An **apple** is a round, edible fruit produced by an **apple tree** (*Malus spp.*, among them the **domestic** or **orchard apple**; ***Malus domestica***). Apple trees are cultivated worldwide and are the most widely grown species in the genus *Malus*. The tree originated in Central Asia, where its wild ancestor, *Malus sieversii*, is still found. Apples have been grown for thousands of years in Eurasia and were introduced to North America by European colonists. Apples have religious and mythological significance in many cultures, including Norse, Greek, and European Christian tradition.

Apples grown from seed tend to be very different from those of their parents, and the resultant fruit frequently lacks desired characteristics. For commercial purposes, including botanical evaluation, apple cultivars are propagated by clonal grafting onto rootstocks. Apple trees grown without rootstocks tend to be larger and much slower to fruit after planting. Rootstocks are used to control the speed of growth and the size of the resulting tree, allowing for easier harvesting.

There are more than 7,500 cultivars of apples.[3] Different cultivars are bred for various tastes and uses, including cooking, eating raw, and cider or apple juice production. Trees and fruit are prone to fungal, bacterial, and pest problems, which can be controlled by a number of organic and non-organic means. In 2010, the fruit's genome was sequenced as part of research on disease control and selective breeding in apple production.

From 2014 to 2023, there have been an average of 78 million tonnes of apples globally produced per year. In 2023, the worldwide production of apples was 83 million tonnes, with China accounting for nearly half of the total.[4]

Etymology

The word *apple*, whose Old English ancestor is *æppel*, is descended from the Proto-Germanic noun **aplaz*, descended in turn from Proto-Indo-European **h₂ébōl*.[5]

As late as the 17th century, the word also functioned as a generic term for all fruit, including nuts. This can be compared to the 14th-century Middle English expression *appel of paradis*, meaning a banana.[6]

Description

The apple is a deciduous tree, generally standing 2 to 4.5 metres (6 to 15 feet) tall in cultivation and up to 9 m (30 ft) in the wild. When cultivated, the size, shape and branch density are determined by rootstock selection and trimming method. The leaves are alternately arranged dark green-colored simple ovals with serrated margins and slightly downy undersides.[7]

Blossoms are produced in spring simultaneously with the budding of the leaves and are produced on spurs and some long shoots. The 3-to-4-centimeter (1-to-1+½-inch) flowers are white with a pink tinge that gradually fades, five petaled, with an inflorescence consisting of a cyme with 4–6 flowers. The central flower of the inflorescence is called the "king bloom"; it opens first and can develop a larger fruit.[7][8]

The fruit is a pome that matures in late summer or autumn, and cultivars exist in a wide range of sizes. Commercial growers aim to produce an apple that is 7 to 8.5 cm (2+¾ to 3+¼ in) in diameter, due to market preference. Some consumers, especially in Japan, prefer a larger apple, while apples less than 5.5 cm (2+¼ in) are generally used for juicing and have little fresh market value.

Skin

Skin, 0% overcolorSkin, 100% overcolor

The groundcolor of ripe apples is yellow, green, yellow-green or whitish yellow. The overcolor of ripe apples can be orange-red, pink-red, red, purple-red or brown-red. The overcolor amount can be 0–100%.[9] The skin may also be wholly or partly russeted (i.e. rough and brown). The skin is covered in a protective layer of epicuticular wax.[10] The exocarp (flesh) is generally pale yellowish-white,[9] though pink, yellow or green exocarps also occur.

Chemistry

Important volatile compounds in apples include acetaldehyde, ethyl acetate, 1-butanal, ethanol, 2-methylbutanal, 3-methylbutanal, ethyl propionate, ethyl 2-methylpropionate, ethyl butyrate, ethyl 2-methyl butyrate, hexanal, 1-butanol, 3-methylbutyl acetate, 2-methylbutyl acetate, 1-propyl butyrate, ethyl pentanoate, amyl acetate, 2-methyl-1-butanol, trans-2-hexenal, ethyl hexanoate, hexanol.[11][12]

Taxonomy

The apple as a species has been given a number of alternative scientific names, or synonyms. In modern times, *Malus pumila* and *Malus domestica* are the two main names in use. *M. pumila* is the older name, but *M. domestica* has become much more commonly used starting in the 21st century, especially in the western world. Two proposals were made to make *M. domestica* a conserved name: the earlier proposal was voted down by the Committee for Vascular Plants of the IAPT in 2014, but in April 2017 the Committee decided, with a narrow majority, that the newly popular name should be conserved.[13] The General Committee of the IAPT decided in June 2017 to approve this change, officially conserving *M. domestica*.[2]

Nevertheless, a number of publications published after 2017 still use *M. pumila* as the correct name, under an alternate taxonomy.[14]

Wild ancestors

The original wild ancestor of *Malus domestica* was *Malus sieversii*, found growing wild in the mountains of Central Asia in southern Kazakhstan, Kyrgyzstan, Tajikistan, and northwestern China.[7][15] Cultivation of the species, most likely beginning on the forested flanks of the Tian Shan mountains, progressed over a long period of time and permitted secondary introgression of genes from other species into the open-pollinated seeds. Significant exchange with *Malus sylvestris*, the crabapple, resulted in populations of apples being more related to crabapples than to the more morphologically similar progenitor *Malus sieversii*. In strains without recent admixture the contribution of the latter predominates.[16][17][18]

Genome

Apples are diploid (though triploid cultivars are not uncommon), have 17 chromosomes and an estimated genome size of approximately 650 Mb. Several whole genome sequences have been completed and made available. The first one in 2010 was based on the diploid cultivar 'Golden Delicious'.[19] However, this first whole genome sequence turned out to contain several errors[20] in part owing to the high degree of heterozygosity in diploid apples which, in combination with an ancient genome duplication, complicated the assembly. Recently, double- and trihaploid individuals have been sequenced, yielding whole genome sequences of higher quality.[21][22]

The first whole genome assembly was estimated to contain around 57,000 genes,[19] though the more recent genome sequences support estimates between 42,000 and 44,700 protein-coding genes.[21][22] The availability of whole genome sequences has provided evidence that the wild ancestor of the cultivated apple most likely is *Malus sieversii*. Re-sequencing of multiple accessions has supported this, while also suggesting extensive introgression from *Malus sylvestris* following domestication.[23]

Distribution and habitat

Central Asia is generally considered the center of origin for apples due to the genetic variability in specimens there.[24]

Cultivation

Wild *Malus sieversii* apple in Kazakhstan

History

The apple is thought to have been domesticated 4,000–10,000 years ago in the Tian Shan mountains, and then to have travelled along the Silk Road to Europe, with hybridization and introgression of wild crabapples from Siberia (*M. baccata*), the Caucasus (*M. orientalis*), and Europe (*M. sylvestris*). Only the *M. sieversii* trees growing on the western side of the Tian Shan mountains contributed genetically to the domesticated apple, not the isolated population on the eastern side.[23]

Chinese soft apples, such as *M. asiatica* and *M. prunifolia*, have been cultivated as dessert apples for more than 2,000 years in China. These are thought to be hybrids between *M. baccata* and *M. sieversii* in Kazakhstan.[23]

Among the traits selected for by human growers are size, fruit acidity, color, firmness, and soluble sugar. Unusually for domesticated fruits, the wild *M. sieversii* origin is only slightly smaller than the modern domesticated apple.[23]

At the Sammardenchia-Cueis site near Udine in Northeastern Italy, seeds from some form of apples have been found in material carbon dated to around 4000 BCE.[25] Genetic analysis has not yet been successfully used to determine whether such ancient apples were wild *Malus sylvestris* or *Malus domesticus* containing *Malus sieversii* ancestry.[26] It is generally also hard to distinguish in the archeological record between foraged wild apples and apple plantations.

There is indirect evidence of apple cultivation in the third millennium BCE in the Middle East. There was substantial apple production in the European classical antiquity, and grafting was certainly known then.[26] Grafting is an essential part of modern domesticated apple production, to be able to propagate the best cultivars; it is unclear when apple tree grafting was invented.[26]

Winter apples, picked in late autumn and stored just above freezing, have been an important food in Asia and Europe for millennia.[27] Of the many Old World plants that the Spanish introduced to Chiloé Archipelago in the 16th century, apple trees became particularly well adapted.[28] Apples were introduced to North America by colonists in the 17th century,[7] and the first apple orchard on the North American continent was planted in Boston by Reverend William Blaxton in 1625.[29] The only apples native to North America are crab apples, which were once called "common apples".[30]

Apple cultivars brought as seed from Europe were spread along Native American trade routes, as well as being cultivated on colonial farms. An 1845 United States apples nursery catalogue sold 350 of the "best" cultivars, showing the proliferation of new North American cultivars by the early 19th century.[30] In the 20th century, irrigation projects in Eastern Washington began and allowed the development of the multibillion-dollar fruit industry, of which the apple is the leading product.[7]

Until the 20th century, farmers stored apples in frostproof cellars during the winter for their own use or for sale. Improved transportation of fresh apples by train and road replaced the necessity for storage.[31][32] Controlled atmosphere facilities are used to keep apples fresh year-round. Controlled atmosphere facilities use high humidity, low oxygen, and controlled carbon dioxide levels to maintain fruit freshness. They were first used in the United States in the 1960s.[33]

Breeding

See also: Fruit tree propagation and Malling series

An apple tree in Germany

Many apples grow readily from seeds. However, more than with most perennial fruits, apples must be propagated asexually to obtain the sweetness and other desirable characteristics of the parent. This is because seedling apples are an example of "extreme heterozygotes", in that rather than inheriting genes from their parents to create a new apple with parental characteristics, they are instead significantly different from their parents, perhaps to compete with the many pests.[34] Triploid cultivars have an additional reproductive barrier in that three sets of chromosomes cannot be divided evenly during meiosis, yielding unequal segregation of the chromosomes (aneuploids). Even in the case when a triploid plant can produce a seed (apples are an example), it occurs infrequently, and seedlings rarely survive.[35]

Because apples are not true breeders when planted as seeds, although cuttings can take root and breed true, and may live for a century, grafting is usually used. The rootstock used for the bottom of the graft can be selected to produce trees of a large variety of sizes, as well as changing the winter hardiness, insect and disease resistance, and soil preference of the resulting tree. Dwarf rootstocks can be used to produce very small trees (less than 3.0 m or 10 ft high at maturity), which bear fruit many years earlier in their life cycle than full size trees, and are easier to harvest.[36]

Dwarf rootstocks for apple trees can be traced as far back as 300 BCE, to the area of Persia and Asia Minor. Alexander the Great sent samples of dwarf apple trees to Aristotle's Lyceum. Dwarf rootstocks became common by the 15th century and later

went through several cycles of popularity and decline throughout the world.[37] The majority of the rootstocks used to control size in apples were developed in England in the early 1900s. The East Malling Research Station conducted extensive research into rootstocks, and their rootstocks are given an "M" prefix to designate their origin. Rootstocks marked with an "MM" prefix are Malling-series cultivars later crossed with trees of 'Northern Spy' in Merton, England.[38]

Most new apple cultivars originate as seedlings, which either arise by chance or are bred by deliberately crossing cultivars with promising characteristics.[39] The words "seedling", "pippin", and "kernel" in the name of an apple cultivar suggest that it originated as a seedling. Apples can also form bud sports (mutations on a single branch). Some bud sports turn out to be improved strains of the parent cultivar. Some differ sufficiently from the parent tree to be considered new cultivars.[40]

Since the 1930s, the Excelsior Experiment Station at the University of Minnesota has introduced a steady progression of important apples that are widely grown, both commercially and by local orchardists, throughout Minnesota and Wisconsin. Its most important contributions have included 'Haralson' (which is the most widely cultivated apple in Minnesota), 'Wealthy', 'Honeygold', and 'Honeycrisp'.

Apples have been acclimatized in Ecuador at very high altitudes, where they can often, with the needed factors, provide crops twice per year because of constant temperate conditions year-round.[41]

Pollination

See also: Fruit tree pollination

Apple blossom from an old Ayrshire cultivarAn orchard mason bee on an apple bloom in British Columbia, Canada

Apples are self-incompatible; they must cross-pollinate to develop fruit. During the flowering each season, apple growers often utilize pollinators to carry pollen. Honey bees are most commonly used. Orchard mason bees are also used as supplemental pollinators in commercial orchards. Bumblebee queens are sometimes present in orchards, but not usually in sufficient number to be significant pollinators.[40][42]

Cultivars are sometimes classified by the day of peak bloom in the average 30-day blossom period, with pollinizers selected from cultivars within a 6-day overlap period. There are four to seven pollination groups in apples, depending on climate:

- Group A – Early flowering, 1 to 3 May in England ('Gravenstein', 'Red Astrachan')

- Group B – 4 to 7 May ('Idared', 'McIntosh')
- Group C – Mid-season flowering, 8 to 11 May ('Granny Smith', 'Cox's Orange Pippin')
- Group D – Mid/late season flowering, 12 to 15 May ('Golden Delicious', 'Calville blanc d'hiver')
- Group E – Late flowering, 16 to 18 May ('Braeburn', 'Reinette d'Orléans')
- Group F – 19 to 23 May ('Suntan')
- Group H – 24 to 28 May ('Court-Pendu Gris' – also called Court-Pendu plat)

One cultivar can be pollinated by a compatible cultivar from the same group or close (A with A, or A with B, but not A with C or D).[43]

Maturation and harvest

See also: Fruit picking and Fruit tree pruning

L. K. Relander, the former President of Finland, with his family picking apples in the 1930s

Cultivars vary in their yield and the ultimate size of the tree, even when grown on the same rootstock. Some cultivars, if left unpruned, grow very large—letting them bear more fruit, but making harvesting more difficult. Depending on tree density (number of trees planted per unit surface area), mature trees typically bear 40–200 kg (90–440 lb) of apples each year, though productivity can be close to zero in poor years. Apples are harvested using three-point ladders that are designed to fit amongst the branches. Trees grafted on dwarfing rootstocks bear about 10–80 kg (20–180 lb) of fruit per year.[40]

Some farms with apple orchards open them to the public so consumers can pick their own apples.[44]

Crops ripen at different times of the year according to the cultivar. Cultivar that yield their crop in the summer include 'Gala', 'Golden Supreme', 'McIntosh', 'Transparent', 'Primate', 'Sweet Bough', and 'Duchess'; fall producers include 'Fuji', 'Jonagold', 'Golden Delicious', 'Red Delicious', 'Chenango', 'Gravenstein', 'Wealthy', 'McIntosh', 'Snow', and 'Blenheim'; winter producers include 'Winesap', 'Granny Smith', 'King', 'Wagener', 'Swayzie', 'Greening', and 'Tolman Sweet'.[30]

Storage

Different kinds of apple cultivars in a wholesale food market

Commercially, apples can be stored for a few months in controlled atmosphere chambers to delay ethylene-induced ripening. Apples are commonly stored in chambers with higher

concentrations of carbon dioxide and high air filtration. This prevents ethylene concentrations from rising to higher amounts and preventing ripening from occurring too quickly.

For home storage, most cultivars of apple can be held for approximately two weeks when kept at the coolest part of the refrigerator (i.e. below 5 °C). Some can be stored up to a year without significant degradation.[*dubious* – *discuss*][45][*verification needed*] Some varieties of apples (e.g. 'Granny Smith' and 'Fuji') have more than three times the storage life of others.[46]

Non-organic apples may be sprayed with a substance 1-methylcyclopropene blocking the apples' ethylene receptors, temporarily preventing them from ripening.[47]