, St, and Ns (Liu et al., 2016). Taxonomic treatment of these species is challenging and often controversial. To reflect the new and robust taxonomic information at either a morphological or molecular level, or both, frequent updates have been made to taxonomic treatments of Triticeae species, leading to the creation of multiple taxonomic names at either the generic or species level for the same taxon (Barkworth and von Bothmer, 2009; Bernhardt, 2015). Based on the most commonly used taxonomy (Barkworth and von Bothmer, 2009; Bernhardt, 2015; Feldman and Levy, 2015; Liu et al., 2016; Wang et al., 1994), the genera of the tribe Triticeae are summarised in Table 1.1..

Table 1.1. The genera of the tribe Triticeae

Genus[1, 2, 3, 4]	Ploidy level[3, 4]	Genomic composition[1, 2, 4, 5]	Growth habit[2, 3, 4]
Aegilops L.	2x-6x	B, C, D, M, N, X, U, BU, CU, CD, DM, DN, MU, DDM, BDM, DMU	Annual
Agropyron Gaertn.	2x-6x	P	Perennial
Amblyopyrum (Jaub. & Spach.) Eig	2x	T	Annual
Anthosachne Steud.	6x	StHW	Perennial
Australopyrum (Tzvelev) Á. Löve	2x	W	Perennial
Crithopsis Jaub. & Spach.	2x	K	Annual
Dasypyrum (Coss. & Dur.) T. Dur.	2x-4x	V	Perennial/Annual
Douglasdeweya C.Yen, J.L. Yang, & B.R. Baum	4x	StP	Perennial
Elymus L.	2x-12x	St plus at least one of H, W, Y	Perennial/Annual
Elytrigia Desv.	2x-10x	St, E, H, N	Perennial
Eremiun Seberg & Linde-Laursen	6x	Ns	Perennial
Eremopyrum (Ledeb.) Jaub.&Spach	2x-4x	F, Xe	Annual
Festucopsis C.E. Hubb	2x	L	Perennial
Henrardia C.E. Hubb	2x	O	Annual
Heteranthelium Jaub.&Spach	2x	Q	Annual
Hordelymus (Jessen) Harz	4x/10x	Ns	Perennial
Hordeum L.	2x-6x	H, I, Xa, Xu, HXa	Perennial/Annual
Hystrix Moench	4x	StH or Ns	Perennial
Kengyilia C. Yen & J.L. Yang	6x	StPY	Perennial
Leymus Hochst	4x-8x	Ns	Perennial
Pascopyrum Á. Löve	8x	St, H, N	Perennial
Peridictyon Seberg, Fred. & Baden	2x	Xp	Perennial
Psathyrostachys Nevski	2x	Ns	Perennial
Pseudoroegneria (Nevski) Á. Löve	2x-4x	St	Perennial
Roegneria K. Koch	4x/6x	St, Y	Perennial
Secale L.	2x	R	Perennial/Annual
Stenostachys Turcz.	4x	HW	Perennial
Taeniatherum Nevski	2x	Ta	Annual
Thinopyrum Á. Löve	4x-12x	E sometimes with P, St, or L	Perennial
Triticum L.	2x-6x	A, B/G, D	Annual

Sources: [1] Bernhardt (2015); [2] Barkworth and von Bothmer (2009); [3] Feldman and Levy (2015); [4] Liu et al. (2016); and [5] Wang et al. (1994).

1.1.2. The Triticum-Aegilops *complex*

The genera *Triticum* and *Aegilops*, sometimes referred to as the wheat group (Feldman and Levy, 2012), contain the diploid species that through hybridisation gave rise to modern cultivated wheat (see Section 1.1.4.). Some *Triticum* and *Aegilops* diploid species are closely related, differing only in small morphological features, and are relatively easy to cross with each other resulting in polyploid species, to the extent that it has even been proposed that these two genera should be merged (Bowden, 1959; Yen, Yang and Yen, 2005).

Aegilops species, commonly known as goatgrass, are annual grasses that occur around the Mediterranean Sea and Central Asia (van Slageren, 1994). The species are diploid, tetraploid or hexaploid and contain the genomes D, U, C, M, N and S. Hybridisation between *Aegilops* and *Triticum* occurs between diploid and polyploid species both naturally and by human-assisted crossing (van Slageren, 1994).

1.1.3. The genus Triticum L.

The genus *Triticum* L. includes bread wheat and its close relatives (Table 1.2.) (Matsuoka, 2011). This genus consists of six species of annual grasses that are diploid (section *Monococcon*), tetraploid (section *Dicoccoidea*), or hexaploid (section *Triticum*). The genomes found in *Triticum* are A, B, D and G. The *Triticum* species exist in cultivated and wild forms, except for *T. urartu* that exists only in a wild form and *T. aestivum* and *T. zhukovskyi* that exist only as cultivated forms (Matsuoka, 2011).

The most important wheat species grown today are the hexaploid bread wheat (*T. aestivum*) and the tetraploid durum or pasta wheat (*T. turgidum* subsp. *durum*) but during the history of wheat domestication other wheats were cultivated.

- Diploid wheat

T. monococcum subsp. *monococcum* or einkorn wheat (genome A^mA^m) arose from the domestication of wild einkorn (Table 1.2.) and was probably the first wheat species widely cultivated, starting around 10,000 years ago in South Eastern Türkiye (Heun et al., 1997; Feuillet, Langridge and Waugh, 2008). Einkorn wheat cultivation has been largely abandoned and replaced by tetraploid and hexaploid wheats (Kilian et al., 2009). Notable locations where it is still grown are provided in Table 1.2., where it is grown as food, feed, or a source of genetic variation for breeding (Nesbitt and Samuel, 1996; Ozkan et al., 2007; Perrino, 1996).

T. urartu (genome AA) was never domesticated but played a critical role in wheat evolution as the donor of the A genome found in polyploid wheats (Kilian et al., 2009).

- Tetraploid wheat

The tetraploid wheat species originated with the hybridisation of diploid species of *Triticum* and *Aegilops*. One of the two lineages of tetraploid wheat is *T. turgidum* (genome BBAA), known as emmer wheat. Domestication of emmer wheat gave rise to a range of subspecies that were cultivated across the globe for thousands of years (Table 1.2.). One of them, durum wheat (*T. turgidum* subsp. *durum*), is widely cultivated today. Durum wheat is consumed as macaroni and semolina products (Matsuoka, 2011).

- Hexaploid wheat

The hexaploid wheat species emerged through natural hybridisation between tetraploid cultivars and diploid *Triticum* and *Aegilops* species (Huang et al., 2002; Kilian et al., 2009). *T. aestivum* (genome BBAADD) accounts for 90% of the world wheat production today and is composed of several subspecies (Table 1.2.).

Table 1.2. The *Triticum* species and subspecies

Section	Species and subspecies[1]	Seed form[2]	Genome composition	Common names	Geographic distribution[3]
Monococcon (2n = 2x = 14)	***T. monococcum* L.**				
	subsp. *aegilopoides* (syn. *T. boeticum*)	Hulled	A^bA^b	Wild einkorn	Balkans, N. Greece, W. Türkiye
	subsp. *monococcum*	Hulled	A^mA^m	Cultivated einkorn	Türkiye, Italy and Spain, Transcaucasia
	T. urartu Tumanian ex Gandilyan	Hulled	AA		Fertile Crescent
Dicoccoidea (2n = 4x = 28)	***T. turgidum*** L.		BBAA		
	subsp. *dicoccoides*	Hulled		Wild emmer	S.E. Türkiye, Israel, S. Syria, N. Iraq, W. Iran
	subsp. *dicoccon*	Hulled		Cultivated emmer	India, Ethiopia, Yemen, Iran, E. Türkiye, Transcaucasia[4], the Volga Basin, ex-Yugoslavia, Central Europe, Italy, Spain
	subsp. *durum*	Naked		Durum or macaroni wheat	Mediterranean climate areas
	subsp. *polonicum*	Naked		Polish wheat	S. Europe, Türkiye, Iraq, Iran, Armenia, N.W. India
	subsp. *turanicum*	Naked		Khorassan wheat	Europe, United States, Iran, Middle East
	subsp. *turgidum*	Naked		Rivet wheat	Portugal, United Kingdom, Spain
	subsp. *carthlicum*	Naked		Persian wheat	Caucasia[5], Iraq, Iran
	subsp. *paleocolchicum*	Hulled		Georgian wheat	Georgia
	T. timopheevii (Zhuk.) Zhuk.		GGAA		
	subsp. *armeniacum*	Hulled		Wild timophevii	Transcaucasia
	subsp. *timopheevii*	Hulled		Cultivated timopheevii	Transcaucasia, Armenia, N. Iraq, Iran
Triticum (2n = 6x = 42)	***T. aestivum*** L.		BBAADD	Common wheat	
	subsp. *aestivum*	Naked		Bread wheat	Temperate regions of the world
	subsp. *compactum*	Naked		Club wheat	Mountains of Afghanistan, Alps
	subsp. *sphaerococcum*	Naked		Indian dwarf wheat	Afghanistan, Bukhara, N.W. India
	subsp. *macha*	Hulled		Macha wheat	Georgia/Transcaucasia
	subsp. *spelta*	Hulled		Spelt	Central Europe, Middle East, United States, Canada
	T. zhukovskyi Menabde & Ericz	Hulled	$GGAAA^mA^m$		Transcaucasia, Armenia, N. Iraq, Iran

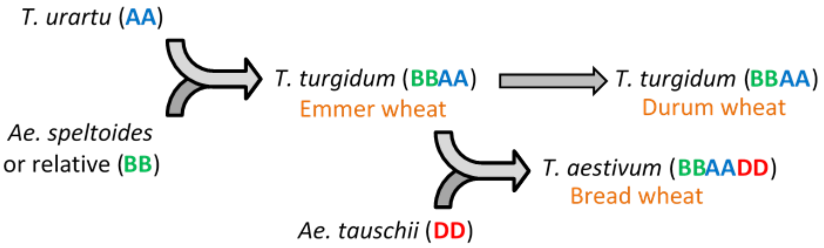
Notes: 1. Based on Van Slageren (1994). For other taxonomic classifications see Wheat Genetic Resource Centre (Kansas State University).
2.Hulled wheat has a hull (dry outer covering) that adheres to the grain. Hull-less wheat or "naked" wheat has an outer hull that is loosely attached to the kernel so it generally falls off during harvesting (see Section 1.2.1.).
3.Based on Matsuoka (2011) and Zaharieva et al. (2010). N, north; S, south; W, west; E, east.
4.Transcaucasia: geographical region in the vicinity of the southern Caucasus Mountains on the border of Eastern Europe and Western Asia. Transcaucasia roughly corresponds to modern Georgia, Armenia, and Azerbaijan.
5. Caucasia: region situated at the border of Eastern Europe and Western Asia between the Black Sea and the Caspian Sea. It extends across territories of the countries Georgia, Armenia, Azerbaijan and Russian Federation.
Source: Adapted from Matsuoka (2011).

1.1.4. The origin of Triticum aestivum

Bread wheat originated from two hybridisation events involving three different diploid progenitors in the Triticum and Aegilops genera (Figure 1.1.). T. urartu was the donor of the A genome of bread wheat (Chapman, Miller and Riley, 1976; Dvořák, 1976; Kimber and Sears, 1987; May and Appels, 1987) while Ae. tauschii was the donor of the D genome (Huang et al., 2002; Kihara, 1944; McFadden and Sears, 1946). Recommended texts for a comprehensive overview of wheat breeding are The World Wheat Book: A History of Wheat Breeding, Volumes 1 and 2 (Bonjean and Angus, 2001; Bonjean, Angus and van Ginkel, 2011). The identity of the B genome donor is still unknown and there is some controversy about this issue (Huang et al., 2002). Much evidence suggests that either *Ae. speltoides* or its undiscovered ancestor from the section Sitopsis were the donor of what became the B genome in tetraploid and hexaploid wheats (Kilian et al., 2006; Petersen et al., 2006; Sallares and Brown, 2004; Sarkar and Stebbins, 1956).

The first step in the creation of bread wheat involved the hybridisation of *T. urartu* (AA) with the B genome donor to generate the tetraploid emmer wheat (*T. turgidum* subsp. *dicoccoides*; genome BBAA) around 0.5 million years ago. Analysis of chloroplast and mitochondrial genomes showed that this hybridisation occurred with the B genome progenitor as the maternal parent (Tsunewaki, 1988). The second step occurred around 8,000 years ago and involved hybridisation between the tetraploid emmer wheat (genome BBAA) and *Ae. tauschii* (genome DD) to form *T. aestivum* (genome BBAADD). Emmer wheat was the maternal parent in this hybridisation event and provided the B genome cytoplasm to *T. aestivum* (Tsunewaki, 1988). Since wild populations of *T. aestivum* have never been found, it is thought that cultivated emmer wheat, not the wild version, hybridised with *Ae. Tauschii.*

Figure 1.1. Origin of *Triticum aestivum*



Note: Diagram representing the two hybridisation events that gave rise to bread wheat and the evolutionary history of durum wheat, the second most cultivated wheat. Letters in brackets represent the genome composition of the species.
Source: Illustration courtesy Maria Alonso, Office of the Gene Technology Regulator (OGTR), Australia.

1.2. Morphological characteristics and uses

1.2.1. Morphological characteristics of bread wheat

The mature bread wheat plant is an annual grass that consists of a central stem from which leaves emerge at opposite sides (Figure 1.2.A). The stem is erect, hollow or pithy, glabrous[7], and up to 1.2 m tall. It is made up of repeating segments which contain a node, a hollow internode, a leaf and a bud and terminates in the ear of the wheat plant (Kirby, 2002). Lateral branches called tillers, which emerge from buds near the base of the stem, can produce an ear at their terminal too (Figure 1.2.A) (Kirby, 2002; Setter and Carlton, 2000b). The root system is composed of seminal roots produced by the young plant during germination, and adventitious roots that arise later from the basal nodes of the plant to become the permanent root system. The root system can grow 1-2 m deep, but most roots are concentrated in the top 30 cm of soil (Kirby, 2002).

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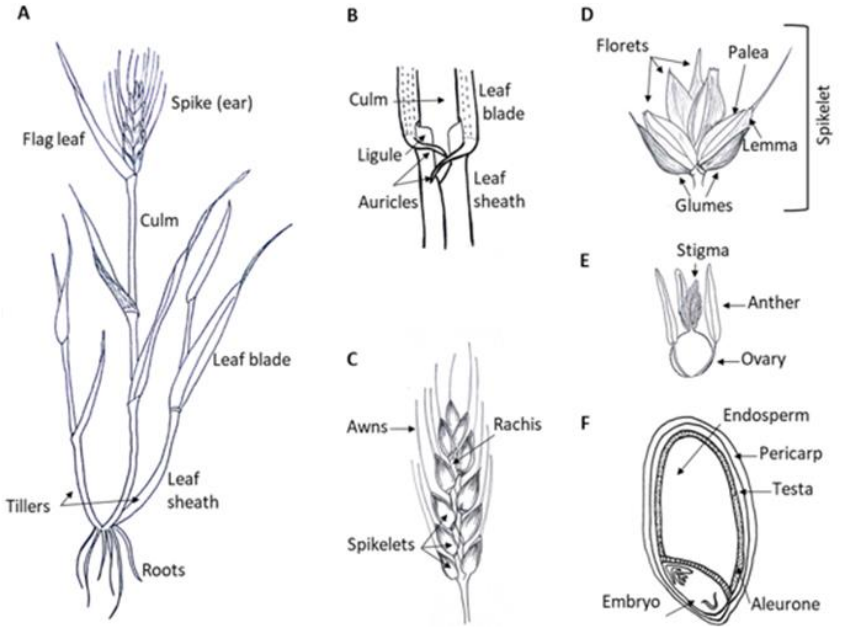
[7] Glabrous: free from plant hairs (trichomes). Smooth.

As in all grasses, the leaves consist of the sheath and the blade (Figure 1.2.A), with the leaf sheath wrapping around the stem (Setter and Carlton, 2000b). The flag leaf blades are 20-38 cm long, about 1.3 cm wide and have an ascending, arching or floppy disposition. At the base of the leaf blade, where it joins the sheath, are a membranous ligule and a pair of small hairy projections known as auricles (Figure 1.2.B) (Kirby, 2002). The aspect of ligules and auricles is used to determine the species of cereal seedlings (Agriculture Victoria, 2012b). The final leaf before the ear is called the flag leaf.

Figure 1.2. Morphology of the *Triticum aestivum* plant



Notes: A, Diagram of a wheat plant. B, Detail of the leaf blade and sheath junction. C, Detail of a spike (ear). D, Different parts of a spikelet. E, Detail of the floral organs. F, Diagram of a cross section of a wheat seed.
Source: Illustration courtesy Maria Alonso, OGTR, Australia.

The ear of bread wheat is an erect floral spike about 5-10 cm long. The spike is made of two rows of spikelets (Figure 1.2.C and D). The spikelets contain the florets (flowers) and are arranged on opposite sides of a central rachis (central stalk of the spike; Setter and Carlton, 2000b). Further details on floral biology are located in Section 2.2.1..

The caryopsis or grain of bread wheat is 7.5-8.5 mm long, 3.5-3.75 mm wide, and ovoid-ellipsoid in shape (Figure 1.2.F). The grain is made up of the bran coat, the endosperm and the embryo (Figure 1.2.F) (Setter and Carlton, 2000b).. The endosperm makes up 83% of the wheat grain and stores the starch and protein (aleurone) important both for the developing plant and flour production (Setter and Carlton, 2000b).

1.2.2. Uses of bread wheat

The primary use of bread wheat is to produce flour, the main ingredient for baking bread. Bread wheat flour is also used to produce other baked goods, confectionery products, noodles and wheat gluten or seitan (a powdered form of purified wheat gluten, used as an alternative to soy based products in vegetarian cooking) (Pomeranz, 1987).

Bread wheat for human food is classified into grades according to a number of quality attributes that dictate its suitability for various end-uses (Table 1.3.). The main quality attributes are grain hardness, protein content and flour strength type (Peña, 2002).

Grain hardness is determined by the way components are packed in the endosperm cells and refers to the grain's resistance to being fractured (Peña, 2002). Hard wheats require longer milling times and more milling energy and produce a larger amount of damaged starch. Hard wheats are preferred for bread making because the damaged starch increases the water absorption of the dough. In contrast, the cookie and cake industries use soft wheat flour since this type of baking requires free water in the form of vapour to expand the doughs and batters.

Table 1.3. Wheat quality characteristics for various food types

Product type	Grain hardness	Protein content (%)	Flour strength type
Leavened breads			
Pan-type, buns	Hard	>13	Strong-extensible
Hearth-French	Hard-medium	11-14	Medium-extensible
Steamed	Hard-soft	11-13	Medium-weak
Unleavened breads			
Arabic	Hard-medium	12-14	Medium-extensible
Chapati, tortilla	Medium	11-13	Medium-extensible
Crackers	Medium-soft	11-13	Medium
Noodles			
Yellow alkaline	Medium	11-13	Medium-strong
White	Medium-soft	10-12	Medium
Cookies, cakes, pastries	Soft-Very Soft	8-10	Weak, Weak-extensible

Source: Peña (2002)

Grain protein content in bread wheat is 8-17%, depending on the genetic make-up and on external factors associated with the crop. Most of the wheat grain protein is gluten. The gluten found in wheat flour forms a viscoelastic mass when in contact with water and determines most of the viscoelastic properties of wheat flour doughs. Gluten viscoelasticity is commonly known as flour or dough strength and it is the main factor dictating the end-use of a wheat variety in bread and pasta making. Flour strength is dependent on both protein content and protein composition of the wheat grain (Peña, 2002).

Other than its primary use as a human food source, bread wheat has a number of alternative uses. These include, but are not limited to, use in animal feed, starch production, bioethanol production, brewing of wheat beer, the production of wheat-based cat and pet litter, wheat-based raw materials for cosmetics and to make wheat straw composites. Wheat straw can also be used as a fuel for heat and electricity (OGTR, 2017; Shevkani et al., 2017).

The use of wheat grain in the animal feed market has increased in recent years concomitantly with the worldwide demand for meat. The amount of wheat used as feed varies each year depending on its price competitiveness with respect to coarse grains like corn and sorghum. Although an average of 19% of wheat was used for feed worldwide in the 2014/2015, 2015/2016 and 2016/2017 seasons, this proportion can reach 42-49% in developed countries in Europe and Australia, which potentially surpasses the amount of wheat destined for food (Heuzé et al., 2015; Tasmanian Institute of Agriculture, 2014). The main consumers of feed wheat are the pork and poultry industries, the beef feedlot industry and the dairy industry. Wheat grain can be fed whole or processed in many different ways like dry rolling, steam rolling, flaking or grinding followed by pelleting (Heuzé et al., 2015). Feed wheat is often surplus to human requirements or is low quality wheat unsuitable for human consumption. However, wheat is increasingly grown specifically for feed purposes, which has led to the introduction of specialty feed wheat lines. Wheat can also be used as winter pasture and forage source (Heuzé, Trann and Baumont, 2015). Wheat forage may be grazed and/or cut for hay and silage. Dual purpose wheat varieties can also be used that provide good quality forage during late fall and winter and harvestable grains the next summer (Heuzé, Trann and Baumont, 2015).

The forecast of industrial utilisation of wheat in 2021/2022 is 24.4 million tonnes (IGC, 2022), the majority of which is for use in the starch industry followed by bioethanol production (FAO, 2021). Wheat-based ethanol production represents a large fraction of production in the EU and Canada that accounted for 4.36% and 1.40% of global ethanol production in 2008, respectively (Saunders, Izydorczyk and Levin, 2011). Production of ethanol from grain wheat involves hydrolysis of extracted starch to glucose or maltose, which is then fermented to produce ethanol and carbon dioxide (Nigam, 2001; Sparks Companies Inc., 2002). The co-product of this process is used in animal feed, which reduces the cost of ethanol production. However, wheat-based ethanol production is less efficient than corn or sugar beet-based production (European Biomass Industry Association, 2017). In countries where wheat is a major agricultural crop, wheat-based ethanol would benefit from the development of high starch, low protein varieties of wheat (similar to feed wheat varieties) with characteristics that are ideally suited for bioethanol production.

1.3. Geographic distribution, natural and managed ecosystems and habitats, cultivation and management practices, and centres of origin and diversity

1.3.1. Geographic distribution

Wheat (*T. aestivum* and *T. durum* combined)[8] is the most abundant crop world-wide, occupying 22% of the total cultivated area in the world (Leff, Ramankutty and Foley, 2004), which accounts for more than 216,000,000 hectares (Monfreda et al., 2008). The most intensive wheat cultivation occurs in the temperate latitudes of both hemispheres (Curtis et al., 2002; Heyne, 1987). Bread wheat production is concentrated between the parallels of latitude 30-60° in the North Temperate Zone and 27-40° in the South Temperate Zone (Briggle and Curtis, 1987; Curtis et al., 2002; Kimber and Sears, 1987; Nuttonson, 1955; Korber-Grohne 1988, Geisler 1991). The northern limit of bread wheat cultivation in Europe lies in southern Scotland (United Kingdom) (60° latitude) and occasionally beyond (central Scandinavia up to 64° latitude) and in North America, wheat is grown to about 55° latitude. Cultivation in the Northern Hemisphere extends as far south as in the mountain regions of Mexico, and at the Equator on the high lands of Ecuador and Colombia (Nuttonson, 1955; Percival, 1921). Wheat grows well from sea level up to heights of about 4500 m above sea level (Briggle and Curtis, 1987; Kimber and Sears, 1987). Wheat is most prevalent in the Great Plains of the United States, the Canadian Prairie Provinces, the Indus and the upper Ganges Valleys, along the Kazakhstan and Russian border, and in southern Australia (Figure 1.3.) (Heyne, 1987; Leff, Ramankutty and Foley, 2004). Wheat is also found throughout Europe, in southern South America, in parts of eastern Africa, and in eastern People's Republic of China (Leff, Ramankutty and Foley, 2004).

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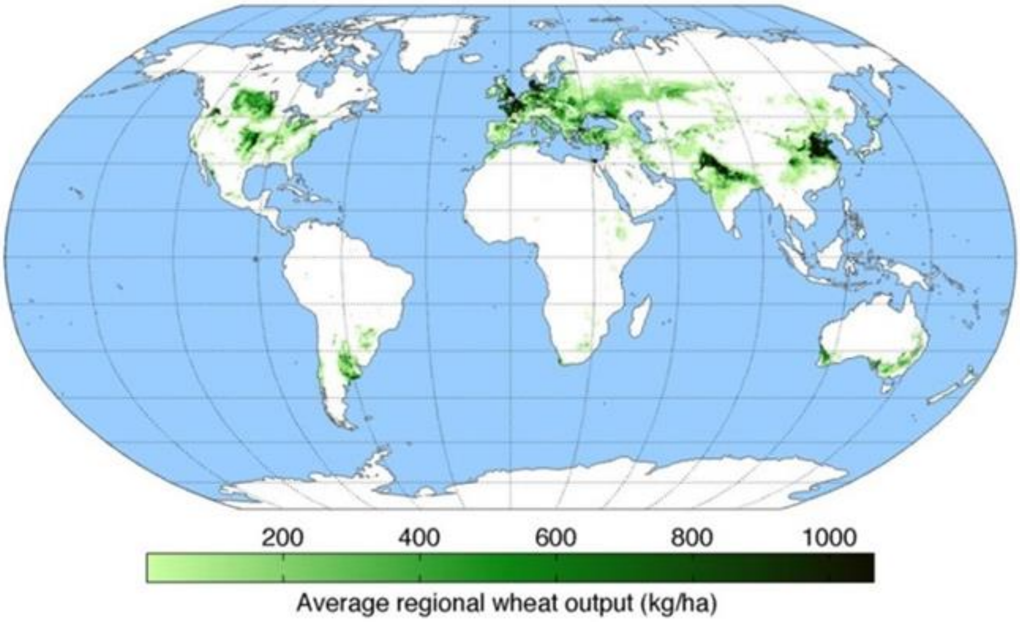
[8] 90-95% of wheat worldwide production corresponds to *T. aestivum* and the rest to *T. turgidum durum*.

Figure 1.3. Map of wheat production across the world



Source: AndrewMT, CC BY-SA 3.0, via Wikimedia Commons.

The global production of wheat (*T. aestivum* and *T. durum* combined) forecast for 2021-2022 is estimated at 785.8 million tonnes (FAO, 2021). Food consumption accounts for most of the global wheat utilisation followed by its use as animal feed (Table 1.4.). Human wheat consumption, per person, was 67.3 kg per annum worldwide (2020-2021) with an average of 62.4 kg per capita in developing countries and 93 kg per capita in developed countries.

Table 1.4. World wheat market in seasons 2020-2021 and 2021-2022

World balance	2020-2021 Estimate*	2021-2022 Forecast*
Production	774.8	785.8
Trade[1]	186.2	187.2
Total utilisation	759.5	778.6
Food	524.7	530.9
Feed	144.7	155.5
Other uses	90.1	92.2
Ending stocks[2]	291.0	298.7

Note: * million tonnes.
[1] Exports based on a common July/June marketing season.
[2] Wheat accumulated in world inventories.
Source: FAO (2021).

The top ten wheat producers in 2021 (listed in decreasing order) were the European Union (hereafter "EU"), People's Republic of China (hereafter "China"), India, Russian Federation (hereafter "Russia"), United States, Canada, Ukraine, Australia, Pakistan and Republic of Türkiye (hereafter "Türkiye"). Of these, the major exporters forecast for 2021/2022 are Russian Federation, European Union, the United States, Canada and Australia, and the total tonnage of wheat exported worldwide is estimated to reach 187.2 million tonnes. The largest importers of wheat are Egypt, China, Indonesia, Türkiye, Algeria, Brazil, Bangladesh, Philippines, Nigeria and Japan (FAO, 2021).

1.3.2. Ecosystems and habitats where the species occur natively, and where it has naturalised

Bread wheat is a crop plant species with low competitive ability, and it has no natural habitat outside cultivation (Tutin, 1980). There are a number of reports of bread wheat becoming naturalised in areas where it is not a native species, including California (Calflora, 2019), the Canadian Prairies and North American central Great Plains (Harker et al., 2005 and references therein). Although bread wheat plants do not have high potential for weediness (Keeler, 1989), they may sometimes be found in 'disturbed' areas where there is little or no competition from other 'weed' species (e.g. waste places, fallow fields, along roadsides). However, their survival at such sites is limited to short periods (Illinois wildflowers, 2019) and there are no indications that bread wheat plants can become established as a self-sustaining population on a long-term basis (Newman, 1990).

1.3.3. Agronomic, silvicultural, and other intensively managed ecosystems where the species is grown or occurs on its own, including management practices

Bread wheat is grown across a wide range of environments around the world. It is a cool season crop requiring a minimum temperature for growth of 3-4°C, with optimal growth occurring around 25°C and tolerance of temperatures to a maximum of about 32°C. Seed germination may occur between 4-37°C, with the optimal temperature ranging from 12-25°C (Acevedo, Silva and Silva, 2002).

Winter and spring wheats differ in the length of their life cycle and temperature requirements (see Section 2.1.). Spring wheat is planted in locations with severe winters and flowers in the same year yielding grain in approximately 90 days. The cold tolerance for seedlings of spring wheat is -5°C and usually require temperatures between 7-18°C for 5-15 days for floral induction (Evans, Wardlaw and Fischer, 1975; Acevedo, Silva and Silva, 2002). Winter wheat is grown in locations with less severe winters and will only head after it has received a cold treatment (vernalization). Winter wheat has a maximum cold tolerance of about -25°C and requires temperatures between 0-7°C for 30- 60 days (Evans, Wardlaw and Fischer, 1975; Acevedo, Silva and Silva, 2002). Winter wheat is therefore planted in the fall and harvested in the spring of the following year. Flowering begins above 14°C (Acevedo, Silva and Silva, 2002).

Wheat grows best in well drained soils. Wheat will grow in areas receiving 250-1750 mm annual precipitation, but most wheat production occurs in areas receiving 375-875 mm annually (Briggle and Curtis, 1987; Kimber and Sears, 1987). Wheat can be grown in dryland (rain-fed) or under irrigation. More than 95% of the developed world's wheat is grown in dryland (Sayre, 2002). Large wheat production areas in the United States, Canada and Australia are produced under low rainfall conditions, whereas most wheat production in Western Europe is produced under favourable rainfall conditions (Sayre, 2002). Winter wheat is grown in Argentina, Australia, Brazil, China, the EU, India, Pakistan, Ukraine and the United States. Spring wheat grown under irrigated conditions is more common in Canada and Russia and is also grown in northwest India, Southern-Central China and the United States (Sayre, 2002; Becker-Reshef et al. 2023).

General agronomic practices for dryland bread wheat

Winter-dominant rainfall areas contribute a major part of the world's dryland wheat production. In these areas 70-100% of the annual rainfall occurs during the growing season, from late fall when wheat is sown to early summer when it is harvested (Anderson and Impiglia, 2002).

No-till or low-till practices in wheat dryland faming are common as they help to conserve moisture and improve soil structure, reduce erosion, increase yields and in some cases decrease disease (Jarvis et al., 2000). Another major trend is stubble retention where the growing surface is covered by previous crop residues. This improves water retention and increases nitrogen availability (Anderson and Impiglia, 2002). Dryland wheat is sown at a rate of 30-50 kg/ha in most regions to achieve a plant population of at least 700,000 plants/ha (70 plants/m^2). In irrigated Mediterranean conditions, highest yields can be achieved at 400-500 plants/m^2 (Lloveras et al., 2004). Plant populations below this density may result in a reduction in yield and increased weed competition (DAF, 2012). Advances in equipment for minimum and no-till systems has incorporated sowing implements that create furrows where seeds are deposited and subsequently covered with soil. The furrow harvests water into the seed row and ensures good seed soil contact (Agriculture Victoria, 2012a). Optimum sowing depth for wheat is around 50-70 mm and seeds are placed in rows from 15-50 cm apart (Anderson and Impiglia, 2002).

Continuous wheat growing is becoming less common and wheat cultivation is more frequently part of cereal-fallow, cereal-grain-legume, cereal-pasture and cereal-oilseed-legume rotations. Continuous wheat is still common in some places, particularly the United Kingdom and other parts of Europe, though it may come with lower yield stability than by using crop rotations, but this potentially evens out in the long-term (Macholdt et al., 2020; Macdonald, 2018; St-Martin et al., 2017; Steinmann and Dobers, 2016). Fixed rotations are common in the more traditional areas around the Mediterranean basin, but in other areas more flexible cropping sequences are likely to be found, driven by fluctuations in the prices of wheat and other products. Crop rotation is practiced to control diseases, weeds and insects, to improve soil fertility (mainly from the inclusion of legumes that fix nitrogen), to spread the risk of crop failure and to stabilise farmer income (Anderson and Impiglia, 2002).

The three main nutrients required for successful production of a wheat crop are nitrogen (N), phosphorus (P) and potassium (K). Depending on soil type and historical use of the land, these nutrients may be deficient in the soil. It is estimated that every two tonnes per hectare of wheat grain takes 42 kg of N, 9 kg of P, 10 kg of K and 2.5 kg of sulphur out of the soil (Laffan, 1999). Protein production in the wheat grain is reliant on substantial nitrogen levels in the soil, therefore higher amounts of N are required if high grain yield and protein levels are expected (GRDC, 2015). Nitrogen fertiliser is commonly added to the field before sowing but it can be added again in fractionated doses prior to flowering, which can be beneficial in Mediterranean growth climates (Laffan, 1999). The trace element deficiencies (zinc, manganese and iron) are most prevalent in winter-rainfall areas and those associated with alkaline soils. These deficiencies can be corrected with small additions to the base fertiliser. The presence of boron and aluminium in the soil can cause toxicity and this is best addressed by using tolerant cultivars (Anderson and Impiglia, 2002).

Weed management can be the most significant cost in wheat production (Bowran, 2000). Seeds of some weeds, when harvested and mixed with the wheat grain, can reduce flour quality (Wolff, 1987). Other costs associated with weeds are yield loss from competition between the crop and the weeds and the cost of applying appropriate control measures (Anderson and Impiglia, 2002). As wheat is most sensitive to weeds during the early stages of its life cycle, the reduction of the weed seed bank in the seasons before cropping and early management of weeds will reduce the weed-associated risks of crop losses (Anderson and Impiglia, 2002). Integrated weed management strategies including agronomic approaches (rotations, row spacing, seed densities, stubble management etc.), biological approaches (for example choice of herbicide resistant cultivars) and chemical approaches to control weeds are likely to be the most effective (Bowran, 2000; GRDC, 2014, 2015).

Leaf and root diseases can affect dryland wheat production but grain yields have seldom been high enough to warrant chemical spray for disease control on a routine basis (Anderson and Impiglia, 2002). The exception is through Europe, where the highest yields have historically been obtained, accompanied by high use of fungicides (Jenkins and Lescar, 1980; Jørgensen et al., 2008). Breeding for resistance and agronomic control methods are more widely used. Root diseases that are transmitted to the wheat crop from alternative grass hosts have been successfully controlled by the use of break crops such as pulses and non-legume broadleaf crops.

Generally, insects do not pose a major threat to wheat in dryland areas. The chances of insect damage are greater in better seasons and in higher yielding crops. Monitoring of pest numbers and establishing economic thresholds can reduce the unnecessary use of pesticides and allow the selection of chemicals that are most effective on the pest species. Breeding for resistance to pests is also an important component of integrated pest management systems (Anderson and Impiglia, 2002).

For more information on wheat pests and diseases see Section 5 and Annex A.

General agronomic practices for irrigated bread wheat

In contrast to dryland wheat, irrigated wheat production systems depend almost entirely on conventional intensive tillage practices especially where irrigation is by flood irrigation or by furrows (Sayre, 2002). In addition, crop residue yields can be quite high in irrigated systems making it difficult to retain stubble or implement zero-tillage planting systems. Irrigated wheat is generally sown on raised beds separated by 70-90 cm wide furrows. The furrows are used for water delivery and to allow better access to the plants which improves mechanical weed control, irrigation water management and fertiliser use efficiency (Sayre, 2002). By using the same beds for successive crops, the need for tillage is reduced and crop residues can be kept and spread in the furrows. Irrigated wheat is sown at a rate of 100-200 kg/ha to achieve a population of 100-150 plants/m^2 of bed area (GRDC, 2012; Rawson and Gómez Macpherson, 2000).

In South and East Asia, irrigated wheat is mostly grown in a continuous rice-wheat rotation (Chhokar et al., 2007; Sayre, 2002). When not grown in rotation with rice, wheat is cultivated in rotation with various upland crops including cotton, soybean, sugar cane, maize and sorghum. In Mexico, Chile, Egypt and Zimbabwe, wheat is grown in annual rotations with maize, soybean or cotton (Sayre, 2002).

Fertiliser use and management is crucial in irrigated production systems since yield potential is high, leading to an extensive removal of essential nutrients from the soil. Nitrogen tends to be the nutrient that is applied at highest rates and costs the most for most farmers growing irrigated wheat (Sayre, 2002). To increase use efficiency, nitrogen is best applied at different developmental stages coinciding with the periods of highest nitrogen demand (Lacy and Giblin, 2006; Ortiz-Monasterio, 2002; Sayre, 2002). Phosphorus may be applied at sowing near the seed when required (Lacy and Giblin, 2006).

Weed control must be undertaken before and after sowing to avoid yield loss (Chhokar et al., 2007). Early removal of weeds with pre-emergent herbicides consistently produces greater yields than if weeds are left until the crop has tillered.

Due to the high plant density in irrigated wheat cultivation, plants are prone to lodging[9] and foliar diseases (Lacy and Giblin, 2006). The profitability of fungicide application increases in high-yielding irrigated wheat. Disease control through a combination of disease-resistant varieties and fungicide seed and leaf treatments is recommended (Sayre, 2002). It is also advisable to sow wheat after a break crop or long fallow to improve soil health and reduce root disease (Rawson and Gómez Macpherson, 2000). Lodging can also be addressed through sowing lodging resistant varieties.

Harvesting and processing bread wheat

Harvest generally occurs in late spring and early summer. Grain must be harvested in a timely manner to minimise pre-harvest losses due to shattering, pre-harvest sprouting, bird damage or weathering. Ideally wheat is harvested when the moisture content is 10-20% (Setter and Carlton, 2000a). Alternately, grain may be harvested at a moisture content higher than is safe for storage and then dried in windrows, sheaves, stooks or shocks (Payne, 2002). During threshing, cracking and breaking the grain should be avoided since damaged grain incurs greater damage from storage moulds and insects, and reduces marketability.

After a crop has been harvested and threshed, the grain, if necessary, is cleaned, i.e. by removal of inert matter, seed of weeds, other crops and other varieties, and seeds that are diseased, damaged and deteriorated. Wheat seed cleaning is performed using mainly screens, indented cylinders and air (for review see Payne, 2002; van Gastel, Bishaw and Gregg, 2002). Wheat seed can be treated with fungicides or insecticides for protection during storage.

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[9] Lodging is when a plant has been flattened in the field or damaged so that it cannot stand upright, e.g. as a result of weather conditions or because the stem is not strong enough to support the plant.

Bread wheat seed production

Since wheat is a self-pollinating crop and the grain can be used as seed, farmers tend to replant their own seed (van Gastel, Bishaw and Gregg, 2002). Wheat farmers typically purchase a relatively small amount of a new variety of improved seed and then save their own seed for planting for quite a long period of time. Depending on the growing region there can be royalty requirements or restrictions on seed saving, particularly where the seeds are protected by intellectual property laws.

When a variety is officially released, the small amount of breeder seed received from the breeder (agricultural research centre or private company) is multiplied through a number of generations before it becomes available to the farmers in larger quantities as certified seed. Each generation is produced under strict supervision and must meet seed quality standards. There are three categories of seed under the OECD Decision Revising the Schemes for the Varietal Certification or the Control of Seed Moving in International Trade (‘OECD Seed Schemes’) [OECD/LEGAL/0308]; Pre-Basic Seed, Basic Seed, and Certified Seed (OECD, 2022). These categories, all derived from the parental material or breeder seed, are summarised by van Gastel, Bishaw and Gregg (2002):

> “Breeder seed is the initial source of seed and is usually produced by the breeder. It is the source for the production of pre-basic or basic seed. Pre-basic seed is the progeny of the breeder seed and is usually produced under the supervision of a breeder or his designated agency. This generation is commonly used for crops that have low multiplication ratios and where large quantities of certified seed are required. Basic seed is the progeny of breeder or pre-basic seed and is usually produced under the supervision of a breeder or his designated agency and under the control of a seed quality control agency. Certified seed is the progeny of basic seed and is produced on contract with selected seed growers under the supervision of the seed enterprise, public or private. Certified seed can be used to produce further generations of certified seed or can be planted by farmers for grain production.” (van Gastel, Bishaw and Gregg, 2002)

The OECD Seed Schemes Rules and Regulations for cereals prescribe, for all self-fertilising species which include wheat, that the basic or certified seed crops must be isolated from other cereal crops by a definite barrier or a space sufficient to prevent seed mixture during harvest. Additional isolation distance and specifications are prescribed for seed crops to produce certified seed of a hybrid variety. Controls on previous uses of the field (previous cropping) include that the field must not have been used to grow wheat for the two previous years (OECD, 2022).

Volunteer bread wheat

As with all crops cultivated and harvested at the field scale, some wheat seeds may escape and remain in the soil until the following season when they germinate giving rise to volunteer plants either before or following seeding of the succeeding crop. Seed loss in wheat crops is the result of natural plant shedding, weather events like hail storms or harvest operations. Wheat seed losses at harvest have been documented as 0.8-6% (Anderson and Soper, 2003). A 2% grain loss at harvest with a crop yield of 3,000 kg/ha and a 1000-seed weight of 25 g will leave approximately 240 seeds/m^2 in the field, noting that current yields can be higher (see Section 2.2.3.) resulting in greater potential for volunteers (Anderson and Soper, 2003). This is similar to a different study in which seed loss after harvest was 219 or 60 seeds/m^2 depending on the harvester used (Komatsuzaki and Endo, 1996). Studies examined persistence of volunteer wheat under a number of different farming systems in Canada and found that most volunteer spring wheat emerged one year after the dispersal of seeds and none persisted after three years (De Corby et al., 2007; Harker et al., 2005). Not all dispersed seeds will germinate the following years as most of them degrade in the soil. The average density of wheat volunteers in the first year post-dispersal was 3.3 plants/m^2 when 190 seeds/m^2 were dispersed (Harker et al., 2005) and 21.5 plants/m^2 after dispersing 500 seeds/m^2 (De Corby et al., 2007). An Australian study found a wheat volunteer density of 0.7-5.6 plants/m^2 post-harvest depending on farming practices (Wicks et al., 2000). Overall, the timing of volunteer emergence and seedling density is variable across growing seasons and locations (Anderson and Nielsen, 1996; Anderson and Soper, 2003; De Corby et al., 2007; Harker et al., 2005). Factors accounting for this variability may be weather conditions, crop management practices and the wheat varieties that differ in their rate of seed shattering and the degree of dormancy of their seeds. In general, volunteer wheat seed emergence is low and as long as volunteer wheat is controlled and not allowed to set seed that would increase the seed bank, it does not represent a major problem to farmers (Harker et al., 2005).

When uncontrolled, volunteer wheat can compete for nutrients and water with succeeding crops and cause severe yield losses (Friesen et al., 1990; Lemerle et al., 2016; Marshall et al., 1989; O'Donovan, Kirkland and Sharma, 1989). Volunteer wheat can also harbour insect pests and diseases that can negatively affect the upcoming wheat crop and neighbouring fields. Diseases that build up on volunteer wheat include cereal rusts, root lesion nematodes, Rhizoctonia bare patch and crown rot (Coutts et al., 2017). Pests commonly found in volunteer wheat include white grub, wireworm, army cutworm, Hessian fly, aphids and mites (Bell et al., 2016). In addition to feeding damage, the latter two pests can transmit viruses that cause wheat diseases. In particular, the wheat curl mite is the vector of *Wheat streak mosaic virus*, *Triticum mosaic virus* and *Wheat mosaic virus*, all of which can be devastating for wheat crops (Coutts et al., 2008; Klein et al., 2016; Thomas, Hein and Lyon, 2004).

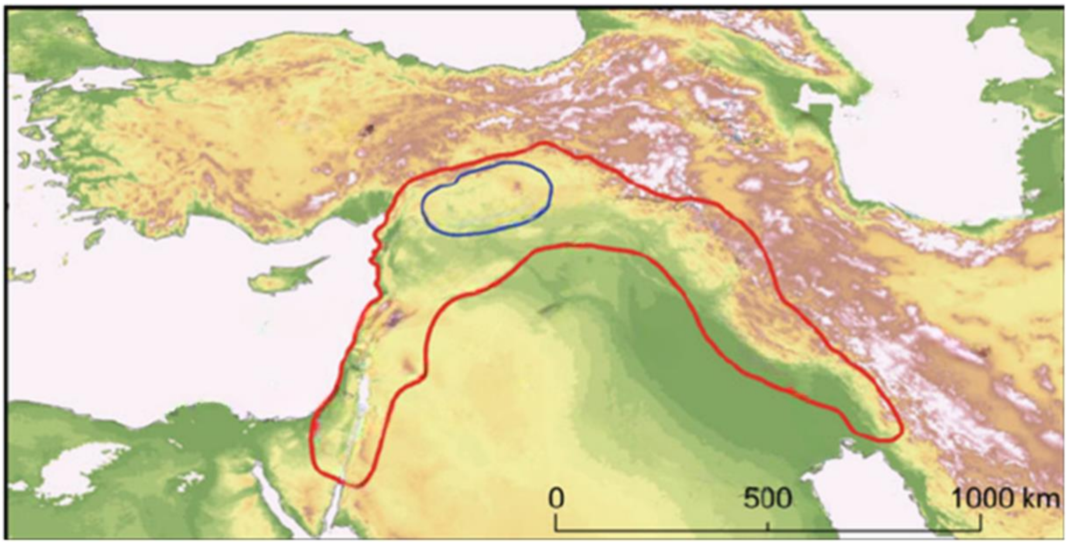
It is recommended to control volunteer wheat at least three weeks prior to the establishment of the next wheat crop in order to reduce the risk of disease transmission (Thomas, Hein and Lyon, 2004). Volunteer wheat can be controlled by tillage and/or herbicides. While tillage is often the most cost-effective method to control volunteer wheat, tillage prior to planting may result in moisture loss due to evaporation from the seed germination zone that is vital for timely crop establishment especially on dryland fields. Herbicides provide a good option for controlling volunteer wheat as well as other weeds (Bell et al., 2016).

1.3.4. Centres of origin and diversity

All *Triticum* species are native to the Fertile Crescent of the Near East, where Western agriculture originated after the last ice age, 12,000-9,500 years ago. The region of the Fertile Crescent extends through the modern-day countries of Israel, Jordan, Türkiye, Syria, Iran and Iraq (Figure 1.4.). Within the Fertile Crescent, agriculture originated in a core area in South Eastern Türkiye where the closest wild relatives of einkorn, emmer, barley, rye, chickpea and lentil still grow (Kilian et al., 2009). Wild cereals were cultivated for centuries in this region but they were gradually replaced due to selection for domesticated cultivars. This domestication process lasted up to one millennium (Kilian et al., 2009).

Tetraploid emmer wheat was domesticated in South Eastern Türkiye. From this area, emmer expanded across Asia, Europe and Africa. North East expansion met the distribution of *Ae. tauschii* and allowed the emergence of hexaploid *T. aestivum* around 8,000 years ago. This hybridisation event took place in the corridor from Armenia to the South Western coast of the Caspian Sea (Feuillet, Langridge and Waugh, 2008; Kilian et al., 2009; Matsuoka, 2011).

Figure 1.4. The Fertile Crescent of the Near East



Note: Red line delimits the region known as the Fertile Crescent while the blue line surrounds the core area in the Karacadag range (KK) where agriculture originated
Source: Modified by Brandon McMahon based on Kilian et al. (2010).

Wheat domestication

Crops differ from their wild ancestors in several plant features, collectively referred to as the domestication syndrome. The most important wheat traits selected for during domestication were the hulled seeds and brittle rachis. Additional selections resulted in the increase in seed size, loss of seed dormancy, reduction of plant height, and changes to photoperiod and vernalisation response (Kilian et al., 2009).

Wild wheats and early-cultivated wheat varieties were characterised by hulled seeds that required drying to be liberated from the chaff. In addition, the spikelets of the wild ears fell apart at ripening through fragmentation of the spike stem (rachis) resulting in seed shattering and dispersal. Most modern varieties of wheat, including bread wheat, have non-hulled or naked seeds. The modified leaves that form the hull (glumes and palea; see Section 1.2.1.) are thinner in these varieties and fall off at harvesting. Modern varieties of wheat also have spikes with a tough non-brittle rachis that keeps the mature spike together until it is harvested. With the introduction of these two traits in cultivated wheat, the harvesting of the grains became efficient (Kilian et al., 2009).

For early wheat varieties to flower, the plants had to experience a period of cold in the winter (a process called vernalisation), followed by exposure to long days in spring (they were responsive to day-length or photoperiod). These responses were adapted to the environmental conditions in the Fertile Crescent. With the spread of agriculture to different environments, better suited wheat types were selected that responded differently to these environmental cues. Today spring and winter-type varieties of wheat are available (see Section 2.1.).

SECTION 2. Reproductive biology

2.1. Generation time and duration under natural circumstances, and where grown or managed

Wheat (*Triticum aestivum* L.) is an annual crop, and its life cycle (from seed to seed) comprises successive but distinct growth-development phases, including emergence, tillering, booting, heading, flowering and ripening (Nuttonson, 1955). Considerable difference exists in the duration of life cycle of different types and varieties of wheat. Furthermore, the duration of each development phase in the wheat life cycle often varies considerably between varieties with different ecological-geographical origins (Nuttonson, 1955).

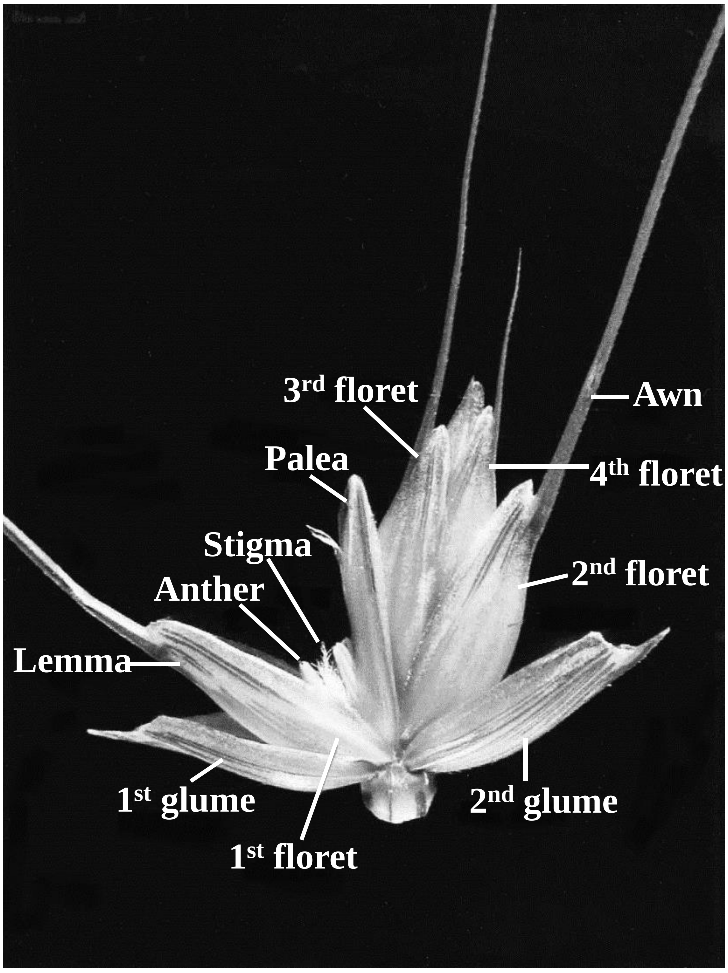
Wheat varieties are broadly categorised into two distinct types, i.e. winter wheat and spring wheat, based on their growth habits (Curtis et al., 2002; Nuttonson, 1955). The life cycle of winter wheat and spring wheat generally lasts about 180-300 days and 100-170 days, respectively, depending on the genotype, geographic location, and environment conditions (Asseng et al., 2012). The main difference between the two types of wheat is that winter wheat requires a vernalisation process (a period of exposure to low temperature for transition from vegetative to reproductive stage), whereas the spring wheat does not require such a vernalisation process (Nuttonson, 1955; Smith, 1995). A third, less clearly defined, type is facultative wheat, noted for a low vernalisation requirement that allows them to be sown earlier in spring (Braun and Sãulescu, 2002). After vernalisation is completed, varieties that are sensitive to photoperiod require a certain day-length to flower. Sensitivity to photoperiod differs amongst modern wheat varieties. Most cultivated wheats today flower faster as the day-length increases, but they do not require a particular length of day to induce flowering (Acevedo, Silva and Silva, 2002). Winter wheat is generally sown in the fall in the Northern Hemisphere, is in a dormant state over winter, flowers in spring, and is harvested around the summer of the next year, while spring wheat is normally sown in the spring and harvested in later summer or early fall (Curtis et al., 2002; Nuttonson, 1955). When winter wheat is sown in the spring, it usually remains prostrate throughout the growing season but will not develop culms or spikes (Nuttonson, 1955). Winter wheat is normally grown in regions where fall seedlings can survive winter, including the central and southern plains of the United States, western Europe, the Balkans, southern Russia, and China (Allan, 1980). Spring wheat is normally grown in colder regions that are unfavourable for winter wheat, including the northern plains of the United States, the Canadian Prairies, Argentina, and northern and central Russia, so plants grow, flower and set seed before the short summer ends. However, spring wheat is also grown as a fall-sown crop in regions with mild winters, such as Mexico, Brazil, India, Australia, and southwestern United States, where plants flower during the warm and wet winter, and are harvested before hot and dry summer conditions set in (Allan, 1980; Nuttonson, 1955).

2.2. Reproduction

2.2.1. Floral biology

The wheat inflorescence is a determinate and composite spike, consisting of two rows of spikelets arranged on opposite sides of a central rachis (Allan, 1980; Lersten, 1987). The rachis is tough, such that it does not disarticulate on maturity and prevents seed shattering. Each spikelet is about 10-15 mm in length, has a short spikelet axis (rachilla) at the bottom, and comprises multiple (usually two to nine) florets, which are encompassed by two small bract leaf-like glumes (Figure 1.2.D, Figure 2.1.) (De Vries, 1971; Lersten, 1987; Waines and Hegde, 2003). In some wheat varieties, the glumes can have awns up to 30 mm long, while the lemmas can have awns up to 80 mm long. As described in the literature (Lersten, 1987; Murai, 2013; Waines and Hegde, 2003; Willenborg and Van Acker, 2008), each floret is enveloped by two leaf-like structures, i.e. a lemma (awn or awnless) and a palea, and comprises the sexual organs that include one pistil, three stamens (each consists of an anther and a filament) and two lodiculae (Figure 1.2.E, Figure 2.1.) (Setter and Carlton, 2000b). The pistil, the centrally located female part of a floret, consists of the ovary, which contains one ovule and two filamentous styles, each terminating with a feathery stigma. The stamen, the male part of a floret, is composed of a filament and an anther containing pollen grains. The two lodiculae are attached to the ovary and swell during anthesis, forcing the lemma and palea apart to facilitate pollination of the stigma from the dehisced anther.

Figure 2.1. Features of the wheat spikelet



Note: The wheat inflorescence (spike or head) is composed of spikelets, which include multiple florets encompassed by two small bracts (glumes). Each floret is enveloped by two leaf-like structures, lemma and palea, and inside sits the reproductive organs, including three stamens and a pistil consisting of the ovary that contains the ovule and two filamentous styles.
Source: Photograph by K-State Research and Extension, Kansas State University. Captions adapted from Waines and Hegde (2003).

2.2.2. Pollination mode, pollen dispersal, pollen viability

The general flowering process in wheat has been investigated for over a century and is well documented (De Vries, 1971; Leighty and Sando, 1924). Wheat starts to flower several days after the spike emerges, flowering generally begins near the upper part of the spike and continues in both an upward and downward direction (De Vries, 1971; Poehlman, 1959b). Flowering occurs throughout the day, and a spikelet requires three to four days while a plant needs up to eight days to finish blooming, which is influenced by both meteorological conditions and genotypes (De Vries, 1971; Leighty and Sando, 1924).

Wheat is predominantly chasmogamous (open) when flowering (De Vries, 1971), but some wheat varieties always keep their flowers closed (cleistogamy) (Ueno and Itoh, 1997). During the flowering process, the two lodiculae within a floret swell, become very turgid, and push the lemma and palea open. While or after the floret opens, the filaments of the stamens rapidly elongate, making anthers extrude from the glumes (De Vries, 1971). The stigmas remain within the glumes in most wheat varieties, but can expose themselves outside the glumes in some varieties or when pollination is delayed. The frequency of chasmogamous flowers varies among different varieties and different meteorological conditions (De Vries, 1971). The percentage of extruding anthers ranges from 12-99% depending on the environmental conditions and genotypes (De Vries, 1971). Low moisture and high stress conditions often promote chasmogamous flowering and increase outcrossing (Waines and Hegde, 2003). The duration of floret opening varies from 11-66 minutes, but it can vary considerably due to differences in genotype and weather conditions (Leighty and Sando, 1924). When conditions are unfavourable for the opening of the glumes, the anthers may not protrude from the glumes, and thus shed all of their pollen inside the flower (Leighty and Sando, 1924; Poehlman, 1959b).

Despite the fact that most of the wheat florets are flowering chasmogamously (De Vries, 1971; Ueno and Itoh, 1997), wheat is predominantly self-pollinating because wheat anther normally dehisces to disperse pollen while the stamens are still within the floret leading to self-pollination (Lersten, 1987; Willenborg and Van Acker, 2008). It is reported that less than 10% of pollen grains fall on the stigma of the same floret, 9-12% remain on the anther (De Vries, 1971) and as much as 30-80% shed outside of the floret into the air from the extruded anthers (Hegde and Waines, 2004; Leighty and Sando, 1924). Once attached to a stigma surface, the pollen tube starts to grow within about 1-2 hours, and fertilisation occurs 30-40 hours later (Chandra and Bhatnagar, 1974; De Vries, 1971). At some time point shortly after the anthers shed pollen, the lodiculae lose their turgidity and collapse, leading to the closing of the floret (De Vries, 1971).

Wheat normally has a very low natural cross-pollination rate of less than 1% (Garber and Quesenberry, 1923; Harrington, 1932; Poehlman, 1959a). Cross-pollination in wheat is mainly facilitated by wind dispersal of pollen because wheat flowers are small, inconspicuous, nectarless, scentless, and unattractive to insect pollinators. The cross-pollination rate varies with cultivars, distance from the pollen source, and environmental conditions (Beri and Anand, 1971; Dong et al., 2016; Hucl, 1996; Joppa, McNeal and Berg, 1968; Khan, Heyne and Arp, 1973; Loureiro et al., 2012; Martin, 1990; Matus-Cádiz, Hucl and Dupuis, 2007). It is estimated that wheat pollen generally travels only one metre in still air due to its relatively heavy weight, which limits mobility (Waines and Hegde, 2003; Willenborg and Van Acker, 2008). Under field conditions, the number of wheat pollen grains decrease significantly as the distance increases from the pollen source (Dong et al., 2016; Hucl and Matus-Cádiz, 2001; Jacot et al., 2004; Khan, Heyne and Arp, 1973; Loureiro et al., 2007b). In studies, most of the pollen grains were found to be concentrated within 5 m of the pollen source and only a few pollen grains were present at >30 m (Dong et al., 2016; Hucl and Matus-Cádiz, 2001; Jacot et al., 2004). However, a pollen slide study conducted by Pioneer Hi-Bred International (Kansas) showed that viable wheat pollen could be found as far as 1,000 m away from a very large pollen source (Hegde and Waines, 2004; Virmani and Edwards, 1983). Hucl and Matus-Cádiz (2001) reported no outcrossing beyond 27 m in their study. Wheat pollen movement is also affected by a number of other factors such as percent of anther extrusion, pollen production per anther, and the number of anthers per unit area (Beri and Anand, 1971; Joppa, McNeal and Berg, 1968; Willenborg and Van Acker, 2008). In addition, high humidity tends to decrease cross-pollination rate (0.1%) while warm and dry weather leads to higher cross-pollination rates (3.7-9.7%) (Mandy, 1970). Thus, genotype and environmental factors such as wind, temperature, and humidity play a strong effect on pollen dispersal.

Both the quantity and viability of wheat pollen are relatively low. As reviewed by De Vries (1971), the number of pollen grains per anther ranged from 581-3,867 in different wheat varieties under various field conditions. The average number of pollen grains per inflorescence of wheat is calculated to be about 10% of rye and 2.5% of maize. Wheat pollen is only viable for a short time period and under field conditions, wheat pollen viability is lost within 15-20 minutes (De Vries, 1971). Optimal viability of wheat pollen is approximate 30 minutes under field conditions at warm temperatures (20°C) and moderate relative humidity (60%) (De Vries, 1971). After flowering, the stigma receptivity can generally last for 7-8 days, but the first 2-4 days are most suitable for pollination (De Vries, 1971).

2.2.3. Seed production and natural dispersal

The number of wheat seeds per area is the product of spikes per area and seeds per spike (Acevedo, Silva and Silva, 2002; Poehlman, 1959b). Spikes per area is dictated by seedling rate, tillering and tiller survival. Seeds per spike is impacted by a number of factors such as genotype, emergence time, tiller population density, weed competition, fertility, and biotic and abiotic stresses (Acevedo, Silva and Silva, 2002). Modern wheat varieties have been bred with high seed production potential. In 1951, the worldwide average wheat seed yield was close to 1 tonne/ha, this then increased to 2 tonnes/ha by the early 1980s (Curtis et al., 2002), and has now climbed to approximately 3.5 tonnes/ha, ranging from 1 tonne/ha to 11 tonnes/ha (OECD, 2021). The significant increases in wheat seed yield are mainly attributed to genetic improvements and better cultural methods (see Section 1.3.3.), particularly the breeding development of the high-yielding, disease-resistant semi-dwarf wheat cultivars (Heyne, 1987; Poehlman, 1959b). It is noted that the development of new wheat cultivars alone cannot deliver such a significant yield increase. It is the simultaneous improvements in varieties and in cropping practices, including the application of agrochemicals (e.g. fertilisers, pesticides, and herbicides), controlled irrigation and new cultivation methods, as a whole that contributes to the wheat yield increase (Pingali, 2012). For example, it is estimated that the average wheat yield in the United States would be reduced by 16% without nitrogen fertiliser (Stewart et al., 2005). Like fertilisers, crop-protection chemicals (pesticides and herbicides) also have contributed to the significant wheat yield increase (Oerke and Dehne, 1997).

Wheat is planted primarily for seed production, and it has been domesticated to reduce the loss of spike fragility to maximise harvest-ability of the produce (Feldman and Levy, 2015; Fuller and Allaby, 2009), thus, natural dehiscence of the seed from the spike at maturation occurs only to a small extent (Anderson and Soper, 2003). However, there exists substantial genotypic variations in natural dehiscence among different wheat cultivars (Anderson and Soper, 2003; Clarke, 1985). Natural dehiscence also varies with season and time (Clarke, 1985; Willenborg and Van Acker, 2008). For example, Clarke (1985) reported that the cumulative natural shattering loss of the five tested wheat cultivars ranged from 4-27 g/m^2 over a period of two weeks.

Wheat seeds shattered from the parent plants may experience different dispersal movement and fates under the biotic and abiotic influences (Bakker et al., 1996; Nathan and Muller-Landau, 2000). Most shattered wheat seeds are anticipated to fall beneath the plant with only a short distance of movement. Some shattered wheat seeds enter the seed bank with different fates, e.g. dead, alive, active or dormant, etc. (see Section 2.2.4.). Wheat seeds on the soil surface or even in the seed bank may be further dispersed by animal or physical forces (wind and water). Wheat seeds can be dispersed through the faeces of birds as the seeds were shown to survive passage through emus (*Dromaius novae-hollandiae*) (Davies, 1978) and other birds (Twigg et al., 2009). Similarly, wheat seeds also can be dispersed via the faeces of mammals such as the white-tailed deer (*Odocoileus virginianus* Zimm.) (Myers et al., 2004), red deer (*Cervus elaphus* L.) and fallow deer (*Dama dama* L.) (Malo and Suárez, 1995). In addition, pest animals such as kangaroos (*Macropus* spp.), rabbits (*Oryctolagus cuniculus*), mice (*Mus musculus*) and rats (*Rattus* spp.) are potential dispersers of viable wheat seeds (OGTR, 2017). Wheat seeds, especially for seeds with awns, can also be dispersed by animals through adhering on their fur (Sorensen, 1986; Yoshioka et al., 2017). However, the long-distance dispersal of seeds by migratory animals is typically rare, but also difficult to measure and predict (Nathan et al., 2008).

Wheat seeds on the soil surface can also be dispersed through abiotic forces such as wind, surface water movement, and soil erosion (Bakker et al., 1996; Nathan and Muller-Landau, 2000). The distance of wind-dispersed seeds depends upon seed mass and meteorological conditions, and only seeds with a mass less than about 0.05 mg have the potential to be dispersed over long distance by wind (Bakker et al., 1996). Wheat seeds have an average mass of about 30 mg and are not expected to be dispersed over a long distance by wind except in a storm. When the intensity and amount of rain cause overland flows, the rain-wash-water can also contribute to the horizontal or surface movement of seeds. There is a lack of specific reports on wheat seed dispersal though abiotic forces. Also, like the seed dispersal by migratory animals, the distance of both wind- and water-mediated wheat seed dispersal is difficult to predict.

2.2.4. Seed viability, longevity and dormancy, germination, seedling viability and establishment

The viability and longevity of wheat seeds are extremely variable depending upon a variety of factors, including genotypes, seed production factors, and environmental conditions (Anderson and Soper, 2003). Wheat seeds in soil may experience several fates, including immediate germination, a short dormant period followed by germination, predation, microbial decomposition, or seed death (Anderson and Soper, 2003; Willenborg and Van Acker, 2008). Because wheat seeds do not have a hard seed coat and are relatively large, they are prone to rapid decomposition, particularly in moist soils, and are generally not very persistent (De Corby et al., 2007; Wilson and Hottes, 1927). Classical burial studies showed that wheat seeds were short-lived in soil, normally persisting for less than one year (Anderson and Soper, 2003). De Corby et al. (2007) investigated the emerging time and recruitment of volunteer spring wheat after broadcasting and incorporating seeds into the soil in fall at 500 seeds/m^2, and showed that wheat seeds emerged early and the wheat seed recruitment level was low. The total cumulative emergence of wheat ranged from 0.9-13.1% (or 5-66 seedlings/m^2), with an overall mean of 4.3%. The majority of the remaining wheat seeds decomposed in the soil (De Corby et al., 2007). However, other field studies showed that volunteer wheat seedlings were still emerging 16 months and occasionally even two years after harvest (Anderson and Soper, 2003). Harker et al. (2005) observed wheat persistence up to three years after seed dispersal at eight sites across Western Canada. Similarly, volunteer spring wheat is reported to persist for even up to five years in the seed bank (Beckie and Owen, 2007). The difference in seed longevity between the burial studies and field studies may be attributed to the after-ripening period of seeds before being destined in seedbank, the seed densities in the soil, and the soil moisture levels (Anderson and Soper, 2003; Percival, 1921).

Dormancy is an effective survival mechanism for wild plant species to prevent or delay germination and maintain longevity under unsuitable or even suitable conditions (Fuller and Allaby, 2009). While wheat has undergone domestication against dormancy, it normally still possesses a sustained level of primary dormancy, which is desirable to prevent pre-harvest sprouting of wheat seeds on the plant and help maintain seed quality (Nyachiro et al., 2002). Wheat seed dormancy levels vary among different genotypes and environmental factors (Komatsuzaki and Endo, 1996; Reddy, Metzger and Ching, 1985). Temperature is shown to be one of the most influential environmental factors affecting the induction of seed dormancy during seed development and expression of dormancy during seed germination. Low temperatures (10-15°C) during the grain-filling period is shown to induce and prolong wheat seed dormancy (Nyachiro et al., 2002; Reddy, Metzger and Ching, 1985). Conversely, low temperature (15°C) during seed germination is effective for breaking seed dormancy (Reddy, Metzger and Ching, 1985). In addition, high nitrogen application rates and high seed nitrogen contents are shown to decrease seed dormancy and increase rain-induced pre-harvest sprouting in genotypes with moderate or low levels of resistance, although results were inconsistent among different environmental conditions (Morris and Paulsen, 1985). There is no reported induction of secondary dormancy in buried wheat seed (De Corby et al., 2007).

The germination and emergence of wheat seeds are impacted by environmental and varietal factors. For germination to be initiated, the wheat seed must be viable, be free of any primary dormancy condition, and be subjected to the appropriate environmental conditions, including a proper temperature range, a suitable degree of moisture, and a supply of oxygen (Percival, 1921). Temperature plays a significant role on wheat seed germination (Nyachiro et al., 2002). Wheat seeds can germinate over a wide range of temperatures from 4-37°C, with the optimal temperature ranging from 12-25°C (Acevedo, Silva and Silva, 2002). Low temperatures of 10-15°C resulted in higher germination percentages than higher temperatures of 25-30°C (Nyachiro et al., 2002; Reddy, Metzger and Ching, 1985; Wilson and Hottes, 1927). Temperature is also shown to have a large effect on emergence time. In the range of 5-20°C, wheat seedling emergence time increases when temperature decreases (Lafond and Fowler, 1989). Wheat seeds are capable of germinating under widely differing moisture conditions, but around 50% seed moisture content of its dry weight appears to be the optimal (Wilson and Hottes, 1927). Low soil water potential is shown to increase the time of emergence, and wheat seeds are capable of germinating and emerging at much lower soil water potentials when the temperature decreases (Lafond and Fowler, 1989). Wheat seedling emergence is also adversely impacted by other environmental factors, such as low oxygen diffusion rate (Hanks and Thorp, 1956), strong soil surface crust (Anzooman et al., 2018; Hanks and Thorp, 1956) and flooding treatments (Ueno, Fujita and Yamazaki, 1999). In addition to environmental factors, both wheat seed germination and emergence also vary significantly between different genotypes (Anzooman et al., 2018; Ueno, Fujita and Yamazaki, 1999).

2.2.5. Asexual propagation (apomixis, vegetative reproduction)

Apomixis is a type of asexual seed development from the maternal tissues of the ovule in flowering plants without the meiosis and fertilisation process (Bicknell and Koltunow, 2004; Koltunow and Grossniklaus, 2003). Apomixis can provide obvious advantages in crop enhancement, including the fixation of heterosis through the formation of true-breeding hybrids, simplification of hybrid seed production without requiring male sterile lines and isolation, and increased opportunity for developing superior gene combinations (Asker, 1979; Baum, Lagudah and Appels, 1992; Hanna and Bashaw, 1987). Apomixis has been described in more than 400 flowering plant taxa, and it has been commonly observed in polyploid wild species of grasses (Bicknell and Koltunow, 2004; Hanna and Bashaw, 1987). However, apomixis is very rare in crop species with the exceptions in tropical forage grasses and subtropical fruit trees, such as mango, mangosteen and citrus (Bicknell and Koltunow, 2004). There has been no report of apomixis in wheat.

In an attempt to use apomixis for crop genetic improvement, numerous attempts have been made to transfer the apomixis trait from wild related species into cultivated crops through wide hybridisations (Savidan, 2001). In Triticeae tribe, *Elymus rectisetus* (Nees in Lehm.) A. Löve & Connor ($2n = 6x = 42$, SSYYWW), which is endemic to Australia and New Zealand, is the only known apomict (Liu, Wang and Carman, 1994). The mechanisms for the high level of or obligate apomixis in *E. rectisetus* have been investigated by Crane and Carman (1987) and Liu, Wang and Carman (1994). To transfer apomixis from *E. rectisetus* to wheat, apomictic *E. rectisetus* has been crossed with wheat (Liu, Wang and Carman, 1994; Peel et al., 1997). Although certain aspects of apomixis in *E. rectisetus* are observed in the hybrids, absolute confirmation of true apomixis in wheat remains elusive (Peel et al., 1997).

A special wheat strain, Salmon, is shown to be able to parthenogenetically produce progenies from egg cells when its nucleus is transferred into heterologous cytoplasms of some related species such as *Aegilops* (Kumlehn et al., 2001; Matzk, 1996). Wheat strain Salmon was derived from a cross between two octoploid Triticales ($2n = 8x = 56$, BBAADDRR), but it possesses the same hexaploid genome formula as that of normal wheat ($2n = 42$, BBAADD) except for two structural chromosomal changes, an 1BL-1RS translocation (the short arm of wheat chromosome 1B is replaced by the short arm of rye chromosome 1R) and a deletion on wheat chromosome 2B (Tsunewaki, 1964). Such a Salmon system of wheat shows a high incidence (up to 90%) of polyhaploid parthenogenesis from the unfertilised but reduced egg cell (Matzk, 1996). Intergeneric hybrids between barley (*Hordeum vulgare*) and wheat were also shown to induce apomixis. Mujeeb-Kazi (1981) successfully made the intergeneric crosses between *H. vulgare* cv. Manker and *T. aestivum* cvs. Bonza and Chinese Spring, resulting in the production of F_1 hybrids ($2n = 4x = 28$, HBAD). However, these F_1 hybrids were all male sterile, and were then backcrossed to wheat parent cultivars to produce backcross-1 (BC_1) seeds. The BC_1 plants were found to contain 28 or 27 chromosomes with the similar genome composition as F_1 hybrids ($2n = 4x = 28$, HABD) rather than the expected BC_1 genome composition ($2n = 7x = 49$, HBBAADD). These BC_1 plants were proved to be derived from haploid parthenogenesis (Mujeeb-Kazi, 1981). Apomixis has also been discovered in wheat rye F_1 hybrids (Silkova, Shchapova and Kravtsova, 2003).

Wheat normally does not naturally reproduce through a vegetative approach, although vegetative reproduction can be artificially induced through *in vitro* tissue culture. Currently, the majority of the methods used for *in vitro* wheat clonal propagation involve plant regeneration from dedifferentiated tissues or cell suspensions (Bhaskaran and Smith, 1990; Vasil, 1987). Plant regeneration, however, is a transient and sporadic event, and only a few genotypes respond favourably to callus induction and plant regeneration (Tanzarella and Greco, 1990). Furthermore, *in vitro* plant regeneration often induces genomic instability and variation (Jain, 2001; Larkin et al., 1984; Larkin and Scowcroft, 1981).

SECTION 3. Genetics and breeding

3.1. Basic genetic information

3.1.1. Cytogenetics

Bread wheat is a polyploid plant that originated with the hybridisation of three diploid grasses, each of them contributing their genomes to the newly formed species (Figure 1.1.). As a result, the genome of bread wheat is formed by three subgenomes: A, B and D (see Section 1.1.4.). Each genome is composed of seven chromosome pairs that are represented by the numbers 1 to 7. To differentiate the subgenome that they belong to, the chromosomes are named as 1A, 1B, 1D to 7A, 7B and 7D, respectively (Figure 3.1.). The 21 pairs of homologous chromosomes of bread wheat fall into seven homoeologous groups. Each group contains one pair of chromosomes from the A, B, D subgenomes. For instance, homoeologous group 1 contains the pairs 1A, 1B and 1D. Homoeologous chromosomes share a high degree of gene synteny and DNA sequence homology, but also differ by a number of non-coding highly repetitive DNA sequences (Feldman and Levy, 2012). A standard karyotype nomenclature has been described (Gill, Friebe and Endo, 1991) that allows ready distinction of the chromosomes. A brief review by Gill (2015) discusses the history and developments of wheat chromosome analysis techniques.

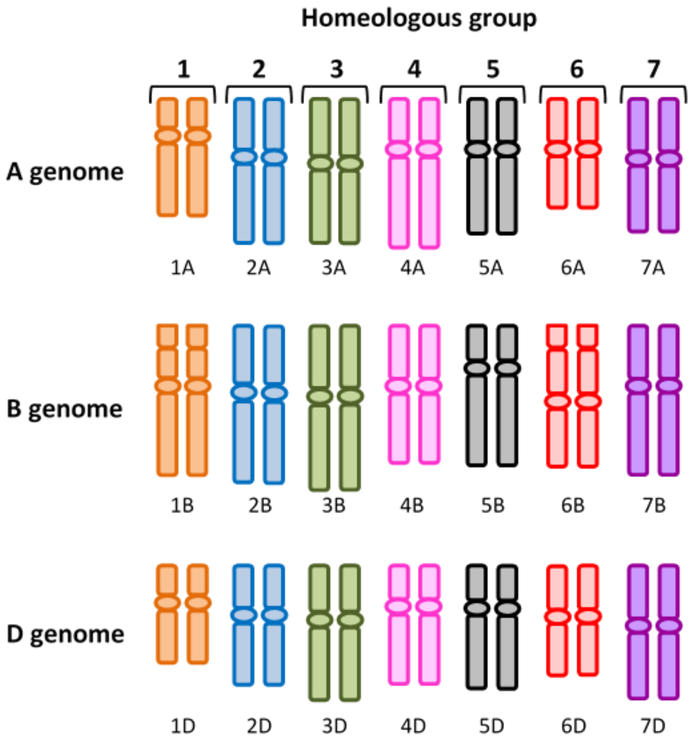
During meiosis, homologous chromosomes are able to pair and recombine (intragenomic pairing) while pairing of homoeologous chromosomes is prevented (intergenomic pairing). This ensures the formation of 21 pairs of chromosomes during meiosis, and results in the regular segregation of chromosomes in the gametes and their subsequent inheritance by the next generation. This diploid like meiotic behaviour in wheat allopolyploids has been critical for their establishment. It ensures high fertility, genetic stability, and diploid-like inheritance of traits (Feldman and Levy, 2012). Two different mechanisms are involved. Firstly, the difference in DNA sequence of homoeologous chromosomes makes it difficult for them to pair at meiosis. Secondly, the gene *Ph1* located on chromosome 5B (Riley and Chapman, 1958; Sears, 1976) restricts pairing to homologous chromosomes (Hegde and Waines, 2004).

3.1.2. Genome characteristics

The genome size of bread wheat is approximately 17 000 000 000 base pairs of DNA (17 Gigabases - Gb). It is approximately forty times bigger than the rice genome (450 Megabases; Goff et al., 2002), six times bigger than the maize genome (2.3 Gb; Schnable et al., 2009) and five times bigger than the human genome (3.2 Gb; Makałowski, 2001). As a hexaploid, the bread wheat genome contains six alleles of each gene in contrast to diploid organisms whose genome contains two alleles per gene. Due to the relatively recent origin of bread wheat, the gene copies found in the different genomes (homoeologous genes) are functional and have more than 97% sequence similarity across coding sequences (IWGSC, 2014; Uauy, 2017).

The advent of next-generation sequencing methods allowed the sequencing of the genome of the reference hexaploid wheat line ‘Chinese Spring’ which was assembled into the 21 constituent chromosomes (IWGSC, 2014). The genomes of five additional varieties have been released; i.e. the bread wheat varieties Robigus, Paragon, Claire and Cadenza and the durum wheat variety Kronos (Uauy, 2017). The complete or partial genomes of the diploid relatives of bread wheat, including *T. urartu*, *T. monococcum*, *Ae. tauschii* and *Ae. speltoides*, have also been sequenced (Brenchley et al., 2012; Jia et al., 2013; Ling et al., 2013).

Figure 3.1. Cartoon karyogram of the bread wheat genome



Note: The cartoon depicts the organisation of the bread wheat genome into 21 pairs of chromosomes, which are derived from three subgenomes.
Source: Illustration courtesy Maria Alonso, OGTR, Australia.

Each bread wheat subgenome has a size of approximately 5.5 Gb with more than 80% comprising highly repetitive transposable elements (IWGSC, 2014). Coding sequences represent less than 2% of the genome. It has been estimated that the wheat genome contains 106,000 functional protein-coding genes, with gene number estimates ranging between 32,000 and 38,000 for each subgenome. This is consistent with the number of genes found in the genomes of the related diploid species (IWGSC, 2014). The genes are also highly conserved, with more than 99% sequence identity between the subgenomes and their respective diploid relatives (IWGSC, 2014). Analysis of gene expression in bread wheat revealed that each subgenome exhibits a high degree of regulatory and transcriptional autonomy and there is no evidence for a genome-wide transcriptional dominance of one of the three subgenomes (IWGSC, 2014). This is in contrast to other polyploid crops like cotton, *Brassica rapa* and maize where one of the genomes is more transcriptionally active than the others (IWGSC, 2014).

3.2. Genetic diversity or variability

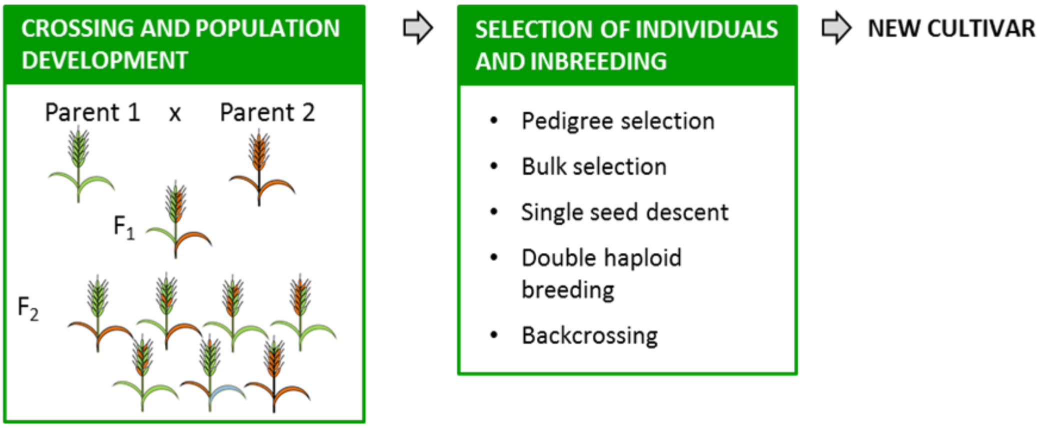
Bread wheat's success as a crop is due to its broad adaptability to different environments. Compared to its diploid and tetraploid relatives, bread wheat has diverse photoperiod and vernalisation requirements; improved tolerance to abiotic stresses; and better resistance to several pests and diseases. It can also be used in producing a greater variety of food products (Dubcovsky and Dvorak, 2007). These characteristics can be explained by the genetic diversity found in bread wheat. The high rate of DNA changes and the buffering effects of polyploidy can quickly lead to a greater diversity of characteristics (Dubcovsky and Dvorak, 2007).

Repetitive transposable elements in the wheat genome have been found to have a high replacement rate (Dubcovsky and Dvorak, 2007). Movement of repetitive transposable elements can generate knock-out mutations by insertion of repetitive elements into genes or by deletion of genes. While knock-out mutations could be lethal or have strong effects in diploid species, they may have only subtle dosage effects in bread wheat, if they affect only one of the three homoeologous genes in the wheat genome. The transposable elements can also facilitate gene duplication, with duplicated genes ending up with new functions. An average of 23.6% of the genes on each chromosome is duplicated on the same chromosome, which is a higher percentage than in other cereals such as rice, sorghum, barley, maize and foxtail millet (IWGSC, 2014). The sequencing of the bread wheat genome has also revealed that its genes contain a higher proportion of mutations leading to amino acid changes with a predicted large impact on protein functionality than their closest diploid and tetraploid relatives (IWGSC, 2014). Therefore, the buffering effect of polyploidy may result in the development of novel protein functions.

3.3. Methods of classical breeding

As with other crops, the ultimate goal of bread wheat breeding is to accumulate favourable traits into one cultivar. In pedigree breeding this is a multi-step process. First, plants that display variation for a given trait of interest must be selected and crossed to generate a breeding population (Figure 3.2.). After crossing the parental lines, the first hybrid generation (F_1) is allowed to self-pollinate (Figure 3.2.). The traits of interest segregate in the F_2 population. The next step of the breeding process is to select the best performing individuals in the F_2 and subsequent generations and to let them self fertilise in order to generate homogenous lines (homozygous genotypes) with fixed traits. These homogenous lines are evaluated at multiple geographic locations to identify the ones best adapted to different environments. Reviews of conventional methods for bread wheat breeding are available (Allard, 1999; Baenziger and DePauw, 2009; Simmonds, 1986).

Figure 3.2. Schematic representation of the breeding process in bread wheat



Source: Illustration courtesy Maria Alonso, OGTR, Australia.

An alternative breeding strategy is composite crossing, used in both organic and conventional systems (Knapp et al., 2019). In this strategy, a population with several traits is grown and replanted over several generations with minimal selection aside from natural condition variations, with the resulting population expected to become better adapted to local conditions over time (Suneson, 1956). Initial trait selection can be important for resulting quality traits (Brumlop, Pfeiffer and Finckh, 2017). See also Section 3.3.2., Bulk Selection.

3.3.1. Methods to create genetic and phenotypic variation

Early breeding programs resulted in an improvement of yield and increased disease resistance in wheat, however these improvements were brought about at the cost of an overall reduction in genetic diversity in the species. Diversity was lost as the improved cultivars, emanating from breeding programmes, replaced wheat landraces across the world (Warburton et al., 2006). Breeders have since focused on expanding the genetic base of wheat by using methods that create genetic variation like the ones mentioned in this section (Warburton et al., 2006).

When a new breeding program is initiated the selected parental varieties must be crossed. Crossing generates variation through genetic recombination at meiosis. Since bread wheat is mostly a self-pollinated species, the crossing of parental lines to generate hybrid wheats usually occurs in the controlled environment of a glasshouse (Simmonds, 1989). The different bread wheat varieties and their wild relatives constitute the genetic sources that provide the starting material for breeding new crop cultivars. Their seeds are stored in gene banks that have been established in many countries and that supply this genetic material to international breeding programs. The International Maize and Wheat Improvement Center (CIMMYT) manages the world's most diverse maize and wheat collections[10]. Other important collections are held at the Svalbard Seed Vault[11] and the Russian Institute of Plant Genetic Resources (VIR[12]).

Many important bread wheat cultivars have genes from wild relatives (Gale and Miller, 1987; Schneider, Molnár and Molnár-Láng, 2008) (For more detail, see Section 4). *In vitro* tissue culture techniques are used when wheat cultivars are crossed with wild relatives to bring new genes into wheat (Baenziger and DePauw, 2009). These embryo rescue techniques support the development of the hybrid embryo that otherwise would die. The *Ph1* gene has been shown to prevent intergenomic pairing at meiosis in hybrids of bread wheat and related *Triticeae* species (Jauhar and Chibbar, 1999; Riley, Chapman and Kimber, 1959). However, intergenomic pairing is advantageous for wheat breeding as meiotic recombination can result in the transfer of beneficial genes into the wheat genome. Wheat breeders have developed several methods to promote homoeologous pairing in hybrids by reducing the activity of the *Ph1* gene (Gale and Miller, 1987).

If a trait of interest does not occur in the existing genetic resources, there are methods to generate genetic variation. Mutations, i.e. changes in DNA sequence, can be induced by exposing wheat seeds to chemical mutagens or to ultraviolet or ionising radiation. These mutagenic techniques are non-targeted, that is genes are mutated at random, and this may generate a trait of interest. An example of novel trait introduction via mutation breeding is resistance to the imidazolinone class of herbicides. Imidazolinone-resistant wheat was originally developed through seed mutagenesis of 'Fidel' winter wheat followed by selection

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[10] http://www.cimmyt.org/tag/germplasm-bank/

[11] https://www.seedvault.no

[12] https://vir.nw.ru

of herbicide resistant plants. Imidazolinone-tolerant wheat cultivars have been released in Argentina, Australia, Canada, and the United States (reviewed in Baenziger and DePauw, 2009).

Hybridisation is another method used to introduce diversity and high-performing crops. Due to self-pollination in wheat it is more difficult to achieve hybridisation than in other crops, and by the year 2012 less than 1% of planted wheat was from hybrid seed (Longin et al., 2012). A range of methods are employed to prepare hybrid seed, reviewed in AGRI-FACTS (2002), though at present it is primarily through use of chemical hybridisation agents (Longin et al., 2012). Strategies continue to be developed to produce hybrids, for example by inducing cytoplasmic male sterility, or using biotechnology techniques (Castillo, Atienza and Martin, 2014; Kempe, Rubtsova and Gils, 2014). For further detail, see Section 4.

3.3.2. Selection methods

Selection is the process of determining the relative worth of individuals from a segregating population and propagating chosen individuals from generation to generation until the traits of interest are fixed. Methods for selecting while inbreeding to develop a cultivar are pedigree selection, bulk selection, single-seed descent, doubled haploid breeding and backcrossing (reviewed in Baenziger and DePauw, 2009).

Pedigree selection. In this method, the breeding of individual plants from a segregating population are selected and propagated and the genealogy of each line is recorded. The pedigree breeding method is the most labour-intensive method but provides the greatest detail of genetic information. It is generally used to create new lines and cultivars that combine the best traits from parent lines.

Bulk selection. In this method, plants are chosen which express individual advantages, and a sample of the aggregate of the seed is propagated in the next cycle of inbreeding. In this case, the breeder often relies extensively on natural selection or relatively simple selection techniques within the bulk population for removing unwanted types or retaining desirable types, as the population is harvested *en masse* with no individual progeny testing.

Single-seed descent. Single-seed descent is a method to achieve homozygosity while often practicing minimal selection. The method consists of selfing a random sample of F_2 derived plants in each generation and advancing only one seed per plant. When inbred lines have been produced, selection can be based on data from replicated field trials for agronomic performance, biotic and abiotic stress tolerance, and end-use quality testing. This method is usually applied when crossing elite wheat varieties in which many of the favourable alleles are already fixed.

Doubled haploid breeding. Doubled haploid technology is used to rapidly generate homozygous lines. The end-point is the production of a random set of inbred lines for subsequent assessment. The method involves production of plants from haploid tissue by doubling the chromosomes. The resultant plant will be completely homozygous and homogeneous. Two predominant methods are available to create doubled haploids (i) anther culture and (ii) the wheat-by-maize system (Tadesse et al., 2013). In anther culture, wheat pollen grains are placed on artificial medium to develop into embryos. Production of wheat haploids through wheat × maize crossing involves using maize pollen to fertilise bread wheat. This results in the production of a haploid embryo that is sustained by embryo rescue techniques. Doubled haploid cultivars have been released in a number of countries and some have become dominant cultivars (reviewed in Baenziger and DePauw, 2009).

Backcrossing. Backcrossing is a method of recurrent crossing to introduce a desirable trait in a specific genetic background. The parental source of the desirable trait is designated the donor parent, and the parent in which the trait is introduced is the recurrent parent. At the end of the breeding, the recurrent parent has the new trait. Backcrossing has been used effectively as a short term breeding strategy to incorporate dominant genes for the control of devastating pathogens, such as those causing stem rust, in otherwise highly productive and adapted cultivars (reviewed in Baenziger and DePauw, 2009).

3.4. Next generation breeding

Deep sequencing and genomics technologies have brought new possibilities to the field of wheat breeding. The availability of a reference genome makes it possible to identify candidate genes responsible for agronomic traits of interest. Some of the applications of new technologies in wheat breeding are outlined in this section.

3.4.1. Marker-assisted selection methods

Traditionally, selection has been based on the phenotype of the individuals. However, contemporary breeding is more reliant on genotypic selection, which is based on molecular markers. Molecular markers are DNA sequences that can be easily tracked and quantified in a population and are linked to a particular trait of interest, such as disease resistance. Detection of markers tightly linked to traits can then rapidly predict the phenotypes of a large selection of segregating individuals at an early stage of development, often well before phenotypic screening would be possible, and at reduced cost. The application of single marker-trait associations to crop breeding is known as marker-assisted selection (MAS) (Hayward et al., 2015). Until now, only a limited number of molecular markers were available for wheat breeding. With the sequencing of multiple bread wheat varieties, more molecular markers are being discovered. Having enough markers across the entire genome makes it possible to have marker-assisted selection on a genomic scale (Genome Wide Marker Assisted Selection or GWAS) (Hayward et al., 2015).

A novel method of wheat breeding called Genomic Selection (GS) has also been deployed (Bassi et al., 2016). In this method, a small population of plants called the training population is genotyped and phenotyped and a statistical model is used to identify which molecular markers are linked to the traits of interest. Then a bigger set of individuals, called the breeding population is only genotyped. The statistical model is then used to predict the performance of the individuals for various traits based on the molecular markers they contain. The individuals predicted to have the best characteristics are propagated in the subsequent breeding cycles.

3.4.2. Mutational genomics

Due to bread wheat being a polyploid, the effects of knock-out mutations in a single gene are often masked by the compensating effect of the two other functional homoeologous genes. This phenomenon is referred to as gene redundancy. Knocking out all three homoeologous genes may uncover hidden genetic variation which may be useful for crop improvement (Uauy, 2017). Recently, a population of chemically induced mutants of bread wheat was produced and the genes in the mutants were sequenced (Krasileva et al., 2017). On average each mutant carried more than 5,000 mutations in different genes. Most importantly, at least one knock-out mutation was identified for almost every gene in the genome. Mutants carrying mutations in one of three homoeologous genes can now be selected from this population and crossed to generate a triple mutant. Thus, gene redundancy can be overcome and the role of these genes elucidated. Introduction of traits into wheat can be accomplished through the use of biotechnology (see Annex B).

3.5. Intraspecific gene flow

Bread wheat is a cultivated species with no known wild or weedy strains (see Section 1). However, cultivated varieties can successfully cross-breed, either naturally or under controlled conditions (for further detail, see Section 4). Gene transfer may occur when the parent lines are grown in proximity to one another and flower simultaneously as they are sexually compatible (Waines and Hegde, 2003). The progeny of such crosses will be fertile (Matus-Cádiz et al., 2004).

Intraspecific pollen-mediated gene flow has been studied at field and commercial scales in Canada (Matus-Cádiz, Hucl and Dupuis, 2007; Matus-Cádiz et al., 2004). The authors showed that intraspecific gene flow in individual plants could be detected at less than 0.01% up to 300 m away when a 16 ha pollinator block was used, or 2.75 km for a 30 ha pollinator block (Matus-Cádiz, Hucl and Dupuis, 2007; Matus-Cádiz et al., 2004). Gene flow was dependent on environmental conditions, with higher gene flow observed in cooler, more humid and wetter conditions (Matus-Cádiz et al., 2004). The authors suggest that the 0.01% trace rate observed in individual samples can be considered a worst-case scenario if compared with gene flow rates averaged across samples (Matus-Cádiz, Hucl and Dupuis, 2007). In the first growing season, one hybrid seed was confirmed out of three million seeds (0.00003% gene flow rate); and in the second season, nine hybrid seeds were confirmed out of ten million seeds (0.00009% gene flow rate; Matus-Cádiz, Hucl and Dupuis, 2007). Isolation distances of up to 45 m were recommended for wheat to reduce pollen-mediated gene flow to negligible levels (Hanson et al., 2005b; Hucl and Matus-Cádiz, 2001).

The rate of intraspecific pollen-mediated gene flow in South-eastern Australia has been shown to be lower than that observed in other countries (Gatford et al., 2006). Using a series of small pollinator blocks, these authors measured a maximum gene flow rate of 0.055% at 8 m from the pollen source (Gatford et al., 2006). The pollinator blocks used in this study were smaller than the ones used in Matus-Cádiz, Hucl and Dupuis (2007), which can lead to lower outcrossing rates. However, this low level of gene flow could also be explained by environmental and morphological factors. Low relative humidity and warmer temperatures could have accelerated pollen desiccation. Hot, dry weather conditions have been shown to lower pollen viability to less than 15 minutes (D’Souza, 1970). It has also been suggested that as most Australian elite cultivars have a closed flower structure, floral morphology of the recipient could play a role in the gene flow rates observed (Gatford et al., 2006). Based on these results, the authors recommended a 12 m separation between GE (genetically engineered, or ‘genetically modified’) and non-GE crops (Gatford et al., 2006).

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

SECTION 4. Hybridisation and introgression

Wide or distant hybridisation between different species or genera provides a way to combine diverged genomes into one nucleus. Such wide hybridisations break what is known as the species and/or genera barrier for gene transfer, and make it possible to exchange genetic information between species or genera (Feuillet, Langridge and Waugh, 2008; Jiang et al., 1993; Mujeeb-Kazi et al., 2013; Sharma and Gill, 1983). Wide hybridisation and introgression are common in natural ecosystems, and have played important roles in plant species evolution, especially for wheat (Abbott, 1992; Anderson, 1949; Feldman and Levy, 2015; Kimber and Sears, 1987; Matsuoka, 2011; Rieseberg and Wendel, 1993). Wide hybridisation has also been increasingly pursued by breeders to increase genetic variations and enhance wheat improvement (Ceoloni et al., 2015; Feldman and Levy, 2015; Feuillet, Langridge and Waugh, 2008; Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi and Rajaram, 2002; Sharma and Gill, 1983).

4.1. Wheat gene pool

The overview of the Triticeae species in Section 1.1., especially their genome compositions, helps with better understanding of wide hybridisations in wheat. The species in the tribe Triticeae are very diverse, including both annual and perennial life cycles, self- or cross-pollinating types, and a wide range of ploidy levels from diploidy to dodecaploidy with extremely diverse genomic compositions (Table 1.1.).

From a genetic perspective, the related species of wheat in the tribe Triticeae can be classified into primary, secondary and tertiary gene pools (Feuillet, Langridge and Waugh, 2008; Harlan and de Wet, 1971; Jiang et al., 1993; Mujeeb-Kazi and Rajaram, 2002). The primary gene pool species consist of hexaploid wheat landraces, cultivated tetraploid *T. turgidum*, wild *T. dicoccoides*, the A genome donor *T. urartu* and D genome donor *Ae. tauschii* (Jiang et al., 1993; Mujeeb-Kazi and Rajaram, 2002; following taxonomy of van Slageren, 1994). Gene transfers from the primary pool species into wheat can occur through homologous chromosome recombination in direct cross and backcross hybridisations (Jiang et al., 1993).

The secondary gene pool species include closely related polyploid *Triticum* and *Aegilops* species, which share one genome with the three genomes of wheat (Jiang et al., 1993). The diploid *Aegilops* species in the Sitopsis section, however, are also placed in this gene pool because of their reduced chromosome pairing and difficulties in achieving gene transfer with wheat. Gene transfers from the secondary pool can occur through homologous recombination between the homologous genomes or recombination among the non-homologous genomes in direct cross and backcross hybridisations (Feuillet, Langridge and Waugh, 2008; Jiang et al., 1993; Mujeeb-Kazi and Rajaram, 2002).

The tertiary gene pool species include the diploid and polyploid species that contain non-homologous genomes compared to wheat genome (Jiang et al., 1993). Thus, wide hybridisation between wheat and its tertiary gene pool species is difficult to make and the gene transfers from this gene pool cannot occur by homologous recombination. However, the genomes of the tertiary pool species are homoeologous (genetically related) to the wheat genomes, and thus gene transfer from these species can be achieved through inducing homoeologous recombination (Feuillet, Langridge and Waugh, 2008; Jiang et al., 1993; Mujeeb-Kazi and Rajaram, 2002).

4.2. Natural facility of interspecific crossing

4.2.1. Natural hybridisation

Relatively few wild relative species within the tribe Triticeae can hybridise with wheat under natural conditions because wheat is primarily a self-pollinated crop and genetic barriers exist between wheat and its wild relative species (Mujeeb-Kazi and Hettel, 1995; Sharma and Gill, 1983). The most important obstacles to wide hybridisation include 1) cross incompatibility between wheat and its wild species, 2) inviability of F_1 hybrid, and 3) sterility of the F_1 hybrid or its progeny (Sharma and Gill, 1983). However, wide hybridisation followed by introgression has occurred during wheat evolution and is an important source of genetic variation in natural populations (Feldman and Levy, 2015; Liu et al., 2016). The origin and domestication of polyploidy *Triticum* species involved natural intergeneric and interspecific hybridisation and introgression (Feldman and Levy, 2015; Marcussen et al., 2014; Matsuoka, 2011).

Natural hybridisation between the polyploidy species of the genera *Triticum* and *Aegilops*, particularly between those sharing one common genome, is a frequent phenomenon (van Slageren, 1994; Zaharieva and Monneveux, 2006). Wheat and *Aegilops* species frequently grow in sympatry in the Mediterranean area, Northern Europe and the United States, and frequent spontaneous intergeneric hybridisation between them have been reported (Arrigo et al., 2011; Hegde and Waines, 2004; van Slageren, 1994; Zaharieva and Monneveux, 2006). For example, jointed goatgrass (*Ae. cylindrica*), a winter annual weedy form of wild wheat (allotetraploid, $2n = 4x = 28$, CCDD), has been widely reported to infest wheat fields and hybridises with wheat to form fertile hybrids under natural field environment conditions (Donald and Ogg, 1991; Gaines et al., 2008; Hanson et al., 2005a; Morrison, Crémieux and Mallory-Smith et al., 2002; Seefeldt et al., 1998; Stone and Peeper, 2004; Zaharieva and Monneveux, 2006; Zemetra, Hansen and Mallory-Smith, 1998). Natural hybrids between *Ae. cylindrica* and *T. aestivum* have been reported in the coasts of the Black Sea of Bulgaria with male sterility frequency between 99.22% and 100% (Stoyanov, 2013). Natural hybrids have been observed and reported between wheat and a number of species in *Aegilops* genus, including *Ae. biuncialis*, *Ae. columnaris*, *Ae. crassa*, *Ae. cylindrica*, *Ae. geniculata*, *Ae. juvenalis*, *Ae. neglecta*, *Ae. speltoides*, *Ae. tauschii*, *Ae. triuncialis*, *Ae. umbellata*, and *Ae. ventricosa*, (Dorofeev, 1969; Loureiro et al., 2006, 2007a; van Slageren, 1994; Zaharieva and Monneveux, 2006).

Many natural wheat × rye hybrids have been discovered (Dorofeev, 1969; Leighty, 1915; Leighty and Sando, 1928; Meister, 1921) since the first wheat × rye hybrid was reported in 1873 (Wilson, 1873). The wheat × rye hybrids are normally male-sterile, and the seeds, if any, set on F_1 hybrid plants are generally due to spontaneous backcrossing with wheat (Briggle, 1969; Muntrzing, 1974). However, intermediate and fertile wheat × rye hybrids that were amphiploid involving wheat plus rye genomes were also reported (Silkova, Shchapova and Kravtsova, 2003). The discovery of amphiploid wheat × rye hybrids resulted in the development of the man-made crop Triticale (Briggle, 1969). The name of Triticale is derived from the combination of the names of two genera involved, *Triticum* and *Secale*, and it is actually a polyploid (principally cultivated as hexaploid, tetraploid to octaploid variants exist) derived from doubling the chromosome number of the sterile F_1 hybrid of a cross between hexaploid wheat (*T. aestivum*) or tetraploid wheat (*T. turgidum*) and diploid rye (*S. cereale*) (Bernard and Bernard, 1987).

4.2.2. Natural introgression

Many domesticated plants hybridise spontaneously with their wild relatives (Felber et al., 2007; Jarvis and Hodgkin, 1999). Detailed analyses of naturally occurring wide hybridisations have shown that the wide cross hybrids often backcrossed to one or both parents repeatedly leading to the infiltration of germplasm of one species into another, and such a process was named “introgressive hybridisation” (Anderson and Hubricht, 1938; Hegde and Waines, 2004), and the consequences were described as the “introgression” of one species into another (Anderson, 1949).

Natural introgression has been shown to have occurred frequently and played an important role for the evolution of and genetic diversity of cultivated wheat. Wild tetraploid wheat (*T. turgidum*, genomes BBAA) has been proved to introgress its genetic materials into cultivated wheat, enriching the genetic diversity of the wheat A and B genomes (Dvorak et al., 2006). Introgression from rye (*S. cereale*) to wheat was also reported to have occurred spontaneously in a Portuguese wheat landrace, ‘Barbela’ (Ribeiro-Carvalho et al., 1997, 2001). Natural crosses and introgression between wheat and the *Aegilops* species, especially the jointed goatgrass (*Ae. cylindrical*, CCDD), have been frequently observed since the early nineteenth century, probably due to their close relationship (Arrigo et al., 2011; Gandhi et al., 2006; Hegde and Waines, 2004; Jacot et al., 2004; Pajkovic et al., 2014; Schneider, Molnár and Molnár-Láng, 2008). The D genome of wheat is considered to have a greater likelihood of being transferred into jointed goatgrass than genes located on A and B genomes of wheat (Hegde and Waines, 2004; Zaharieva and Monneveux, 2006). Alternatively, natural introgression of genes can also occur from wheat into its wild relative species such as jointed goatgrass (Gandhi et al., 2006; Hegde and Waines, 2004). It is noteworthy that the transfer of genes related to the fitness or competitiveness from wheat to its wild relative species could pose a potential weediness risk (Hegde and Waines, 2004).

4.3. Experimental crosses

Wheat breeders are facing challenges to make further genetic improvements due to the scarcity of wheat varieties and landraces with desired genetic variations. The ample number of wild relatives of wheat in tribe Triticeae can provide tremendous genetic variability, and breeders have been attempting to make artificial wide cross hybridisations to tap new genes in wild species for wheat genetic improvement (Ceoloni et al., 2015; Kimber and Feldman, 1987; Mujeeb-Kazi, 1995; Mujeeb-Kazi et al., 2013; Ogbonnaya et al., 2013). With the advancement of hybridisation techniques and embryo culture, numerous hybridisations have been successfully made, not only between wheat and its related species within the genus *Triticum* (interspecific), but also between wheat and more distant relatives in other genera of the Triticeae tribe (intergeneric), and wide hybridisation has become a common approach used in genetic improvement of wheat (Ceoloni et al., 2015; Jiang et al., 1993; Liu et al., 2016; Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi and Rajaram, 2002; Mujeeb-Kazi et al., 2013; Sharma and Gill, 1983).

4.3.1. Interspecific hybridisations

Interspecific crosses have been successfully made between wheat and other *Triticum* species that have genomes similar to the wheat A, B, or D genome. These *Triticum* species include diploid wheat (*T. monococcum* and *T. urartu*), tetraploid wheat (*T. turgidum*, *T. timopheevii*, *T. carthlicum*, *T. durum*, *T. dicoccum*, *T, dicoccoides*, and *T. araraticum*) and hexaploid wheat (*T. spelta*, *T. zhukovskyi*, *T. compactum*, *T. sphaerococcum*, and *T. macha*) (Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi et al., 2013; Sharma and Gill, 1983).

4.3.2. Intergeneric hybridisations

In contrast to the above-described interspecific crosses, the species used in intergeneric crosses are very diverse genomically and normally difficult to cross with wheat; even when successful, the resulting hybrids have little or no intergenomic chromosome association (Mujeeb-Kazi, 1995). Significant genotypic variations in crossability of wheat varieties and wild relatives exist (Jiang et al., 1993; Zeven, 1987). The crossability of common wheat with its related genera is controlled by several crossability genes (*Kr* genes) or QTLs (Lein, 1943; Liu et al., 2014; Luo, 1989). Other factors, including the ploidy level, the species choice for the female parent, and various wide cross techniques such as emasculation, pre-pollination chemical treatments and embryo rescue culture also have a big effect on the success of intergeneric hybridisation (Gupta, Mishra and Kumar, 2018; Jiang et al., 1993; Mujeeb-Kazi, 1995; Sharma and Gill, 1983).

Wheat has been successfully crossed with many species of the allied genera within the tribe Triticeae, such as *Aegilops*, *Agropyron*, *Secale*, *Dasypyrum* (synonym of *Haynaldia*), *Hordeum* and *Elymus* (Baum, Lagudah and Appels, 1992; Ceoloni et al., 2015; Jiang et al., 1993; Liu et al., 2016; Mujeeb-Kazi and Hettel, 1995; Sharma and Gill, 1983). In particular, the genus *Aegilops* can be crossed readily with common wheat since it is the most closely related genus to wheat in Triticeae tribe (Schneider, Molnár and Molnár-Láng, 2008; Zhang et al., 2015). The majority of hybrid wheat lines, including chromosome additions, substitution, and translocation lines have been produced between common wheat and *Aegilops* (Schneider, Molnár and Molnár-Láng, 2008). It is worthy to note that *Aegilops* had been subsumed into *Triticum* genus in the past due to their close relationship, resulting in different names for *Aegilops* species at the generic level (Kimber and Feldman, 1987; Mujeeb-Kazi and Hettel, 1995). The *Thinopyrum* genus (synonymously *Agropyron* or *Elytrigia*) is the most widely used perennial to cross with wheat (Ceoloni et al., 2015; Mujeeb-Kazi, 1995; Mujeeb-Kazi et al., 2013). Almost all of the basic genomes in the Triticeae species have been combined, either singly or in combination, with the genomes of bread wheat through wide hybridisations (Ceoloni et al., 2015; Jiang et al., 1993; Liu et al., 2016; Mujeeb-Kazi, 1995). A summary list of genera and species in tribe Triticeae that have been successfully crossed with wheat to form intergeneric hybrids is shown in Table 4.1.. This summary table by no means represents a complete list of all the successful wide hybridisations, and the number of new intergeneric hybrids with more distantly related species is expected to be constantly increasing.

Table 4.1. List of intergeneric species that have been crossed with wheat

Genera	Species
Aegilops	*bicornis*, *biuncialis*, *caudata*, *columnaris*, *comosa*, *crassa*, *cylindrica*, *dichasians*, *geniculata*, *juvenalis*, *kotschyi*, *longissima*, *mutica*, *ovata*, *peregrina*, *searsii*, *sharonensis*, *speltoides*, *squarrosa*, *tauschii*, *triaristata*, *tripsaccoides*, *truncialis*, *umbellulata*, *uniaristata*, *variabilis*, *ventricosa*
Agropyron	*caespitosum*, *ciliare*, *cristatum*, *desertorum*, *distichum*, *elongatum*, *intermedium*, *junceum*, *michnoi*, *mongolicum*, *podperae*, *smithii*, *scirpeum*, *trachycaulum*, *villosum*, *yezoense*
Dasypyrum	*villosum*
Elymus	*altissimus*, *anthosachnoides*, *canadensis*, *caninus*, *caucasicus*, *ciliaris*, *cylindricus*, *dahuricus*, *dolichatherus*, *fibrosus*, *giganteus*, *kamoji*, *nipponicus*, *parviglumis*, *pendulinus*, *rectisetus*, *repens*, *scabrus*, *semicostatus*, *shandongensis*, *tibeticus*, *trachycaulus*, *tschimganicus*, *tsukushiensis*
Elytrigia	*acutum*, *pungens*, *repens*, *varnense*
Hordeum	*bogdanii*, *bulbosum*, *californicum*, *chilense*, *depressum*, *distichum*, *geniculatum*, *jubatum*, *marinum*, *pubiflorum*, *pussillum*, *spontaneum*, *vulgare*
Leymus	*angustus*, *cinereus*, *innovatus*, *mollis*, *multicaulis*, *racemosus*, *triticoides*
Psathyrostachys	*fragilis*, *huashanica*, *juncea*
Pseudoroegneria	*geniculata*, *scythica*, *stipifolia*, *strigosa*
Secale	*africanum*, *ancestrale*, *cereale*, *montanum*, *vavilovii*
Thinopyrum	*bessarabicum*, *curvifolium*, *distichum*, *elongatum*, *gentryi*, *intermedium*, *junceiforme*, *junceum*, *ponticum*, *sartorii*

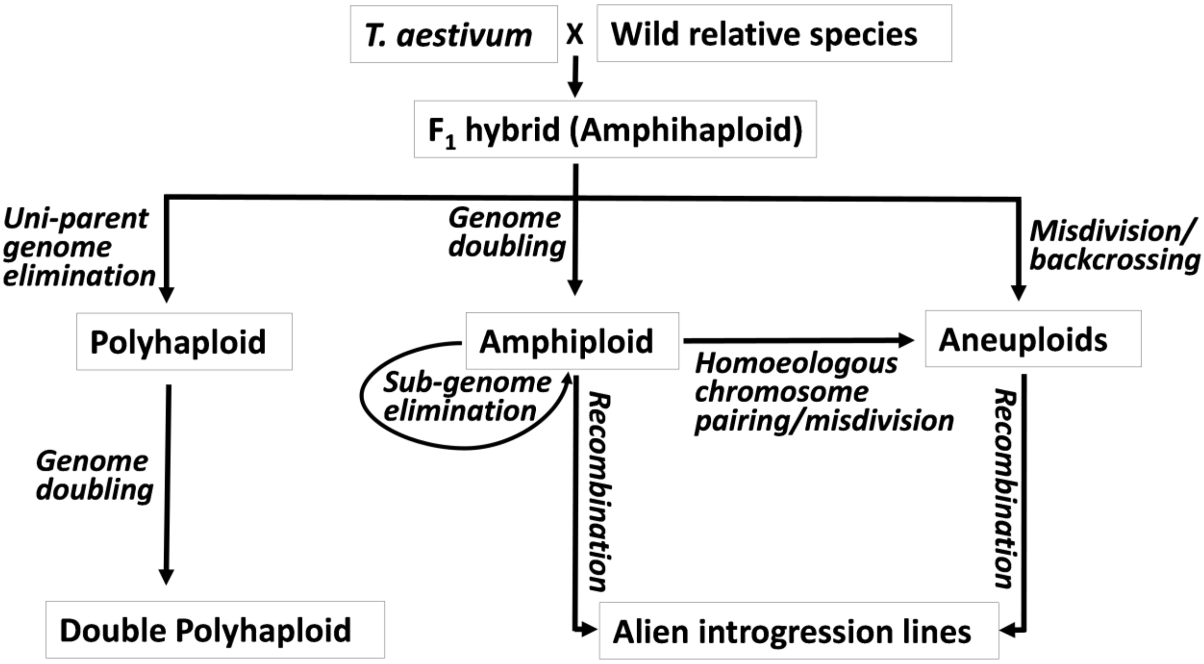
Sources: Ceoloni et al., 2015; Jacot et al., 2004; Jiang et al., 1993; Liu et al., 2016; Molnár-Láng, Linc and Szakács, 2013; Mujeeb-Kazi, 1995; Mujeeb-Kazi et al., 2013; Schneider, Molnár and Molnár-Láng, 2008; Sharma and Gill, 1983; Smith, 1942; Wang, 2011.

Species outside the tribe Triticeae have also been tested for intergeneric crosses with wheat, including maize (*Zea mays*) and sorghum (*Sorghum bicolor*) (Liu et al., 2014). The cross between wheat (*T. aestivum*, 2n = 42) and maize (*Z. mays*, 2n = 20) led to the production of hybrid zygotes with one complete haploid chromosome set from each parent (Laurie and Bennett, 1986). Maize chromosomes, however, are subsequently eliminated, resulting in the production of haploid wheat (Laurie and Bennett, 1986, 1988b). Similarly, wheat had been crossed with sorghum (*S. bicolor*, 2n = 20) as well as pear millet (*Pennisetum glaucum*, 2n = 14), resulting in fertilised hybrid zygotes with one complete haploid chromosome set from each parent followed by the rapid elimination of the sorghum or pear millet chromosomes (Laurie, 1989; Laurie and Bennett, 1988a).

4.3.3. Genetic manipulations of wide hybrids for alien gene introgressions

The success of wide hybridisations between wheat and its allied species in the tribe Triticeae and beyond, as described above, is only the first necessary step for gene introgression. In many wide hybridisations, there exists post-hybridisation barriers such as: homologous chromosome not being present for paring during meiosis, sterility and genome elimination/loss that can impede the gene transfer between wheat and its related wild relatives (Ceoloni et al., 2015; Gupta, Mishra and Kumar, 2018; Jiang et al., 1993; Liu et al., 2014; Mujeeb-Kazi and Rajaram, 2002). To overcome these barriers and facilitate gene introgression, a variety of genetic strategies have been used to manipulate the hybrid genomes for genetic improvement (Table 4.1.).

Figure 4.1. Genetic manipulations of interspecific and/or intergeneric hybrids for chromosomal interchanges and alien gene introgression



Source: Based on Liu et al. (2014).

F_1 hybrids and amphihaploids

Wide crosses between two distantly related species lead to the generation of the F_1 hybrids, bringing distantly-related parental genomes together into the same nucleus (Ceoloni et al., 2015; Jiang et al., 1993; Liu et al., 2016; Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi and Rajaram, 2002; Mujeeb-Kazi et al., 2013; Sharma and Gill, 1983). F_1 hybrid genomes normally are amphihaploids (containing the haploid set of chromosomes from each of the parent species) and in most cases exhibit little or no intergenomic chromosome association and exchange because the non-homologous chromosomes from each parental genome cannot pair with each other during meiosis (Baum, Lagudah and Appels, 1992; Jiang et al., 1993; Maan, 1987). Furthermore, such F_1 amphihaploid hybrids are normally sterile because the irregular meiotic division of single set of non-homologous chromosomes results in the gametes with incomplete set of chromosomes (Baum, Lagudah and Appels, 1992; Maan, 1987; Mujeeb-Kazi et al., 2013). Both the sterility and absence of intergenomic association in F_1 amphihaploid hybrids hinder the introgression of genes between wheat and its wild relative species (Loureiro et al., 2009; Mujeeb-Kazi et al., 2013).

Ploidy alterations

F_1 amphihaploids can sometimes go through certain ploidy alterations either at the whole ploidy or individual chromosome level, resulting in the conversion of amphihaploids into amphiploids (containing at least one complete diploid set of chromosomes from each parent species) or leading to the generation of aneuploidy progenies with the addition, deletion or substitution of one or a few chromosomes (De Storme and Mason, 2014; Feldman and Levy, 2012; Mujeeb-Kazi and Rajaram, 2002; Sharma and Gill, 1983). The ploidy alterations via chromosome doubling or backcrossing can often restore the fertility of hybrid progenies, facilitate the introgression of genes from wild related species into wheat, and play an important role in the speciation and diversification of wheat (Mujeeb-Kazi and Hettel, 1995; Zaharieva and Monneveux, 2006). In addition, some F_1 amphihaploids can eliminate the entire set of genomes from one parent followed by genome doubling, resulting in the formation of double polyhaploid (Figure 4.1.) (Laurie, 1989; Laurie and Bennett, 1986, 1988a). These ploidy alterations can occur either spontaneously or through cytogenetic manipulation (De Storme and Mason, 2014; Maan, 1987; Mujeeb-Kazi and Hettel, 1995).

Whole genome duplication and amphiploids

As described above, wheat itself was derived from two wide crosses, each resulting in the formation of complete amphiploids and eventually the generation of the allohexaploid wheat (Feuillet, Langridge and Waugh, 2008). Like many other crop species such as oats, cotton and tobacco, wheat is presumed to have undergone a spontaneous whole genome duplication through unreduced gametogenesis (with somatic chromosome number) followed by subsequent fertilisation of unreduced female and male gametes, leading to the generation of an amphiploid from natural wide hybridisations (De Storme and Mason, 2014; Matsuoka, 2011). See also Section 1.1.1.. The whole genome duplication can also be achieved through artificial treatment with antimicrotubule chemicals such as colchicine, oryzalin, amiprophosmethyl (APM), trifluralin, and pronamide (Liu et al., 2014). Artificial whole genome duplication processes have been employed in a variety of applications, e.g. developing new alloploid crops such as the creation of Triticale (X *Triticosecale* Wittmack), production of double haploids lines, and generation of amphidiploids as the bridge of alien gene introgression into crops (Liu et al., 2016).

Amphiploid F_1 hybrid plants between three species of the *Aegilops* genus and different *T. aestivum* cultivars can show certain self-fertility, with averages of F_1 hybrids bearing F_2 seeds of 8.17%, 5.12% and 48.14% for *Ae. biuncialis*, *Ae. geniculata* and *Ae. triuncialis*, respectively (Loureiro et al., 2009). All the F_2 seeds studied were spontaneous amphiploids (2n = 10x = 70) (Loureiro et al., 2009), evidence for possible spontaneous formation of amphiploids between these three *Aegilops* species and hexaploid wheat.

A large number of synthetic amphiploids (complete or partial) have been developed with many species and genera in tribe Triticeae (Liu et al., 2016). Triticale as the first man made cereal crop was an amphiploid developed through the artificial cross between wheat and rye (Briggle, 1969; Falk and Kasha, 1981; Li et al., 2015; Oettler, 2005). Synthetic hexaploid wheat (2n = 6x = 42, BBAADD) has been produced by several approaches, including: 1) crossing *T. turgidum* (2n = 4x = 28, BBAA) × *Ae. tauschii* (2n = 2x = 14, DD) followed by artificial whole genome duplication; 2) crossing wheat (2n = 6x = 42, BBAADD) × *Ae. tauschii* (2n = 2x = 14, DD); 3) crossing wheat (2n = 6x = 42, BBAADD) × *T. turgidum* (2n = 4x = 28, BBAA) (Liu et al., 2016; Mujeeb-Kazi and Hettel, 1995; Ogbonnaya et al., 2013). The A-genome synthetic hexaploids (2n = 6x = 42, BBAAAA) have also been produced through crossing durum wheat (2n = 4x = 28, BBAA) with A genome diploid species *T. monococcum* or *T. urartu* (2n = 2x = 14, AA) (Mujeeb-Kazi and Hettel, 1995). Unlike the amphiploid crops such as wheat, Triticale, oat, and cotton that have already gone through a long domestication and evolution process, the synthetic amphiploids are unsuitable for being directly used as crops because they contain excessive alien genetic materials with many undesirable genes, known as linkage drag, and are often associated with genome shock and meiotic instability (Gaeta and Chris Pires, 2010). However, the synthetic amphiploid wheat lines are easy to cross with wheat and provide a convenient way to transfer genes from *T. turgidum* and *Ae. tauschii* into wheat (Ogbonnaya et al., 2013). Thus, wide hybridisation-derived amphiploids are mostly used as potent bridge germplasm from which further genetic manipulations can lead to exploitable products such as alien gene introgression or alien chromosome substitution, addition, and translocation lines where undesired linkage drag is largely minimised (Ceoloni et al., 2015; Jiang et al., 1993; Mujeeb-Kazi et al., 2013).

Aneuploidy

Aneuploidy lines contain increased or lost dosage of chromosomes compared to their wild type counterparts. The hexaploid nature of wheat makes it tolerant to a certain level of chromosome dosage changes and can lead to the generation of aneuploids at relatively high frequency (De Storme and Mason, 2014; Feldman and Levy, 2005). The systematic production of aneuploid lines in wheat was first reported in 1954, and these lines include monosomic (2n = 20II + 1I = 41), nullisomic (2n = 20II = 40), trisomic (2n = 20II + 1III = 43), tetrasomic (2n = 20II + 1IV = 44), and nulli-tetrasomic (2n = 19II + 1IV = 42) (Joppa, 1987; Sears, 1954). In addition, more complicated forms of aneuploids exist, such as a double monosomic line missing one chromosome from each of two pairs of homologous chromosomes (2n = 19II + 1I + 1I = 40) or a double tetrasomic line with an additional pair of two pairs of homologous chromosomes (2n = 20II + 1IV + 1IV = 46) (Heyne, 1987; Joppa, 1987; McIntosh, 1987). There are also aneuploidy lines called ditelosomic that lacks a pair of chromosome arms rather than the whole chromosomes as well as deletion lines lacking a segment of a chromosome (Endo and Gill, 1996). These aneuploids have been used extensively for the genetic and genomic studies of wheat (Joppa, 1987; McIntosh, 1987; Qi et al., 2007).

Aneuploid F_1 progenies have been reported in many interspecific and intergeneric crosses such as the crosses of wheat with *H. vulgare*, *Thinopyrum repens* and *Agropyron desertorum* (Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi et al., 2013). Aneuploids can also be generated from the selfed progenies or the backcross progenies of wide cross-derived amphiploids (Mujeeb-Kazi and Hettel, 1995; Mujeeb-Kazi et al., 2013). From the wheat genetic improvement point of view, the aneuploids are often more preferred over the amphiploids (complete or partial) and this is especially true for the single chromosome addition, substitution and translocation lines with a wheat genetic background. This is because aneuploids carry less alien genetic material, with a reduced likelihood of linkage drag and are much easier and more efficient to lead to translocations or subtle exchanges through cytogenetic manipulation and breeding selection (Mujeeb-Kazi et al., 2013; Qi et al., 2007). The rapid development of molecular cytogenetic, molecular marker, and sequencing technologies further aid the development and identification of addition, substitution and translocation lines (Qi et al., 2007). A variety of disease resistance genes and abiotic stress tolerance genes have been transferred from wild Triticeae species into wheat through the use of chromosome addition, substitution and translocation lines (Ceoloni et al., 2015; Jiang et al., 1993; Liu et al., 2016; Mujeeb-Kazi and Rajaram, 2002; Mujeeb-Kazi et al., 2013; Sharma and Gill, 1983). One of the most prominent examples of the transfer of alien genetic variation into wheat is the 1BL/1RS translocation, in which the short arm of rye chromosome one (1RS) was substituted for the long arm of Group 1 wheat Chromosome B (1BL) (Gupta and Vasistha, 2018).

Preferential elimination of constituent subgenome(s)

In some cases, the hybrid amphidiploids of some wide crosses preferentially eliminate chromosomes from constituent subgenome(s) (Laurie, 1989; Laurie and Bennett, 1988b, 1986; Liu et al., 2016). For example, in the man-made octaploid Triticale that comprises the R genome from its rye parent and A, B and D genomes from its wheat parent, either the D genome or R genome was preferentially eliminated (Li et al., 2015; Liu et al., 2016). The loss of D genome from octaploid Triticale led to the production of hexaploid Triticale with complete A, B, and R genomes (Hao et al., 2013; Li et al., 2015) or hexaploid lines with complete A and B genomes, and a composite genome consisting of the chromosomes of D and R genomes (Dou et al., 2006). In F_3 progenies derived from a cross between wheat × *Psathyrostachys huashanica* amphiploid (2n = 56, ABBDDNsNs) and hexaploid Triticale (2n = 42, BBAARR), it was found that both the A and B genomes remained complete but the chromosomes of D, Ns and R genomes were eliminated. Comparatively, the R genome chromosomes from rye were more likely to be retained in the progenies than the Ns genome chromosomes from *P. huashanica* and D genome chromosomes from wheat (Xie et al., 2012).

Uniparental genome elimination and polyhaploids

Unlike the normal F_1 hybrids, which contains a complete haploid genome from each parent species, some wide hybrids contain only one parent species' haploid genome while the other parent species' haploid genome is eliminated, resulting in the production of haploid hybrids (Mujeeb-Kazi, 1995). Such phenomenon of uniparental genome elimination has been observed in a variety of crosses between *Triticum* and other genera within tribe Triticeae, such as *Hordeum*, *Elymus*, and *Agropyron* as well as in wide crosses between wheat and more distantly related species outside tribe Triticeae, such as *Z. mays*, *S. bicolor*, *Pennisetum glaucum*, *Coix lacryma-jobi*, and *Imperata cylindrica* (Laurie, 1989; Laurie and Bennett, 1988b, 1986; Liu et al., 2014, 2016; Mujeeb-Kazi, 1995). Chromosome elimination of one parental genome after fertilisation can occur either spontaneously or through modified pollination methods *in vivo*, or by *in vitro* culture of immature male or female gametophytes in intraspecific, interspecific, intergeneric, or more distant hybrids in many species (Dunwell, 2010). This uniparental genome elimination process leads to the generation of polyhaploid wheat. For example, wide crosses between wheat and maize has become a main approach for double haploid production in wheat (Niu et al., 2014). No introgression of maize DNA into wheat has been found (Brazauskas, Pasakinskiene and Jahoor, 2004). The polyhaploid wheat can then lead to the production of double haploids through either spontaneous or artificial chromosome doubling. Double haploids in wheat can benefit breeders to quickly fix genetic recombination and increase breeding efficiency.

Genetic recombination (transfer)

Polyploidisation and genetic recombination are two important driving factors for speciation and evolution of many plant species (De Storme and Mason, 2014; Gaeta and Chris Pires, 2010; Lambing et al., 2017; Pelé, Rousseau-Gueutin and Chèvre, 2018). From the standpoint of crop genetic improvement, genetic recombination also plays an important role in facilitating the transfer of desirable genes from wild relative species to wheat. This is because wide hybrids and their derivatives with different ploidy levels of alien genomes are usually associated with a number of undesirable characteristics, such as: poor fertility, low yield and late maturation, to list a few, and genetic recombination between wheat and its wild relative chromosomes will help remove or at least minimise these linkage drags (Feuillet, Langridge and Waugh, 2008; Mujeeb-Kazi et al., 2013; Qi et al., 2007).

Homologous and homoeologous recombination are two major genetic recombination mechanisms in allopolyploid species such as wheat (Jiang et al., 1993; Qi et al., 2007). Chromosome pairs originating from a common ancestry are considered homologous, whereas chromosomes derived from different species are considered homoeologous (Glover, Redstig and Dessimoz, 2016). While recombination predominantly occurs among DNA sequences on homologous chromosomes, it may also occur among sequences on homoeologous chromosomes in allopolyploids (Gaeta and Chris Pires, 2010).

Homologous recombination

As described above, wheat, an allohexaploid, comprises three subgenomes (A, B and D) derived from three ancestral diploid progenitors. However, the allohexaploid wheat behaves cytologically like a diploid during its meiosis process because only homologous chromosomes can pair and the meiotic pairing of homoeologous chromosomes is suppressed by a pairing homoeologous (*Ph*) gene system in wheat (Kimber and Sears, 1987; Sears, 1976). This *Ph* gene system includes a major gene called *Ph1* on the long arm of chromosome 5B (Kimber and Sears, 1987; Riley, 1966; Riley, Chapman and Kimber, 1959), an intermediate effect gene, *Ph2*, on chromosome 3D and several minor loci (Sears, 1976). The pairing suppression genes *Ph1* and *Ph2* are also shown to suppress the pairing between wheat and alien chromosomes in wide cross hybrids (Liu et al., 2014). Homologous chromosomes undergo crossing over (reciprocal exchange) and non-crossover gene conversion events during meiosis, leading to novel genetic variations (Lambing et al., 2017).

As previously described, common wheat and the species in primary and secondary gene pools share at least one subgenome, and when brought together through wide crossing these homologous subgenomes can exchange genetic information via homologous recombination. A number of desirable genes have been successfully transferred from primary and secondary gene pool species into wheat through the homologous recombination between the shared subgenomes of wheat and its wild relative species (Liu et al., 2016; Mujeeb-Kazi and Rajaram, 2002; Mujeeb-Kazi et al., 2013). Numerous examples of alien genes transferred from different wheat wild relatives into wheat have been summarized by (Molnár-Láng, Ceoloni and Doležel et al., 2015).

Homoeologous recombination

The species within the tertiary gene pool contain genomes that are non-homologous to the wheat genomes, and thus their genes cannot be transferred to wheat by homologous recombination, making the exploitation of tertiary gene species more difficult (Mujeeb-Kazi and Rajaram, 2002). However, technologies that assist homoeologous gene transfers can be achieved through techniques such as, genetic manipulations of *Ph* genes controlling chromosome pairing, irradiation, and tissue culture-induced translocations (Griffiths et al., 2006; Mujeeb-Kazi and Rajaram, 2002).

To achieve the transfer of desirable genes into wheat from a wild species with non homologous genomes, chromosomes of such wild species must be able to pair with wheat chromosomes. As described above, *Ph1* and *Ph1*-like genes normally suppress intergenomic chromosome paring. When the *Ph1* gene is absent or inactivated, considerable pairing can occur between homoeologous chromosomes (Mujeeb-Kazi and Rajaram, 2002). The genetic manipulation of the *Ph1* gene to promote homoeologous chromosome paring and the subsequent recombination has been extensively used for alien gene introgression (Liu et al., 2016; Mujeeb-Kazi and Rajaram, 2002; Qi et al., 2007). Segmental introgression lines have been developed from the hybridisation between wheat and perennial wheat relatives. As reviewed by Hegde and Waines (2004), the effect of the *Ph1* gene can also be suppressed under certain genetic backgrounds such as the diploid *Aegilops* species (Chen, Tsujimoto and Gill, 1994; Hegde and Waines, 2004). The facilitation of homoeologous chromosome pairing through manipulating *Ph* genes can enhance intergenomic recombination between wheat chromosomes and their homoeologous chromosomes in related species, promoting the transfer of the desired gene from certain alien chromatin segments while reducing the amounts of unwanted alien DNA (Baum, Lagudah and Appels, 1992; Liu et al., 2014). In addition to the manipulation of *Ph* genes, irradiation mutation and tissue culture-mediated somaclonal variations also have been used to induce chromosome breakage and rearrangement in wheat wide hybridisation (Baum, Lagudah and Appels, 1992; Jauhar and Chibbar, 1999).

It is worth noting that while homoeologous recombination can generate novel gene combinations and phenotypes, it may also destabilise the karyotype and lead to aberrant meiotic behaviour and reduced fertility (De Storme and Mason, 2014; Gaeta and Chris Pires, 2010). Selection, either naturally or artificially, plays a significant role to retain the lines with the desirable fertility, stabilised chromosome inheritance, and advantageous variations (Gaeta and Chris Pires, 2010).

SECTION 5. General interactions with other organisms (ecology)

5.1. Interactions in agricultural ecosystems

5.1.1. Weeds

Competition with other plants for light, water and nutrition can reduce the yield of wheat crops. There are a number of weeds which are associated with wheat crops, however not all warrant control in wheat production or in all seasons. Weeds common in wheat crops world-wide include wild oats (*Avena fatua* L.), fat hen (*Chenopodium album*), canary grass (*Phalaris minor*) and cleavers (*Galium aparine*) (Jabran et al., 2017). Examples of weeds affecting wheat in specific countries are shown in Table 5.1.. Herbicide resistance is an important problem in the management of weeds and several of the most common weeds, namely wild oats, canary grass and annual ryegrass exhibit resistance to herbicides globally (Heap, 2018).

5.1.2. Vertebrate pests

Damage to wheat crops by birds has been noted around the world. Birds such as geese (Cummings, 2016), crows (Kennedy and Connery, 2008), cockatoos (Temby and Marshall, 2003) and sparrows (Dawson, 1970) feed on seeds, dig and tear out plants, or otherwise damage cereal crops. Birds may also damage grain stored on farm (GRDC, 2014, 2015).

Animals such as feral pigs, wild boars, kangaroos, rabbits, moose and deer can also cause considerable damage to wheat plants by feeding on seedlings or trampling mature plants (Amici et al., 2012; Gentle, Phinn and Speed, 2010).

Rodents cause significant losses to wheat crops worldwide both directly by gnawing and feeding and indirectly by spoilage and contamination. This damage can be highly variable and strongly dependent on rodent density (Brown et al., 2007). Rodents are opportunistic feeders and their diet can include seeds, the pith of stems and other plant materials (Caughley et al., 1998). Rodents may eat seeds at the seed source or they may hoard seed (AGRI-FACTS, 2002). The dominant rodent pest in wheat crops depends on the geographical location. For example, the lesser bandicoot rat (*Bandicota bengalensis*) in India (Parshad, 1999), the montane vole (*Microtus montanus*) in North America (Witmer et al., 2007), the common vole (*Microtus arvalis*) in Europe (Jacob and Tkadlec, 2010) and the house mouse (*Mus musculus*) in Australia (ACIAR, 2003) are the predominating rodent pests, respectively.

Table 5.1. Common weeds in wheat crops

Location	Scientific name	Common name	References
Australia	*Raphanus raphanistrum* *Lolium rigidum* Gaudin *Phalaris paradoxa* L. *Echinochloa colona* (L.) Link. *Conyza* spp. *Bromus* spp.	wild radish annual ryegrass paradoxa grass awnless barnyard grass fleabane brome grasses	GRDC, 2014, 2015
Canada	*Polygonum convolvulus* L. *Stellaria media* L. *Sinapsis arvensis* L. *Cirsium arvense* L.	wild buckwheat chickweed wild mustard Canada thistle	Mason and Spaner, 2006
Europe	*Alopecurus myosuroides* *Agrostis* spp. *Bromus sterilis* *Lolium* spp. *Poa annua* *Tripleurospermum inodorum* *Stellaria media* L. *Papaver rhoeas* *Veronica* spp. *Cirsium arvense* L. *Viola arvensis* *Raphanus raphanistrum* *Sinapsis arvensis* L. *Capsella bursa-pastoris* *Bifora* spp. *Convolvulus arvensis* *Galeopsis* spp. *Polygonum* spp.	blackgrass bentgrass sterile brome ryegrass annual meadowgrass scentless chamomile common chickweed corn poppy speedwells Canada thistle field pansy wild radish wild mustard shepherds' purse bifora field bindweed hemp nettle knotweed	Gianessi, Sankula and Reigner, 2003
China (People's Republic of) and India	*Calystegia* spp. *Capsella bursa-pastoris* *Cirsium* spp.	bindweed shepherds' purse thistles	Jabran et al., 2017
United States	*Kochia scoparia* *Avena fatua* *Polygonum convolvulus* *Setaria* spp. *Chenopodium album* *Bromus* spp. *Lamium* spp.	kochia wild oat wild buckwheat green foxtail common lambsquarters cheatgrass henbit or deadnettle	Van Wychen, 2017

5.1.1. Invertebrate pests

Many insects have been described to affect wheat worldwide. Although damage caused by most of these insects is either insignificant or limited to isolated areas, some pests inflict serious yield and forage losses. Some of these pest problems are directly linked to the unique farming system employed in a particular area, while other pests are opportunistic or generalist herbivores that do not specifically target wheat as a host (Miller and Pike, 2002). Insects usually do not cause major direct damage in wheat, unless populations reach very high levels (Duveiller, Singh and Nicol, 2007). More information on insect pests affecting wheat can be found in Miller and Pike (2002) and Annex A.

Wheat stored as grain is subject to a number of insect and mite pests, many of which have developed cosmopolitan distributions over the years (Miller and Pike, 2002). Proper storage involves ensuring that stored grain is free from insects and then maintaining grain moisture and temperature at sufficiently low levels to inhibit insect activity and development. Treatment of contaminated grain with appropriate chemicals prevents pest outbreaks. Many insect species have developed resistance to frequently used pesticides. Current research on stored product integrated pest management seeks to develop biological and cultural control methods for managing pests (Miller and Pike, 2002).

5.1.2. Pathogens

Wheat diseases can reduce the quantity and quality of grain yield. It has been estimated that 12.4% of world-wide wheat yield is lost annually due to diseases (Oerke, 2006). The incidence and impact of pathogens varies across and within wheat growing regions but typically increases with the intensity of the crop productivity (Oerke, 2006). Foliar diseases are the most important yield constraints in irrigated wheat systems that are characterised by dense stands and high tiller density. In contrast, soil borne pathogens are more frequently found in rain-fed wheat cropping (Duveiller, Singh and Nicol, 2007). Disease management plans rely on cultural practices that break the disease cycles, the application of biocide chemicals and planting disease resistant wheat varieties. Disease resistant varieties are developed by breeding programs that survey for sources of genetic resistance and combine a number of resistance factors in a single variety. There are also coordinated international surveillance programs that monitor the progress of diseases worldwide and guide management strategies (e.g. RustTracker.org[13]).

Information on wheat diseases commonly found in agricultural systems can be found in specialised compendia (Bockus et al., 2010; Mehta, 2014; Wiese, 1987) and Annex A.

Foliar diseases caused by fungi

Some of the most important wheat diseases caused by fungi are wheat rusts, the blotch diseases and Fusarium head blight/scab disease.

Wheat rust diseases are caused by fungi belonging to the genus *Puccinia*. *P. graminis* f. sp. *tritici*, *P. striiformis* f. sp. *tritici* and *P. triticina* are the causal agents of the stem, stripe and leaf rusts, respectively. Wheat rust diseases cause substantial losses in global wheat production annually. A large percentage of wheat varieties cultivated worldwide are susceptible to these diseases and in some cases susceptibility leads to 80-100% yield losses. The constant emergence of new virulent strains of wheat rusts constitutes a threat to wheat production across the globe (Figueroa, Hammond-Kosack and Solomon, 2018).

Three different diseases caused by Ascomycete fungi are known as the blotch diseases: Septoria tritici blotch (caused by *Zymoseptoria tritici*), Septoria nodorum blotch (*Parastagonospora nodorum*) and tan spot (*Pyrenophora tritici-repentis*). Septoria tritici blotch is the primary leaf disease of wheat in temperate growing regions and is regarded as the primary threat to wheat production in Europe. Septoria nodorum blotch and tan spot are prominent diseases in Australia (Figueroa, Hammond-Kosack and Solomon, 2018). Tan spot is also common in other parts of the wheat-growing world. The use of minimum or zero tillage practices may be increasing the incidence of tan spot.

Fusarium head blight disease, also known as wheat scab or ear blight, is the most serious and hazardous floral disease of wheat. The disease is caused by the Ascomycete fungus *Fusarium graminearum* and leads to the premature senescence of the wheat head. Wheat crops are particularly prone to Fusarium head blight if rain prevails just prior to and during crop flowering. Fusarium head blight causes a reduction in grain yield and quality, but also

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[13] https://rusttracker.cimmyt.org/

leads to the accumulation in the grain of various mycotoxins that represent a major food safety risk and health hazard to humans and animals. In many countries, legal limits are in place on the permitted mycotoxin levels for the various end-uses (Figueroa, Hammond-Kosack and Solomon, 2018).

Soilborne pathogens

Soilborne pathogens have a global distribution and cause economic yield losses in areas of the world where cereals dominate the cropping system and result in suboptimal growing conditions. Soilborne disease pathogens of cereals invade the crown and root tissues, diminishing their capacity for efficient nutrient and water uptake (Singleton, 2002). In dryland areas, a complex of soilborne fungi and nematodes cause root rot diseases. Some of the most important diseases caused by soilborne pathogens include the root lesion and the cereal cyst nematode complex, caused by the nematodes *Pratylenchus thornei* and *Heterodera* spp. respectively. Similarly, soilborne fungi *Fusarium graminearum* and *Bipolaris sorokiniana* cause crown rot and common root rot diseases, respectively.

Viral pathogens

A number of viral diseases of wheat are present regionally and globally; refer to Annex A for a list. Viruses have high potential for economic impact, capable of causing high (up to 96%) localised yield losses when coinfection by multiple viruses occurs (Byamukama et al., 2014). Viral diseases may become more prevalent with climate change, as elevated CO_2 levels can increase viral titres (Trębicki et al., 2015).

The predominant and most economically relevant virus in North America is the *Wheat streak mosaic virus* (WSMV, genus *Tritimovirus*) (Byamukama et al., 2014), which can contribute to significant losses. WSMV is increasingly globally relevant, found in the Americas, Australia, Europe, Asia, and North Africa (Brunt et al., 1996; Dwyer et al., 2007; Singh et al., 2018). *Barley yellow dwarf virus* (BYDV, genus *Luteovirus*) is another significant viral disease (Choudhury et al., 2019) that is found globally. In individual wheat fields prone to infection, it can cause average yield loss of between 11% and 33% (reviewed by Walls III, Rajotte and Rosa, 2019).

An important vector of the WSMV and at least four other viruses is wheat curl mite (WCM), *Aceria tosichella* (reviewed by Skoracka, Rector and Hein, 2018). Transmission occurs by wind dispersion of viruliferous WCMs from infected plants (Singh et al., 2018). Other transmission vectors include aphids (e.g. for BYDV transmission) and seeds, with vectors and viruses benefitting from ‘green bridges’ between growing seasons where viruses may be harboured by alternate host organisms (Dwyer et al., 2007; Singh et al., 2018).

Infected wheat displays symptoms that are dependent on the virus. Typically, chlorosis and streaking of leaves are observed for mosaic viruses, and purpling for yellow dwarf viruses. Mixed infections produce more severe symptoms, but no additional unique symptoms (Burrows et al., 2009). Symptoms are fewer and milder as plants mature and they become more resistant to infection (Somsen and Sill, 1970).

5.1.3. Non-domesticated animals and incidental human contact

Wheat is generally considered non-toxic to animals, supported by the diversity of pest species (see Sections 5.1.2. and 5.1.3.) and its use as food and feed. Wheat pollen is able to induce grass pollen allergic reactions (Constantin et al., 2009). High exposure is limited to peak flowering season (Andersson and Lidholm, 2003) and by the limited travelling distance of wheat pollen (see Section 2.2.). Details on food allergens and the use of wheat in food and feed can be found in the OECD ‘Consensus document on compositional considerations for new varieties of bread wheat (*Triticum aestivum*): key food and feed nutrients, anti-nutrients and toxicants' (OECD, 2003).

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Annex A. Most common diseases and pests in *Triticum aestivum*

Specialised Compendia

Bockus et al. (2010), Chelkowski (1991), Mehta (2014), Wiese (1987).

Online databases

- Wheat Diseases and Pests: a guide for field identification (CIMMYT)[14]
- GrainGenes database (USDA)[15]
- Wheat Doctor (CIMMYT)[16]
- Diseases of wheat (*Triticum* spp. L.) (The American Phytopathological Society)[17]
- European and Mediterranean Plant Protection Organization (EPPO) database[18]

Table A.1. Viruses, mycoplasms

Disease	Agent
Agropyron mosaic virus	*Agropyron mosaic virus* (AgMV). Geographic occurrence, e.g. in Eurasia, Canada and the United States
Barley stripe mosaic hordeivirus	*Barley stripe mosaic hordeivirus* (BSMV). Geographic occurrence, e.g. in Eurasia, Northern America and the Pacific
Barley yellow dwarf virus	Barley yellow dwarf virus (BYDV). Geographic occurrence world-wide; wheat varieties show different tolerance level (Baltenberger, Ohm and Foster, 1987); tolerance level had been increased through cross breeding with resistant Agropyron varieties (Goulart et al., 1993; Sharma et al., 1989).
Barley yellow streak mosaic virus	*Barley yellow streak mosaic virus*. Geographic occurrence, e.g. in Canada and the United States
Barley yellow striate mosaic cytorhabdovirus	*Barley yellow striate mosaic cytorhabdovirus* (BYSMV). Geographic occurrence, e.g. in Africa, Eurasia, Middle East and Pacific
Brome mosaic virus	*Brome mosaic virus* (BMV). Geographic occurrence, e.g. in Eurasia, Australia, South Africa and the United States
European wheat striate mosaic tenuivirus	*European wheat striate mosaic tenuivirus* (EWSMV). Geographic occurrence e.g. in Czechia, Poland, Romania, Denmark, Finland, Sweden, Germany, United Kingdom and Spain
Wheat American striate mosaic virus	*Wheat American striate mosaic cytorhabdovirus* (WASMV). Geographic occurrence, e.g. in Canada and the United States
Wheat dwarf virus	*Wheat dwarf virus* (WDV). Geographic occurrence, e.g. in Bulgaria, Czechia, Slovak Republic, Hungary, former USSR, France and Sweden
Wheat soilborne mosaic virus	*Wheat soilborne mosaic virus*. Geographic occurrence, e.g. in China, Japan, Italy and the United States
Wheat spindle streak mosaic virus	*Wheat spindle streak mosaic virus* (WSSMV). Geographic occurrence, e.g. in France, Germany, Italy, India, Japan, China, and United States
Wheat streak mosaic virus	*Wheat streak mosaic virus* (WSMV). Geographic occurrence e.g. in Canada, the United States, Romania and Jordan
Wheat yellow leaf virus	*Wheat yellow leaf virus* (WYLV). Geographic occurrence, e.g. in Japan and Italy
Wheat yellow mosaic bymovirus	*Wheat yellow mosaic bymovirus* (WYMV). Geographic occurrence e.g. in China, Japan, Korea, Canada and France

Source: Brunt et al. (1996).

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[14] https://repository.cimmyt.org/xmlui/handle/10883/1115

[15] https://graingenes.org/GG3/

[16] http://wheatdoctor.cimmyt.org/seed

[17] https://www.apsnet.org/edcenter/resources/commonnames/Pages/Wheat.aspx

[18] https://gd.eppo.int/

Table A.2. Bacteria

Disease	Agent
Basal glume rot	*Pseudomonas syringae* pv. *atrofaciens* (McCulloch)
Black chaff, Bacterial leaf streak	*Xanthomonas translucens* pv. *undulosa* and *Xanthomonas translucens* pv. *translucens*. This pathogen causes disease mainly in wheat, but can infect a number of other Poaceae species, such as barley, triticale and rye

Source: Brunt et al. (1996)

Table A.3. Fungi

Disease	Agent
Ergot	*Claviceps purpurea*: infects florets and produces grain-like sclerotia containing mycotoxins (ergot alkaloids). The fungal grains are harvested with the wheat grains and, if not removed, mycotoxin contamination of products occurs
Eyespot, stembreak, straw breaker	*Oculimacula yallundae* (Wallwork and Spooner). Syn: *Pseudocercosporella herpotrichoides* (Fron.) Deight.
Fusarium diseases	Numerous *Fusarium* species play a part in the pathology of the cereal fusaria. The major species are: – *Fusarium culmorum* (W.G. Smith) Sacc. var. *culmorum* – *Fusarium avenaceum* (Fr.) Sacc. var. *avenaceum* – *Fusarium graminearum* Schwabe (perfect form: *Gibberella zeae* (Schw.) Petch): widespread, especially harmful not only to wheat but also to maize. – *Fusarium poae* (Peck) Wollenw.: occurs sporadically, often in conjunction with the grass mite (*Siteroptes graminum* [Reuter]), which feeds on the fungus and helps it to proliferate. – Other species found in wheat include: *Fusarium acuminatum* Ell. et Kellerm. (*Gibberella acuminata* Wollenw.), *Fusarium dimerum* Penzig, *Fusarium equiseti* (Corda) Sacc. (*Gibberella intricans* Wollenw.), *Fusarium sporotrichioides* Sherb., *Fusarium tricinctum* (Corda) Sacc. and, *Fusarium moniliforme* Sheldon sensu Wollenw. et Reinking.
Mould	*Aspergillus* ssp./*Penicillium* ssp. can proliferate during storage. Both are potential mycotoxin producers (Ochratoxin A).
Phoma leaf spot	*Phoma glomerata* (Cda.) Wr. et Hochaf.
Powdery mildew of cereals	*Blumeria graminis* (DC) Speer f. sp. *tritici*. Syn: *Erysiphe graminis* DC. f. sp. *tritici* March Resistance genes, e.g. *Mlk*, *Pm1* to *Pm9*, *M1Ax*, *U1* and *U2*, can be found in different wheat varieties and related species (Heun and Fischbeck, 1987, 1989; Hovmøller, 1989; Zeller, Lutz and Stephan, 1993).
Rhizoctonia root rot	*Rhizoctonia* spp., *Thanatephorus cucumeris* (Frank) Donk.
Rusts	
- Yellow/stripe rust	*Puccinia striiformis* f. sp. *tritici* West., Syn.: *Puccinia glumarum* Erikss. et Henn. Formation of pathotypes which specialize in wheat or barley. In exceptional cases wheat stripe rust strains may attack highly susceptible barley varieties or vice versa.
- Leaf rust of wheat	*Puccinia triticina* Erikss., Syn.: *Puccinia recondita* Rob. ex Desm. f. sp. *tritici*, Syn.: *Puccinia rubigovera* Wint. Formation of pathotypes, alternate host *Thalictrum* spp.
- Black stem rust of wheat	*Puccinia graminis* Pers. f. sp. *tritici*. Development of formae speciales specialised in rye, barley, oats, wheat and grasses. Numerous pathotypes formed.
Septoria nodorum blotch, *Stagonospora nodorum* blotch	*Parastagonospora nodorum* (Berk.), Syn.: *Leptosphaeria nodorum* (E. Müll.), conidial form *Septoria nodorum* Berk., Syn.: *Phaesopheria nodorum* (E. Müll.) Hejarude. Only partial resistance in wheat found (Bostwick, Ohm and Shaner, 1993; Jeger et al., 1983).
Septoria tritici blotch	*Zymoseptoria tritici*. Syns: *Mycosphaerella graminicola* (Fckl.) Sanderson, conidial form: *Septoria tritici* Rob. ex Desm.
Smuts	
- Loose smut of wheat	*Ustilago tritici* (Pers.) Rostr.
- Stinking smut (Common bunt)	Various *Tilletia* species with different sori, including: – *Tilletia caries* (DC.) Tul. Syn.: *Tilletia tritici* (Bjerk.) Wint. – *Tilletia foetida* (Wallr.) Liro, Syn.: *Tilletia laevis* Kühn or *Tilletia foetens* (Bjerk. Et Curt.) Schroet. – *Tilletia intermedia* (Gassner) Savul. Syn.: *Tilletia tritici* f. sp. *intermedia* Gassner
- Dwarf bunt of wheat	*Tilletia controversa* Kühn

- Karnal bunt	*Tilletia indica* Mitra. Syn: *Neovossia indica* (Mit.) Mund.
- Stripe/flag smut	*Urocystis agropyri* (Preuss.) Schroet.
Take-all	*Gaeumannomyces graminis* (Sacc.) v. Arx. et Olivier var. *tritici* Walker Several varieties with overlapping hosts, var. *tritici* attacks wheat, triticale, barley and rye.
Tan spot	*Pyrenophora tritici-repentis* (Died.) Drechsl. Syns: *Drechslera tritici-repentis* (Died.) Shoem., perfect form: *Pyrenophora trichostoma* (Fr.) Fckl.

Source: Brunt et al. (1996)

Table A.4. Animals

Pest	Agent
Aphids:	
- Grain aphids	*Macrosiphum avenae* (Fabr.), Syn.: *Sitobion avenae* (Fabr.) Also in barley, oats, rye, maize, fodder grasses. Aphid species which does not alternate hosts.
- Oat or bird cherry aphid	*Rhopalosiphum padi* (L.) Alternate-host aphid with broad host plant profile among cereal and grass species, e.g. barley, oats, maize, fodder grasses.
- Rose grain aphid	*Metopolophium dirhodum* (Walk.) Alternate-host aphid (also in barley, oats, rye, maize, fodder grasses).
- Apart from the above-mentioned species of aphid, the following species may cause damage to cereals, maize and grasses:	Bromegrass aphid (*Diuraphis bromicola* [H.R.L.]), cat's-tail aphid (*Diuraphis mühlei* [Börn.]), corn leaf aphid (*Rhopalosiphum maidis* [Fitch.]), yellow cherry/reed canary grass aphid (*Rhopalomyzus lonicerae* [Siebold], *Rhopalomyzus poae* [Gill.]), cocksfoot aphid (*Hyalopteroides humilis* [Walk.]), *Laingia psammae* (Theob.), *Schizaphis nigerrima* H.R.L., *Metopolophium festucae* (Theob.), green grain aphid (*Schizaphis graminum* [Rond.]), grain aphid (*Sitobion granarium* [Kirby]), cob aphid (*Sipha maydis* [Pass.], *Sipha glyeriae* [Kalt.]), black (bean) aphid (*Aphis fabae* Scop.), green peach aphid (*Myzus persicae* [Sulz.])
Cereal cyst nematodes, cereal stem eelworm	*Heterodera avenae* Woll. Also attacks barley, oats, rye, fodder grasses. Several biotypes distinguished by their host profile.
Cereal leaf beetle	Red-throated cereal leaf beetle (*Oulema melanopus* [L.], Syn.: *Lema melanopa* [L.]), Blue cereal leaf beetle (*Oulema lichenis* [Voet], Syn.: *Lema lichenis* [Voet])
Corn beetle	*Zabrus tenebroides* Goeze (corn ground beetle) Also found in barley, oats, rye, maize, fodder grasses.
Crane-fly larvae	Larvae of the marsh crane-fly (*Pales* (*Tipula*) *paludosa* Meig.), Common crane-fly (*Pales* (*Tipula*) *oleracea* L.), Autumn crane-fly (*Pales* (*Tipula*) *czizeki* de Jong). Also in barley, oats, rye, maize, fodder grasses.
March fly larvae	*Bibio hortulans* (L.), *Bibio marci* (L.), *Bibio johannis* (L.), *Bibio clavipes* (Meig.) Also in barley, oats, rye, maize, fodder grasses.
Myriapods	Various species of myriapods, notably the common millipedes *Cylindroiulus teutonicus* (Pocock) and *Blaniulus guttulatus* (Bosc.) Also in barley, oats, rye, maize, fodder grasses.
Root aphids	*Anoecia corni* (Fabr.), *Anoecia vagans* (Koch), *Aploneura graminis* (Buckt.), *Aploneura lentisci* Pass., *Byrsocrypta personata* Börner, *Forda marginata* Koch, *Forda formicaria* V. Heyden, *Geoica discreta* Börner, *Tetraneura ulmi* (L.) Also in barley, oats, rye, maize, fodder grasses.
Slugs	Various species of slug, notably the field slug (*Deroceras reticulatum* O.F. Müll., *Deroceras agreste* L.), the garden/blackfield slug (*Arion hortensis* [Fér.], *Arion rufus* [L.]). Also in barley, oats, rye, maize, fodder grasses.
Wheat and grass bugs	Wheat and grass bugs are a non-homogeneous group of pests. The greatest economic damage is caused by wheat bugs (*Eurygaster* spp.).

	Also in barley, oats, rye, maize, fodder grasses.
Wheat seed gall nematode	*Anguina tritici* (Steinbuch) Filipjev.

Source: Brunt et al. (1996)

Annex B. Biotechnology applications for wheat improvement

Wheat breeding, like other crop breeding, has relied heavily on spontaneously occurring natural genetic variations and induced genetic variations using radiation such as gamma rays or mutagenic chemicals such as ethyl methanesulfonate (EMS). Biotechnological tools provide an expanded toolset for wheat breeders to introduce novel genetic variation into wheat plants for breeding selection.

One way to introduce a new trait in wheat is through genetic engineering or modification. Typically, this process allows the introduction of a DNA sequence from one or more organisms into the genome of a recipient organism. Because genetic engineering in wheat involves a phase of tissue culture, only the few wheat varieties that are amenable to this process can be genetically engineered (also named ‘genetically modified’ or ‘transgenic’). These varieties can then be crossed with elite cultivars to transfer the new trait. Argentina has authorised one transgenic drought and herbicide tolerant wheat variety known as HB4 for commercial planting. After Argentina in 2020, Brazil approved HB4 wheat for cultivation in March 2023, following feed and food use approvals in 2021. Several countries have approved HB4 wheat for feed and food uses since 2020 (ISAAA, 2023). Field trials of transgenic bread wheat been undertaken in Argentina[19], Australia[20], the Europe Union[21], Canada[22] and the United States[23] with traits including herbicide tolerance, pathogen resistance, insect resistance, abiotic stress tolerance, yield enhancement and improved nutritional quality.

The development of emerging genome-editing technologies provides another way to introduce new traits into wheat, and/or alter existing traits. The method known as clustered regulatory interspaced short palindromic repeats (CRISPR/Cas9) has been used to create genetic and phenotypic variation in wheat related to disease resistance (Wang et al., 2014; Zhang et al., 2017; Su et al., 2019), yield (Zhang et al., 2016; Wang et al., 2018), herbicide tolerance (Zhang et al., 2019), and quality traits (Li et al., 2020; Sanchez-Leon et al., 2018). An advantage of genome editing for wheat is the potential for altering multiple genes simultaneously. Wheat has a large and complex hexaploidy genomes with high functional redundancy and complementarity among it’s A, B, and D subgenomes, resulting in six alleles for most wheat genes. This genome complexity makes it challenging to alter multiple or all copies of a target gene through naturally occurring mutations or conventional mutation breeding methods. One example of overcoming this challenge is the use of multiplexed CRISPR/Cas9 for the simultaneous mutation of up to 35 of the 45 different α-gliadin genes (Sanchez-Leon et al., 2018). It is also possible to use CRISPR in wheat without integrating heterologous DNA into the genome, because the vectors are either not

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[19] National Bioeconomy Directorate at the Ministry of Agriculture, Livestock and Fisheries, Argentina, https://www.argentina.gob.ar/agricultura/alimentos-y-bioeconomia/ogm-vegetal-eventos-con-autorizacion-comercial.

[20] Office of Gene Technology Regulator, Australia. http://www.ogtr.gov.au/.

[21] European Commission GMO Register, https://ec.europa.eu/food/plant/gmo/eu_register_en.

[22] Canadian Food Inspection Agency, http://www.inspection.gc.ca/.

[23] United States Department of Agriculture, https://www.aphis.usda.gov/aphis/home/.

integrated into the wheat genome (Zhang et al., 2016; Liang et al., 2017) or are segregated out through crossing (Wang et al., 2017).

While the biotechnologies described above have been applied to wheat improvement by introducing new genetic variations and traits into wheat, these technologies are continuously being refined (Puchta 2017; Nasti and Voytas 2021) and new technologies and approaches are expected to emerge. Collectively these tools are expected to expand opportunities for wheat improvement.

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