

Wheat is a grass widely cultivated for its seed, a cereal grain that is a worldwide staple food. The many species of wheat together make up the genus *Triticum* (/ˈtrɪtɪkəm/); the most widely grown is common wheat (*T. aestivum*). The archaeological record suggests that wheat was first cultivated in the regions of the Fertile Crescent around 9600 BC. Botanically, the wheat kernel is a caryopsis, a type of fruit.

Wheat is grown on more land area than any other food crop (220.7 million hectares or 545 million acres in 2021). World trade in wheat is greater than for all other crops combined. In 2021, world wheat production was 771 million tonnes (850 million short tons), making it the second most-produced cereal after maize (known as corn in the US and Australia; wheat is often called corn in other countries). Since 1960, world production of wheat and other grain crops has tripled and is expected to grow further through the middle of the 21st century. Global demand for wheat is increasing because of the usefulness of gluten to the food industry.

Wheat is an important source of carbohydrates. Globally, it is the leading source of vegetable proteins in human food, having a protein content of about 13%, which is relatively high compared to other major cereals but relatively low in protein quality (supplying essential amino acids). When eaten as the whole grain, wheat is a source of multiple nutrients and dietary fiber. In a small part of the general population, gluten – which comprises most of the protein in wheat – can trigger coeliac disease, noncoeliac gluten sensitivity, gluten ataxia, and dermatitis herpetiformis.

## Description

A: Plant; B ripe ear of corn; 1 spikelet before flowering; 2 the same, flowering and spread, enlarged; 3 flowers with glumes; 4 stamens 5 pollen; 6 and 7 ovaries with juice scales; 8 and 9 parts of the scar; 10 fruit husks; 11, 12, 13 seeds, natural size and enlarged; 14 the same cut up, enlarged.

Wheat is a stout grass of medium to tall height. Its stem is jointed and usually hollow, forming a straw. There can be many stems on one plant. It has long narrow leaves, their bases sheathing the stem, one above each joint. At the top of the stem is the flower head, containing some 20 to 100 flowers. Each flower contains both male and female parts. The flower, which is wind-pollinated, is housed in a pair of small leaflike glumes. The two (male) stamens and (female) stigmas protrude outside the glumes. The flowers are grouped into spikelets, each with between two and six flowers. Each fertilised carpel develops into a wheat grain or berry; botanically a fruit, it is often called a seed. The grains ripen to a golden yellow; a head of grain is called an ear.

Leaves emerge from the shoot apical meristem in a telescoping fashion until the transition to reproduction i.e. flowering. The last leaf produced by a wheat plant is known as the flag leaf. It is denser and has a higher photosynthetic rate than other leaves, to supply carbohydrate to the developing ear. In temperate countries the flag leaf, along with the second and third highest leaf

on the plant, supply the majority of carbohydrate in the grain and their condition is paramount to yield formation. Wheat is unusual among plants in having more stomata on the upper (adaxial) side of the leaf, than on the under (abaxial) side. It has been theorised that this might be an effect of it having been domesticated and cultivated longer than any other plant. Winter wheat generally produces up to 15 leaves per shoot and spring wheat up to 9 and winter crops may have up to 35 tillers (shoots) per plant (depending on cultivar).

Wheat roots are among the deepest of arable crops, extending as far down as 2 metres (6 ft 7 in). While the roots of a wheat plant are growing, the plant also accumulates an energy store in its stem, in the form of fructans, which helps the plant to yield under drought and disease pressure, but it has been observed that there is a trade-off between root growth and stem non-structural carbohydrate reserves. Root growth is likely to be prioritised in drought-adapted crops, while stem non-structural carbohydrate is prioritised in varieties developed for countries where disease is a bigger issue.

Depending on variety, wheat may be awned or not awned. Producing awns incurs a cost in grain number, but wheat awns photosynthesise more efficiently than their leaves with regards to water usage, so awns are much more frequent in varieties of wheat grown in hot drought-prone countries than those generally seen in temperate countries. For this reason, awned varieties could become more widely grown due to climate change. In Europe, however, a decline in climate resilience of wheat has been observed.

## History

Origin and 21st century production areas of wheat

Domestication

Further information: Domestication

Hunter-gatherers in West Asia harvested wild wheats for thousands of years before they were domesticated, perhaps as early as 21,000 BC, but they formed a minor component of their diets. This phase of pre-domestication cultivation lasted at least a thousand years, during which early cultivars were spread around the region and slowly developed the traits that would come to characterise their domesticated forms.

Repeated harvesting and sowing of the grains of wild grasses led to the creation of domestic strains, as mutant forms ('sports') of wheat were more amenable to cultivation. In domesticated wheat, grains are larger, and the seeds (inside the spikelets) remain attached to the ear by a toughened rachis during harvesting. In wild strains, a more fragile rachis allows the ear to shatter easily, dispersing the spikelets. Selection for larger grains and non-shattering heads by farmers might not have been deliberately intended, but simply have occurred because these traits made gathering the seeds easier; nevertheless such 'incidental' selection was an

important part of crop domestication. As the traits that improve wheat as a food source involve the loss of the plant's natural seed dispersal mechanisms, highly domesticated strains of wheat cannot survive in the wild.

Wild einkorn wheat (*T. monococcum* subsp. *boeoticum*) grows across Southwest Asia in open parkland and steppe environments. It comprises three distinct races, only one of which, native to Southeast Anatolia, was domesticated. The main feature that distinguishes domestic einkorn from wild is that its ears do not shatter without pressure, making it dependent on humans for dispersal and reproduction. It also tends to have wider grains. Wild einkorn was collected at sites such as Tell Abu Hureyra (c. 10,700–9000 BC) and Mureybet (c. 9800–9300 BC), but the earliest archaeological evidence for the domestic form comes after c. 8800 BC in southern Turkey, at Çayönü, Cafer Höyük, and possibly Nevalı Çori. Genetic evidence indicates that it was domesticated in multiple places independently.

Wild emmer wheat (*T. turgidum* subsp. *dicoccoides*) is less widespread than einkorn, favouring the rocky basaltic and limestone soils found in the hilly flanks of the Fertile Crescent. It is more diverse, with domesticated varieties falling into two major groups: hulled or non-shattering, in which threshing separates the whole spikelet; and free-threshing, where the individual grains are separated. Both varieties probably existed in prehistory, but over time free-threshing cultivars became more common. Wild emmer was first cultivated in the southern Levant, as early as 9600 BC. Genetic studies have found that, like einkorn, it was domesticated in southeastern Anatolia, but only once. The earliest secure archaeological evidence for domestic emmer comes from Çayönü, c. 8300–7600 BC, where distinctive scars on the spikelets indicated that they came from a hulled domestic variety. Slightly earlier finds have been reported from Tell Aswad in Syria, c. 8500–8200 BC, but these were identified using a less reliable method based on grain size.

## Early farming

Sickles with stone microblades were used to harvest wheat in the Neolithic period, c. 8500–4000 BC

Einkorn and emmer are considered two of the founder crops cultivated by the first farming societies in Neolithic West Asia. These communities also cultivated naked wheats (*T. aestivum* and *T. durum*) and a now-extinct domesticated form of Zanduri wheat (*T. timopheevii*), as well as a wide variety of other cereal and non-cereal crops. Wheat was relatively uncommon for the first thousand years of the Neolithic (when barley predominated), but became a staple after around 8500 BC. Early wheat cultivation did not demand much labour. Initially, farmers took advantage of wheat's ability to establish itself in annual grasslands by enclosing fields against grazing animals and re-sowing stands after they had been harvested, without the need to systematically remove vegetation or till the soil. They may also have exploited natural wetlands and floodplains to practice *décrue* farming, sowing seeds in the soil left behind by receding floodwater. It was harvested with stone-bladed sickles. The ease of storing wheat and other

cereals led farming households to become gradually more reliant on it over time, especially after they developed individual storage facilities that were large enough to hold more than a year's supply.

Wheat grain was stored after threshing, with the chaff removed. It was then processed into flour using ground stone mortars. Bread made from ground einkorn and the tubers of a form of club rush (*Bolboschoenus glaucus*) was made as early as 12,400 BC. At Çatalhöyük (c. 7100–6000 BC), both wholegrain wheat and flour was used to prepare bread, porridge and gruel. Apart from food, wheat may also have been important to Neolithic societies as a source of straw, which could be used for fuel, wicker-making, or wattle and daub construction.

## Spread

Domestic wheat was quickly spread to regions where its wild ancestors did not grow naturally. Emmer was introduced to Cyprus as early as 8600 BC and einkorn c. 7500 BC; emmer reached Greece by 6500 BC, Egypt shortly after 6000 BC, and Germany and Spain by 5000 BC. "The early Egyptians were developers of bread and the use of the oven and developed baking into one of the first large-scale food production industries." By 4000 BC, wheat had reached the British Isles and Scandinavia. Wheat likely appeared in China's lower Yellow River around 2600 BC.

The oldest evidence for hexaploid wheat has been confirmed through DNA analysis of wheat seeds, dating to around 6400–6200 BC, recovered from Çatalhöyük. As of 2023, the earliest known wheat with sufficient gluten for yeasted breads was found in a granary at Assiros in Macedonia dated to 1350 BC. From the Middle East, wheat continued to spread across Europe and to the Americas in the Columbian exchange. In the British Isles, wheat straw (thatch) was used for roofing in the Bronze Age, and remained in common use until the late 19th century. White wheat bread was historically a high status food, but during the nineteenth century it became in Britain an item of mass consumption, displacing oats, barley and rye from diets in the North of the country. It became "a sign of a high degree of culture". After 1860, the enormous expansion of wheat production in the United States flooded the world market, lowering prices by 40%, and (along with the expansion of potato growing) made a major contribution to the nutritional welfare of the poor.

Sumerian cylinder seal impression dating to c. 3200 BC showing an ensi and his acolyte feeding a sacred herd wheat stalks; Ninurta was an agricultural deity and, in a poem known as the "Sumerian Georgica", he offers detailed advice on farming

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## Evolution

## Phylogeny

Wheat origins by repeated hybridization and polyploidy. Not all species are shown.

Some wheat species are diploid, with two sets of chromosomes, but many are stable polyploids, with four sets of chromosomes (tetraploid) or six (hexaploid). Einkorn wheat (*Triticum monococcum*) is diploid (AA, two complements of seven chromosomes,  $2n=14$ ). Most tetraploid wheats (e.g. emmer and durum wheat) are derived from wild emmer, *T. dicoccoides*. Wild emmer is itself the result of a hybridization between two diploid wild grasses, *T. urartu* and a wild goatgrass such as *Ae. speltoide*s. The hybridization that formed wild emmer (AABB, four complements of seven chromosomes in two groups,  $4n=28$ ) occurred in the wild, long before domestication, and was driven by natural selection. Hexaploid wheats evolved in farmers' fields as wild emmer hybridized with another goatgrass, *Ae. squarrosa* or *Ae. tauschii*, to make the hexaploid wheats including bread wheat.

A 2007 molecular phylogeny of the wheats gives the following not fully-resolved cladogram of major cultivated species; the large amount of hybridisation makes resolution difficult. Markings like "6N" indicate the degree of polyploidy of each species:

## Taxonomy

During 10,000 years of cultivation, numerous forms of wheat, many of them hybrids, have developed under a combination of artificial and natural selection. This complexity and diversity of status has led to much confusion in the naming of wheats.

## Major species

Hexaploid species (6N)

Common wheat or bread wheat (*T. aestivum*) – The most widely cultivated species in the world.

Spelt (*T. spelta*) – Another species largely replaced by bread wheat, but in the 21st century grown, often organically, for artisanal bread and pasta.

Tetraploid species (4N)

Durum (*T. durum*) – A wheat widely used today, and the second most widely cultivated wheat.

Emmer (*T. turgidum* subsp. *dicoccum* and *T. t. conv. durum*) – A species cultivated in ancient times, derived from wild emmer, *T. dicoccoides*, but no longer in widespread use.

Khorasan or Kamut (*T. turgidum* ssp. *turanicum*, also called *T. turanicum*) is an ancient grain type; Khorasan is a historical region in modern-day Afghanistan and the northeast of Iran. The grain is twice the size of modern wheat and has a rich nutty flavor.

Diploid species (2N)

Einkorn (*T. monococcum*). Domesticated from wild einkorn, *T. boeoticum*, at the same time as emmer wheat.

Hulled versus free-threshing species

Hulled wheat & Einkorn. Note how the einkorn ear breaks down into intact spikelets.

The four wild species of wheat, along with the domesticated varieties einkorn, emmer and spelt, have hulls. This more primitive morphology (in evolutionary terms) consists of toughened glumes that tightly enclose the grains, and (in domesticated wheats) a semi-brittle rachis that breaks easily on threshing. The result is that when threshed, the wheat ear breaks up into spikelets. To obtain the grain, further processing, such as milling or pounding, is needed to remove the hulls or husks. Hulled wheats are often stored as spikelets because the toughened glumes give good protection against pests of stored grain. In free-threshing (or naked) forms, such as durum wheat and common wheat, the glumes are fragile and the rachis tough. On threshing, the chaff breaks up, releasing the grains.

## As a food

### Naming of grain classes

Wheat grain classes are named by color, season, and hardness. The classes used in the United States are:

Durum – Hard, translucent, light-colored grain used to make semolina flour for pasta and bulghur; high in protein, specifically, gluten protein.

Hard Red Spring – Hard, brownish, high-protein wheat used for bread and hard baked goods. Bread flour and high-gluten flours are commonly made from hard red spring wheat. It is primarily traded on the Minneapolis Grain Exchange.

Hard Red Winter – Hard, brownish, mellow high-protein wheat used for bread, hard baked goods and as an adjunct in other flours to increase protein in pastry flour for pie crusts. Some brands of unbleached all-purpose flours are commonly made from hard red winter wheat alone. It is primarily traded on the Kansas City Board of Trade. Many varieties grown from Kansas south are descendant from a variety known as "turkey red", which was brought to Kansas by Mennonite immigrants from Russia. Marquis wheat was developed to prosper in the shorter growing season in Canada, and is grown as far south as southern Nebraska.

Soft Red Winter – Soft, low-protein wheat used for cakes, pie crusts, biscuits, and muffins. Cake flour, pastry flour, and some self-rising flours with baking powder and salt added, for example, are made from soft red winter wheat. It is primarily traded on the Chicago Board of Trade.

Hard White – Hard, light-colored, opaque, chalky, medium-protein wheat planted in dry, temperate areas. Used for bread and brewing.

Soft White – Soft, light-colored, very low protein wheat grown in temperate moist areas. Used for pie crusts and pastry.

#### Food value and uses

Wheat is used in a wide variety of foods.

Wheat, hard red winter

Nutritional value per 100 g (3.5 oz)

Energy 1,368 kJ (327 kcal)

Carbohydrates

71.18 g

Sugars 0.41

Dietary fiber 12.2 g

Fat

1.54 g

Protein

12.61 g

Vitamins      Quantity%DV†

Thiamine (B1) 33%0.383 mg

Riboflavin (B2) 10%0.115 mg

Niacin (B3) 5.464 mg

Pantothenic acid (B5) 19%0.954 mg

Vitamin B6 23%0.3 mg

Folate (B9) 10%38 µg

Choline 6%31.2 mg

Vitamin E 7%1.01 mg

Vitamin K 2%1.9 µg

Minerals      Quantity%DV†

Calcium	3%29 mg
Iron	25%3.19 mg
Magnesium	35%126 mg
Manganese	190%3.985 mg
Phosphorus	41%288 mg
Potassium	12%363 mg
Sodium	0%2 mg
Zinc	28%2.65 mg
Other constituents	Quantity
Water	13.1 g
Selenium	70.7 µg

[Link to USDA Database Entry](#)

Units

µg = micrograms • mg = milligrams

IU = International units

†Percentages are roughly approximated using US recommendations for adults.

Source: USDA FoodData Central

Wheat is a staple cereal worldwide. Raw wheat berries can be ground into flour or, using hard durum wheat only, can be ground into semolina; germinated and dried creating malt; crushed or cut into cracked wheat; parboiled (or steamed), dried, crushed and de-branned into bulgur also known as groats. If the raw wheat is broken into parts at the mill, as is usually done, the outer husk or bran can be used in several ways. Wheat is a major ingredient in such foods as bread, porridge, crackers, biscuits, muesli, pancakes, pasta, pies, pastries, pizza, semolina, cakes, cookies, muffins, rolls, doughnuts, gravy, beer, vodka, boza (a fermented beverage), and breakfast cereals. In manufacturing wheat products, gluten is valuable to impart viscoelastic functional qualities in dough, enabling the preparation of diverse processed foods such as breads, noodles, and pasta that facilitate wheat consumption.

## Nutrition

Raw red winter wheat is 13% water, 71% carbohydrates including 12% dietary fiber, 13% protein, and 2% fat (table). Some 75–80% of the protein content is as gluten. In a reference amount of 100 grams (3.5 oz), wheat provides 1,368 kilojoules (327 kilocalories) of food energy and is a rich source (20% or more of the Daily Value, DV) of multiple dietary minerals, such as manganese, phosphorus, magnesium, zinc, and iron (table). The B vitamins, niacin (36% DV), thiamine (33% DV), and vitamin B6 (23% DV), are present in significant amounts (table).



Wheat is a significant source of vegetable proteins in human food, having a relatively high protein content compared to other major cereals. However, wheat proteins have a low quality for human nutrition, according to the DIAAS protein quality evaluation method. Though they contain adequate amounts of the other essential amino acids, at least for adults, wheat proteins are deficient in the essential amino acid lysine. Because the proteins present in the wheat endosperm (gluten proteins) are particularly poor in lysine, white flours are more deficient in lysine compared with whole grains. Significant efforts in plant breeding are made to develop lysine-rich wheat varieties, without success, as of 2017. Supplementation with proteins from other food sources (mainly legumes) is commonly used to compensate for this deficiency, since the limitation of a single essential amino acid causes the others to break down and become excreted, which is especially important during growth.

## Health advisories

Consumed worldwide by billions of people, wheat is a significant food for human nutrition, particularly in the least developed countries where wheat products are primary foods. When eaten as the whole grain, wheat supplies multiple nutrients and dietary fiber recommended for children and adults. In genetically susceptible people, wheat gluten can trigger coeliac disease. Coeliac disease affects about 1% of the general population in developed countries. The only known effective treatment is a strict lifelong gluten-free diet. While coeliac disease is caused by a reaction to wheat proteins, it is not the same as a wheat allergy. Other diseases triggered by eating wheat are non-coeliac gluten sensitivity (estimated to affect 0.5% to 13% of the general population), gluten ataxia, and dermatitis herpetiformis. Certain short-chain carbohydrates present in wheat, known as FODMAPs (mainly fructose polymers), may be the cause of non-coeliac gluten sensitivity. As of 2019, reviews have concluded that FODMAPs only explain certain gastrointestinal symptoms, such as bloating, but not the extra-digestive symptoms that people with non-coeliac gluten sensitivity may develop health disorders. Other wheat proteins, amylase-trypsin inhibitors, have been identified as the possible activator of the innate immune system in coeliac disease and non-coeliac gluten sensitivity. These proteins are part of the plant's natural defence against insects and may cause intestinal inflammation in humans.

## Production and consumption

### Global

#### Wheat production, 2021

Country	Millions of tonnes
China	136.9
India	109.6
Russia	78.1
United States	44.8
France	36.6
Ukraine	32.2

Pakistan 27.5

World 771

In 2021, world wheat production was 771 million tonnes, led by China, India, and Russia which collectively provided 42% of the world total. As of 2019, the largest exporters were Russia (32 million tonnes), United States (27), Canada (23) and France (20), while the largest importers were Indonesia (11 million tonnes), Egypt (10.4) and Turkey (10.0). In 2021, wheat was grown on 220.7 million hectares or 545 million acres worldwide, more than any other food crop. World trade in wheat is greater than for all other crops combined. Global demand for wheat is increasing due to the unique viscoelastic and adhesive properties of gluten proteins, which facilitate the production of processed foods, whose consumption is increasing as a result of the worldwide industrialization process and westernization of diets.

## Historical factors

### Wheat prices in England, 1264–1996

Wheat became a central agriculture endeavor in the worldwide British Empire in the 19th century, and remains of great importance in Australia, Canada and India. In Australia, with vast lands and a limited work force, expanded production depended on technological advances, especially regarding irrigation and machinery. By the 1840s there were 900 growers in South Australia. They used "Ridley's Stripper", to remove the heads of grain, a reaper-harvester perfected by John Ridley in 1843. In Canada, modern farm implements made large scale wheat farming possible from the late 1840s. By 1879, Saskatchewan was the center, followed by Alberta, Manitoba and Ontario, as the spread of railway lines allowed easy exports to Britain. By 1910, wheat made up 22% of Canada's exports, rising to 25% in 1930 despite the sharp decline in prices during the worldwide Great Depression. Efforts to expand wheat production in South Africa, Kenya and India were stymied by low yields and disease. However, by 2000 India had become the second largest producer of wheat in the world. In the 19th century the American wheat frontier moved rapidly westward. By the 1880s 70% of American exports went to British ports. The first successful grain elevator was built in Buffalo in 1842. The cost of transport fell rapidly. In 1869 it cost 37 cents to transport a bushel of wheat from Chicago to Liverpool. In 1905 it was 10 cents.

In the 20th century, global wheat output expanded by about 5-fold, but until about 1955 most of this reflected increases in wheat crop area, with lesser (about 20%) increases in crop yields per unit area. After 1955 however, there was a ten-fold increase in the rate of wheat yield improvement per year, and this became the major factor allowing global wheat production to increase. Thus technological innovation and scientific crop management with synthetic nitrogen fertilizer, irrigation and wheat breeding were the main drivers of wheat output growth in the second half of the century. There were some significant decreases in wheat crop area, for instance in North America. Better seed storage and germination ability (and hence a smaller requirement to retain harvested crop for next year's seed) is another 20th-century technological innovation. In Medieval England, farmers saved one-quarter of their wheat harvest as seed for

the next crop, leaving only three-quarters for food and feed consumption. By 1999, the global average seed use of wheat was about 6% of output. In the 21st century, rising temperatures associated with global warming are reducing wheat yield in several locations.

## Peak wheat

Food production per person increased since 1961.

Peak wheat is the concept that agricultural production, due to its high use of water and energy inputs, is subject to the same profile as oil and other fossil fuel production. The central tenet is that a point is reached, the "peak", beyond which agricultural production plateaus and does not grow any further, and may even go into permanent decline.

Based on current supply and demand factors for agricultural commodities (e.g., changing diets in the emerging economies, biofuels, declining acreage under irrigation, growing global population, stagnant agricultural productivity growth), some commentators are predicting a long-term annual production shortfall of around 2% which, based on the highly inelastic demand curve for food crops, could lead to sustained price increases in excess of 10% a year – sufficient to double crop prices in seven years.

According to the World Resources Institute, global per capita food production has been increasing substantially for the past several decades.

## Agronomy

### Growing wheat

Wheat is an annual crop. It can be planted in autumn and harvested in early summer as winter wheat in climates that are not too severe, or planted in spring and harvested in autumn as spring wheat. It is normally planted after tilling the soil by ploughing and then harrowing to kill weeds and create an even surface. The seeds are then scattered on the surface, or drilled into the soil in rows. Winter wheat lies dormant during a winter freeze. It needs to develop to a height of 10 to 15 cm before the cold intervenes, so as to be able to survive the winter; it requires a period with the temperature at or near freezing, its dormancy then being broken by the thaw or rise in temperature. Spring wheat does not undergo dormancy. Wheat requires a deep soil, preferably a loam with organic matter, and available minerals including soil nitrogen, phosphorus, and potassium. An acid and peaty soil is not suitable. Wheat needs some 30 to 38 cm of rain in the growing season to form a good crop of grain.

The farmer may intervene while the crop is growing to add fertilizer, water by irrigation, or pesticides such as herbicides to kill broad-leaved weeds or insecticides to kill insect pests. The farmer may assess soil minerals, soil water, weed growth, or the arrival of pests to decide timely and cost-effective corrective actions, and crop ripeness and water content to select the right

moment to harvest. Harvesting involves reaping, cutting the stems to gather the crop; and threshing, breaking the ears to release the grain; both steps are carried out by a combine harvester. The grain is then dried so that it can be stored safe from mould fungi.

## Crop development

### Wheat developmental stages on the BBCH and Zadok's scales

Wheat normally needs between 110 and 130 days between sowing and harvest, depending upon climate, seed type, and soil conditions. Optimal crop management requires that the farmer have a detailed understanding of each stage of development in the growing plants. In particular, spring fertilizers, herbicides, fungicides, and growth regulators are typically applied only at specific stages of plant development. For example, it is currently recommended that the second application of nitrogen is best done when the ear (not visible at this stage) is about 1 cm in size (Z31 on Zadoks scale). Knowledge of stages is also important to identify periods of higher risk from the climate. Farmers benefit from knowing when the 'flag leaf' (last leaf) appears, as this leaf represents about 75% of photosynthesis reactions during the grain filling period, and so should be preserved from disease or insect attacks to ensure a good yield. Several systems exist to identify crop stages, with the Feekes and Zadoks scales being the most widely used. Each scale is a standard system which describes successive stages reached by the crop during the agricultural season. For example, the stage of pollen formation from the mother cell, and the stages between anthesis and maturity, are susceptible to high temperatures, and this adverse effect is made worse by water stress.

## Farming techniques

Technological advances in soil preparation and seed placement at planting time, use of crop rotation and fertilizers to improve plant growth, and advances in harvesting methods have all combined to promote wheat as a viable crop. When the use of seed drills replaced broadcasting sowing of seed in the 18th century, another great increase in productivity occurred. Yields of pure wheat per unit area increased as methods of crop rotation were applied to land that had long been in cultivation, and the use of fertilizers became widespread.

Improved agricultural husbandry has more recently included pervasive automation, starting with the use of threshing machines, and progressing to large and costly machines like the combine harvester which greatly increased productivity. At the same time, better varieties such as Norin 10 wheat, developed in Japan in the 1930s, or the dwarf wheat developed by Norman Borlaug in the Green Revolution, greatly increased yields.

In addition to gaps in farming system technology and knowledge, some large wheat grain-producing countries have significant losses after harvest at the farm and because of poor roads, inadequate storage technologies, inefficient supply chains and farmers' inability to bring the produce into retail markets dominated by small shopkeepers. Some 10% of total wheat

production is lost at farm level, another 10% is lost because of poor storage and road networks, and additional amounts are lost at the retail level.

In the Punjab region of the Indian subcontinent, as well as North China, irrigation has been a major contributor to increased grain output. More widely over the last 40 years, a massive increase in fertilizer use together with the increased availability of semi-dwarf varieties in developing countries, has greatly increased yields per hectare. In developing countries, use of (mainly nitrogenous) fertilizer increased 25-fold in this period. However, farming systems rely on much more than fertilizer and breeding to improve productivity. A good illustration of this is Australian wheat growing in the southern winter cropping zone, where, despite low rainfall (300 mm), wheat cropping is successful even with relatively little use of nitrogenous fertilizer. This is achieved by crop rotation with leguminous pastures. The inclusion of a canola crop in the rotations has boosted wheat yields by a further 25%. In these low rainfall areas, better use of available soil-water (and better control of soil erosion) is achieved by retaining the stubble after harvesting and by minimizing tillage.

## Pests and diseases

Pests – or pests and diseases, depending on the definition – consume 21.47% of the world's wheat crop annually.

## Diseases

### Rust-affected wheat seedlings

There are many wheat diseases, mainly caused by fungi, bacteria, and viruses. Plant breeding to develop new disease-resistant varieties, and sound crop management practices are important for preventing disease. Fungicides, used to prevent the significant crop losses from fungal disease, can be a significant variable cost in wheat production. Estimates of the amount of wheat production lost owing to plant diseases vary between 10 and 25% in Missouri. A wide range of organisms infect wheat, of which the most important are viruses and fungi.

The main wheat-disease categories are:

Seed-borne diseases: these include seed-borne scab, seed-borne *Stagonospora* (previously known as *Septoria*), common bunt (stinking smut), and loose smut. These are managed with fungicides.

Leaf- and head- blight diseases: Powdery mildew, leaf rust, *Septoria tritici* leaf blotch, *Stagonospora* (*Septoria*) *nodorum* leaf and glume blotch, and *Fusarium* head scab.

Crown and root rot diseases: Two of the more important of these are 'take-all' and *Cephalosporium* stripe. Both of these diseases are soil borne.

Stem rust diseases: Caused by *Puccinia graminis* f. sp. *tritici* (basidiomycete) fungi e.g. Ug99

Wheat blast: Caused by *Magnaporthe oryzae* *Triticum*.

Viral diseases: Wheat spindle streak mosaic (yellow mosaic) and barley yellow dwarf are the two most common viral diseases. Control can be achieved by using resistant varieties.

A historically significant disease of cereals including wheat, though commoner in rye is ergot; it is unusual among plant diseases in also causing sickness in humans who ate grain contaminated with the fungus involved, *Claviceps purpurea*.

## Animal pests

Pupa of the wheat weevil, *Sitophilus granarius*, inside a wheat kernel

Among insect pests of wheat is the wheat stem sawfly, a chronic pest in the Northern Great Plains of the United States and in the Canadian Prairies. Wheat is the food plant of the larvae of some Lepidoptera (butterfly and moth) species including the flame, rustic shoulder-knot, setaceous Hebrew character and turnip moth. Early in the season, many species of birds and rodents feed upon wheat crops. These animals can cause significant damage to a crop by digging up and eating newly planted seeds or young plants. They can also damage the crop late in the season by eating the grain from the mature spike. Recent post-harvest losses in cereals amount to billions of dollars per year in the United States alone, and damage to wheat by various borers, beetles and weevils is no exception. Rodents can also cause major losses during storage, and in major grain growing regions, field mice numbers can sometimes build up explosively to plague proportions because of the ready availability of food. To reduce the amount of wheat lost to post-harvest pests, Agricultural Research Service scientists have developed an "insect-o-graph", which can detect insects in wheat that are not visible to the naked eye. The device uses electrical signals to detect the insects as the wheat is being milled. The new technology is so precise that it can detect 5–10 infested seeds out of 30,000 good ones.

## Breeding objectives

In traditional agricultural systems, wheat populations consist of landraces, informal farmer-maintained populations that often maintain high levels of morphological diversity. Although landraces of wheat are no longer extensively grown in Europe and North America, they continue to be important elsewhere. The origins of formal wheat breeding lie in the nineteenth century, when single line varieties were created through selection of seed from a single plant noted to have desired properties. Modern wheat breeding developed in the first years of the twentieth century and was closely linked to the development of Mendelian genetics. The standard method of breeding inbred wheat cultivars is by crossing two lines using hand emasculation, then selfing or inbreeding the progeny. Selections are identified (shown to have the genes responsible for the varietal differences) ten or more generations before release as a variety or cultivar.

Major breeding objectives include high grain yield, good quality, disease- and insect resistance and tolerance to abiotic stresses, including mineral, moisture and heat tolerance. Wheat has been the subject of mutation breeding, with the use of gamma-, x-rays, ultraviolet light (collectively, radiation breeding), and sometimes harsh chemicals. The varieties of wheat created through these methods are in the hundreds (going as far back as 1960), more of them being created in higher populated countries such as China. Bread wheat with high grain iron and zinc content has been developed through gamma radiation breeding, and through conventional selection breeding. International wheat breeding is led by the International Maize and Wheat Improvement Center in Mexico. ICARDA is another major public sector international wheat breeder, but it was forced to relocate from Syria to Lebanon in the Syrian Civil War.

Pathogens and wheat are in a constant process of coevolution. Spore-producing wheat rusts are substantially adapted towards successful spore propagation, which is essentially to say its  $R_0$ . These pathogens tend towards high- $R_0$  evolutionary attractors.

## For higher yields

Breeding has increased yields over time

The presence of certain versions of wheat genes has been important for crop yields. Genes for the 'dwarfing' trait, first used by Japanese wheat breeders to produce Norin 10 short-stalked wheat, have had a huge effect on wheat yields worldwide, and were major factors in the success of the Green Revolution in Mexico and Asia, an initiative led by Norman Borlaug. Dwarfing genes enable the carbon that is fixed in the plant during photosynthesis to be diverted towards seed production, and they also help prevent the problem of lodging. "Lodging" occurs when an ear stalk falls over in the wind and rots on the ground, and heavy nitrogenous fertilization of wheat makes the grass grow taller and become more susceptible to this problem. By 1997, 81% of the developing world's wheat area was planted to semi-dwarf wheats, giving both increased yields and better response to nitrogenous fertilizer.

*T. turgidum* subsp. *polonicum*, known for its longer glumes and grains, has been bred into main wheat lines for its grain size effect, and likely has contributed these traits to *Triticum petropavlovskyi* and the Portuguese landrace group Arrancada. As with many plants, MADS-box influences flower development, and more specifically, as with other agricultural Poaceae, influences yield. Despite that importance, as of 2021 little research has been done into MADS-box and other such spikelet and flower genetics in wheat specifically.

The world record wheat yield is about 17 tonnes per hectare (15,000 pounds per acre), reached in New Zealand in 2017. A project in the UK, led by Rothamsted Research has aimed to raise wheat yields in the country to 20 t/ha (18,000 lb/acre) by 2020, but in 2018 the UK record stood at 16 t/ha (14,000 lb/acre), and the average yield was just 8 t/ha (7,100 lb/acre).

## For disease resistance

Different strains have been infected with the stem rust fungus. The strains bred to be resistant have their leaves unaffected or relatively unaffected by the fungus.

Wild grasses in the genus *Triticum* and related genera, and grasses such as rye have been a source of many disease-resistance traits for cultivated wheat breeding since the 1930s. Some resistance genes have been identified against *Pyrenophora tritici-repentis*, especially races 1 and 5, those most problematic in Kazakhstan. Wild relative, *Aegilops tauschii* is the source of several genes effective against TTKSK/Ug99 - Sr33, Sr45, Sr46, and SrTA1662 - of which Sr33 and SrTA1662 are the work of Olson et al., 2013, and Sr45 and Sr46 are also briefly reviewed therein.

Lr67 is an R gene, a dominant negative for partial adult resistance discovered and molecularly characterized by Moore et al., 2015. As of 2018 Lr67 is effective against all races of leaf, stripe, and stem rusts, and powdery mildew (*Blumeria graminis*). This is produced by a mutation of two amino acids in what is predicted to be a hexose transporter. The product then heterodimerizes with the susceptible's product, with the downstream result of reducing glucose uptake.

Lr34 is widely deployed in cultivars due to its abnormally broad effectiveness, conferring resistance against leaf- and stripe-rusts, and powdery mildew. Krattinger et al. 2009 finds Lr34 to also be an ABC transporter and conclude that this is the probably means of its effectiveness and the reason that it produces a 'slow rusting'/adult resistance phenotype.

Pm8 is a widely used powdery mildew resistance introgressed from rye (*Secale cereale*). It comes from the rye 1R chromosome, a source of many resistances since the 1960s.

Resistance to *Fusarium* head blight (FHB, *Fusarium* ear blight) is also an important breeding target. Marker-assisted breeding panels involving kompetitive allele specific PCR can be used. Singh et al. 2019 identify a KASP genetic marker for a pore-forming toxin-like gene providing FHB resistance.

## To create hybrid vigor

Because wheat self-pollinates, creating hybrid seed to provide the possible benefits of heterosis, hybrid vigor (as in the familiar F1 hybrids of maize), is extremely labor-intensive; the high cost of hybrid wheat seed relative to its moderate benefits have kept farmers from adopting them widely despite nearly 90 years of effort. Commercial hybrid wheat seed has been produced using chemical hybridizing agents, plant growth regulators that selectively interfere with pollen development, or naturally occurring cytoplasmic male sterility systems. Hybrid wheat has been a limited commercial success in Europe (particularly France), the United States and South Africa.



Synthetic hexaploids made by crossing the wild goatgrass wheat ancestor *Aegilops tauschii*, and other *Aegilops*, and various durum wheats are now being deployed, and these increase the genetic diversity of cultivated wheats.

## For gluten content

Modern bread wheat varieties have been cross-bred to contain greater amounts of gluten, which affords significant advantages for improving the quality of breads and pastas from a functional point of view. However, a 2020 study that grew and analyzed 60 wheat cultivars from between 1891 and 2010 found no changes in albumin/globulin and gluten contents over time. "Overall, the harvest year had a more significant effect on protein composition than the cultivar. At the protein level, we found no evidence to support an increased immunostimulatory potential of modern winter wheat."

## For water efficiency

Stomata (or leaf pores) are involved in both uptake of carbon dioxide gas from the atmosphere and water vapor losses from the leaf due to water transpiration. Basic physiological investigation of these gas exchange processes has yielded carbon isotope based method used for breeding wheat varieties with improved water-use efficiency. These varieties can improve crop productivity in rain-fed dry-land wheat farms.

## For insect resistance

The gene *Sm1* protects against the orange wheat blossom midge.

## Genomics

### Decoding the genome

In 2010, 95% of the genome of Chinese Spring line 42 wheat was decoded. This genome was released in a basic format for scientists and plant breeders to use but was not fully annotated. In 2012, an essentially complete gene set of bread wheat was published. Random shotgun libraries of total DNA and cDNA from the *T. aestivum* cv. Chinese Spring (CS42) were sequenced to generate 85 Gb of sequence (220 million reads) and identified between 94,000 and 96,000 genes. In 2018, a more complete Chinese Spring genome was released by a different team. In 2020, 15 genome sequences from various locations and varieties around the world were reported, with examples of their own use of the sequences to localize particular insect and disease resistance factors. Wheat Blast Resistance is controlled by *R* genes which are highly race-specific.

## Genetic engineering

For decades, the primary genetic modification technique has been non-homologous end joining (NHEJ). However, since its introduction, the CRISPR/Cas9 tool has been extensively adopted, for example:

To intentionally damage three homologs of TaNP1 (a glucose-methanol-choline oxidoreductase gene) to produce a novel male sterility trait, by Li et al. 2020

Blumeria graminis f.sp. tritici resistance has been produced by Shan et al. 2013 and Wang et al. 2014 by editing one of the mildew resistance locus o genes (more specifically one of the Triticum aestivum MLO (TaMLO) genes)

Triticum aestivum EDR1 (TaEDR1) (the EDR1 gene, which inhibits Bmt resistance) has been knocked out by Zhang et al. 2017 to improve that resistance

Triticum aestivum HRC (TaHRC) has been disabled by Su et al. 2019 thus producing Gibberella zeae resistance.

Triticum aestivum Ms1 (TaMs1) has been knocked out by Okada et al. 2019 to produce another novel male sterility

and Triticum aestivum acetolactate synthase (TaALS) and Triticum aestivum acetyl-CoA-carboxylase (TaACC) were subjected to base changes by Zhang et al. 2019 (in two publications) to confer herbicide resistance to ALS inhibitors and ACCase inhibitors respectively

As of 2021 these examples illustrate the rapid deployment and results that CRISPR/Cas9 has shown in wheat disease resistance improvement.

## In art

Wheatfield with Crows, an 1890 painting by Vincent van Gogh. Van Gogh Museum, Amsterdam

The Dutch artist Vincent van Gogh created the series Wheat Fields between 1885 and 1890, consisting of dozens of paintings made mostly in different parts of rural France. They depict wheat crops, sometimes with farm workers, in varied seasons and styles, sometimes green, sometimes at harvest. Wheatfield with Crows was one of his last paintings, and is considered to be among his greatest works.

In 1967, the American artist Thomas Hart Benton made his oil on wood painting Wheat, showing a row of uncut wheat plants, occupying almost the whole height of the painting, between rows of freshly-cut stubble. The painting is held by the Smithsonian American Art Museum.

In 1982, the American conceptual artist Agnes Denes grew a two-acre field of wheat at Battery Park, Manhattan. The ephemeral artwork has been described as an act of protest. The harvested wheat was divided and sent to 28 world cities for an exhibition entitled "The International Art Show for the End of World Hunger".