

1 Strawberries: a General Account

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1.1. Origin and History of Strawberry Cultivation

The genus *Fragaria* belongs to the family Rosaceae. Recorded history of the *Fragas* dates back to 23–79 AD in the writings of Pliny (Darrow, 1966). Early colonists in North America cultivated the native strawberry, *Fragaria virginiana*, which was a hardy plant with the ability to withstand cold temperature and drought. In the early 1600s, *F. virginiana* was imported to Europe from North America. In the 1700s, explorers found a wild strawberry in Chile, *Fragaria chiloensis*, which grew large fruit but was not well suited to a wide range of climates. Northern Europe, including France, cultivated the woodland strawberry, *Fragaria vesca* (L.), as early as 1300. It was appreciated as much for its flowers as for the fruit.

Additionally, musky strawberries, *Fragaria moschata*, were also cultivated in Europe and Russia for centuries. Musky strawberries are light red to purple, and have a strong vinous flavour like Muscat grapes.

In 1714, the most important event in the history of the modern strawberry took place (Darrow, 1966). Amédée-Francois Frézier, a member of the French army, returned from duty in Peru and Chile with some plants of *F. chiloensis*. When he arrived, he distributed his plants. One of them was interplanted alongside *F. virginiana* in Brest, France (Hancock and Luby, 1995). A natural hybrid comprising a hardy plant with large fruit developed by natural crossing and was therefore noticed. This natural hybrid was called *Fragaria* × *ananassa* Duch., and many former species have been supplanted by its cultivation ever since.

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1.2. Taxonomy and Biology

The French botanist Antoine Nicolas Duchesne is credited with identification of the natural hybrid *Fragaria* × *ananassa*. The cultivated strawberry *F.* × *ananassa* Duch. is a member of the family Rosaceae, subfamily Rosoideae, along with blackberries and raspberries. There are about 34 species of *Fragaria* found in Asia, America (North and South) and Europe, of which two are cultivated commercially for their fruit: *F. moschata*, the musky or Hautboy strawberry, and *F. vesca*, the woodland or alpine strawberry. These species were cultivated for centuries, but there is very little production of them today, due to the success of *F.* × *ananassa*.

The *F.* × *ananassa* is a perennial and arises from a crown of meristematic tissue or compressed stem tissue. The leaves, stems, runners, axillary crowns, inflorescences and roots all arise from the crown. The plant has trifoliate leaves that spiral around the crown, with buds in the leaf axils giving rise to the runners. The runners have two nodes, with a plant produced at the distal node. Strawberry blossoms contain many pistils, each with its own style and stigma attached to the receptacle. Botanically, the strawberry fruit is an 'accessory fruit' and is not a true berry. When fertilization occurs, the receptacle develops into a fleshy fruit. The flesh consists of the greatly enlarged flower receptacle and is embedded with the many true fruits, or achenes, which are popularly called seeds. These seeds are arranged on the outside of the receptacle tissue. The growth of the receptacle is dependent on successful fertilization of the ovules, with its size and shape

dependent on the number of achenes formed (Darnell, 2003).

Strawberries can be diploid, tetraploid, hexaploid, octoploid and even decaploid. The woodland strawberry, *F. vesca*, and most of the native species around the world are diploid. They range from dioecious to hermaphroditic and self-fertile to self-incompatible. Three known tetraploids are *Fragaria moupinensis*, *Fragaria orientalis*, and *Fragaria corymbosa*. *F. moschata* is a hexaploid strawberry and is known for its musky flavour. *F. chiloensis* and *F. virginiana* are both octoploid, with their flowers mostly being dioecious although some are hermaphroditic (Hancock *et al.*, 1996). This polyploidy of the *Fragaria* spp. makes selection of desirable traits via traditional breeding using cross-pollination of the flowering plants tedious and time consuming (Husaini *et al.*, 2011).

1.3. Area, Production and Yield

Strawberry is a highly popular crop and is in great demand for fresh markets as well as in the fruit processing industry for preparing jams and other products (Husaini and Abdin, 2008). Its popularity can be judged from the fact that the production of strawberries has increased considerably in recent years (Table 1.1, Figs 1.1–1.3).

The figures clearly show that worldwide strawberry production has shown a remarkable increase of about 53.5% and an expansion in area of about 12% in the period between 2003 and 2013. The steepest increase has been observed in Africa, where the production increased by 125.9% and area increased by 70.7%

Table 1.1. Total area and production of strawberry across major regions.

Region	Production (t)		Area (ha)	
	2003	2013	2003	2013
World	5,041,331	7,739,622	320,990	361,662
Europe	1,224,692	1,484,987	162,543	162,315
Asia	2,334,869	3,845,553	113,121	143,036
USA	977,945	1,360,869	19,587	23,549
Africa	184,582	417,135	6,250	10,671

Source: <http://faostat.fao.org/>.

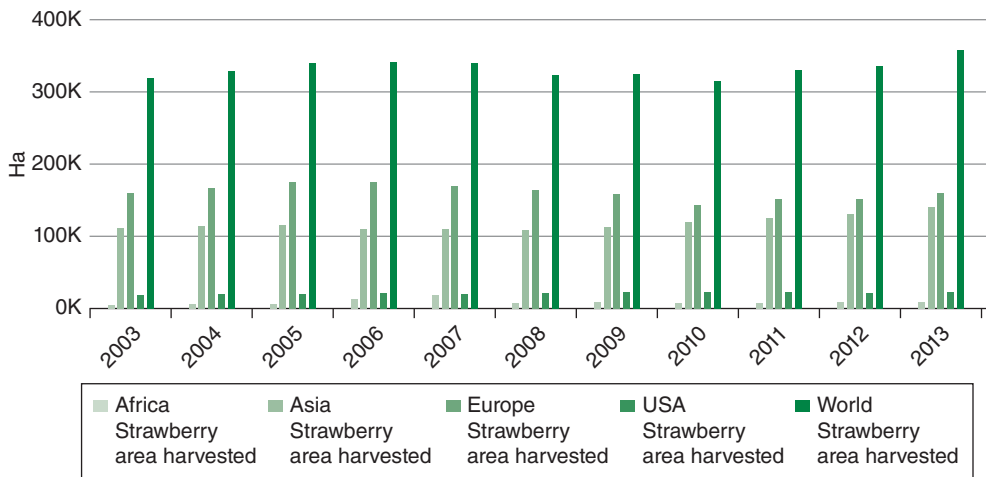


Fig. 1.1. Trend in strawberry area harvested across major regions. K, thousand.

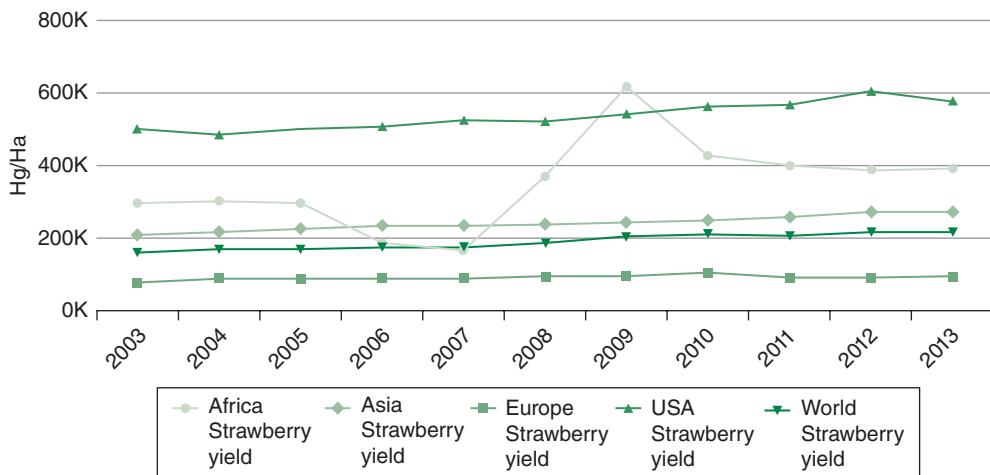


Fig. 1.2. Trend in strawberry yield across major regions. K, thousand.

in this decade. Next in rank comes Asia, where there has been 64.7% increase in production and 26.4% increase in area. The production and area in USA have increased by 39.1 and 20.2%, respectively. Europe has recorded an increase of 21.2% in production, despite a small decrease of 0.1% in the area under cultivation. Overall, the figures are encouraging, revealing the profitability and popularity of this glamour fruit across all major regions of the world.

There are hundreds of different strawberry cultivars. These have been produced

by plant breeders to fit particular environmental or marketing niches, and generally no single cultivar is grown worldwide or even nationwide. Each cultivar performs differently, depending on the climate and conditions in which it is grown. Octoploid strawberry accessions are extremely variable in morphology, photoperiod sensitivity and fruit quality (Husaini, 2010). To maximize strawberry production, it is important to choose a suitable strawberry cultivar that is well suited to a growing region. A good source of this information can be found on websites such as

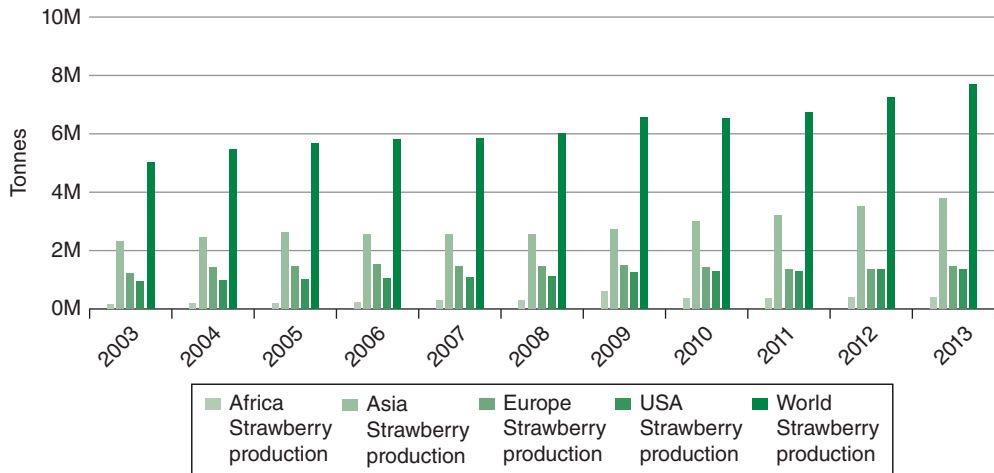


Fig. 1.3. Trend in strawberry production across major regions. M, million.

Strawberry Plants.org (<http://strawberryplants.org/2010/05/strawberry-varieties/>). Due to the difficulties imposed by the complicated octoploid genome on conventional breeding strategies, manipulation through recombinant DNA technology, Golden Gate cloning and CRISPR (clustered regularly interspaced short palindromic repeats)/Cas systems are favourable options in strawberry improvement. The problem of strawberry fruit softening is a classic example of this kind of intervention by biotechnological tools. Genetic transformation has also improved strawberries for many traits that confer adaptive advantage to these plants such as the challenges imposed by climate change (Husaini *et al.*, 2012) (see Chapter 14, this volume).

1.4. Health-promoting Properties

In the past few years, the antioxidant power of fruit has been considered an indicator of the beneficial bioactive compounds present in foodstuffs and therefore of their healthfulness. Indeed, strawberry phenolics are best known for their antioxidant and anti-inflammatory action, and possess direct and indirect antimicrobial, anti-allergy, and anti-hypertensive properties, as well as the capacity for inhibiting the activities of some physiological enzymes and receptors, preventing oxidative

stress-related diseases (Wang *et al.*, 1996). The major class of strawberry polyphenols is flavonoids, mainly anthocyanins. The most quantitatively important phenolic compounds present in strawberries are in the form of pelargonidin and cyanidin derivatives (Giampieri *et al.*, 2012, 2013, 2014).

There is consolidated evidence to classify strawberries as a functional food with several preventive and therapeutic health benefits (Basu *et al.*, 2014). Strawberries possess anticarcinogenic, antioxidative and genoprotective properties against multiple human and mouse cancer cell types both *in vitro* (Wang *et al.*, 2005; Zhang *et al.*, 2008) and *in vivo* in animal models (Carlton *et al.*, 2001; Stoner *et al.*, 2007), but human studies are still rare, and investigations particularly focused on patients with precancerous conditions are strongly advisable. Strawberry phenolics are able to: (i) detoxify free radicals, blocking their production; (ii) modulate the expression of genes involved in metabolism, cell proliferation and antioxidant defence; and (iii) protect and repair DNA damage. Several polyphenolic compounds such as anthocyanins, kaempferol, quercetin, fisetin, ellagitannins and ellagic acid have been reported in strawberries (Giampieri *et al.*, 2012, 2013, 2014). Fisetin possesses antioxidant, anti-inflammatory and anti-proliferative effects in a wide variety

of cancers (Ravichandran *et al.*, 2011). Most of the studies have been performed *in vivo*, in particular in lung cancer (Ravichandran *et al.*, 2011; Touil *et al.*, 2011), prostate cancer (Khan *et al.*, 2008), teratocarcinoma (Tripathi *et al.*, 2011) and skin cancer (Syed *et al.*, 2011).

A highly prevalent problem affecting nearly 21% of the world population is depression, and its prevalence has increased significantly by 6% during the past two decades. According to the World Health Organization, depression will become the second leading cause of disease-related disability by the year 2020. The antidepressant potential of fisetin has been investigated in two classical mouse models of despair tasks: tail suspension and forced swimming tests. Fisetin application (10 and 20 mg kg⁻¹, *per os*) inhibited the immobility time in both behavioural tests in a dose-dependent way, while the doses that affected the immobile response did not affect locomotor activity. In addition, neurochemical assays showed that fisetin produced an increase in serotonin and noradrenaline levels in the frontal cortex and hippocampus (Zhen *et al.*, 2012). These findings indicate that fisetin could serve as a novel natural antidepressant agent.

Anticarcinogenic effects of strawberries are mediated mainly through the detoxification of carcinogens, scavenging of reactive oxygen species, the decrease in oxidative DNA damage (Xue *et al.*, 2001; Stoner *et al.*, 2008), the reduction of cancer cell proliferation through apoptosis (Seeram *et al.*, 2006) and cell-cycle arrest (Stoner *et al.*, 2007), downregulation of activator protein 1 and nuclear factor- κ B, inhibition of Wnt signalling, tumour necrosis factor- α

(Zhang *et al.*, 2008) and angiogenesis (Atalay *et al.*, 2003; Duthie, 2007).

Strawberries (*F. × ananassa* Duch.) are a rich source of a wide variety of nutritive compounds such as sugars, vitamins and minerals, as well as non-nutritive, bioactive compounds such as flavonoids, anthocyanins and phenolic acids. The most abundant class of phytochemicals in strawberries is ellagitannins (i.e. sanguin-H-6), followed by flavonols (i.e. quercetin and kaempferol-3-malonyl glucoside), flavanols (i.e. catechins and procyanidins), and phenolic acids (i.e. caffeic and hydroxybenzoic acid derivatives) (Wang *et al.*, 1996; Giampieri *et al.*, 2012, 2013, 2014). All of these compounds exert a synergistic and cumulative effect on human health promotion and in disease prevention. Of its many positive characteristics, the nutritional value of strawberries is nearly perfect (Table 1.2). Eight medium strawberries contain more vitamin C than an orange, 20% of the recommended daily allowance for folic acid, no fat and no cholesterol, and are considered high in fibre. Another significant nutritional feature is the concentration of folate (24 μ g per 100 g of fresh fruit); among fruit, strawberries are one of the richest natural sources of this indispensable micronutrient, which represents an essential factor in health promotion and disease prevention (Tulipani *et al.*, 2008, 2009). Strawberries are also a notable source of manganese, and a good source of iodine, magnesium, copper, iron and phosphorus. Moreover, both their dietary fibre and fructose contents may contribute to regulating blood sugar levels by slowing digestion, while the fibre content may control calorie intake by its satiating effect.

Table 1.2. Nutritional composition of strawberry (*Fragaria × ananassa* Duch.). (From US Department of Agriculture: <http://ndb.nal.usda.gov/ndb/search/list?qlookup=09316&format=Full.>)

Component	Per 100 g	Standard error	Component	Per 100 g	Standard error
Nutrient			Lipids		
Water (g)	90.95	0.214	Fatty acids, total saturated (g)	0.015	–
Energy (kcal)	32	–	16:00 (g)	0.012	–
Energy (kJ)	136	–	18:00 (g)	0.003	–
Protein (g)	0.67	0.026	Fatty acids, total monounsaturated (g)	0.043	–
Total lipid (fat) (g)	0.3	0.047	16:1 undifferentiated (g)	0.001	–
Ash (g)	0.4	0.021	18:1 undifferentiated (g)	0.042	–
Carbohydrate, by difference (g)	7.68	–	Fatty acids, total polyunsaturated (g)	0.155	–
Fibre, total dietary (g)	2	0.152	18:2 undifferentiated (g)	0.09	–
Sugars, total (g)	4.89	–	18:3 undifferentiated (g)	0.065	–
Sucrose (g)	0.47	0.328	18:4 (g)	0	–
Glucose (dextrose) (g)	1.99	0.194	20:4 undifferentiated (g)	0	–
Fructose (g)	2.44	0.198	20:5 <i>n</i> -3 (EPA) (g)	0	–
Lactose (g)	0	0	22:5 <i>n</i> -3 (DPA) (g)	0	–
Maltose (g)	0	0	22:6 <i>n</i> -3 (DHA) (g)	0	–
Galactose (g)	0	0	Cholesterol (mg)	0	–
Starch (g)	0.04	0.029	Phytosterols (mg)	12	–
Vitamins			Amino acids		
Vitamin C, total ascorbic acid (mg)	58.8	2.473	Tryptophan (g)	0.008	–
Thiamin (mg)	0.024	0.003	Threonine (g)	0.02	–
Riboflavin (mg)	0.022	0.008	Isoleucine (g)	0.016	–
Niacin (mg)	0.386	0.037	Leucine (g)	0.034	–
Pantothenic acid (mg)	0.125	0.003	Lysine (g)	0.026	–
Vitamin B-6 (mg)	0.047	0.012	Methionine (g)	0.002	–
Folate, total (µg)	24	5.465	Cystine (g)	0.006	–
Folic acid (µg)	0	–	Phenylalanine (g)	0.019	–
Folate, food (µg)	24	5.465	Tyrosine (g)	0.022	–
Folate, DFE (µg)	24	–	Valine (g)	0.019	–
Choline, total (mg)	5.7	–	Arginine (g)	0.028	–
Betaine (mg)	0.2	–	Histidine (g)	0.012	–
Vitamin B-12 (µg)	0	–	Alanine (g)	0.033	–
Vitamin B-12, added (µg)	0	–	Aspartic acid (g)	0.149	–
Vitamin A, RAE (µg)	1	0.031	Glutamic acid (g)	0.098	–

Retinol (µg)	0	–	Glycine (g)	0.026	–
Carotene, β (µg)	7	0.22	Proline (g)	0.02	–
Carotene, α (µg)	0	0	Serine (g)	0.025	–
Cryptoxanthin, β (µg)	0	0	Minerals		
Vitamin A, (IU)	12	0.625	Calcium (Ca) (mg)	16	0.562
Lycopene (µg)	0	0	Iron (Fe) (mg)	0.41	0.026
Lutein + zeaxanthin (µg)	26	8.04	Magnesium (Mg) (mg)	13	0.222
Vitamin E (α-tocopherol) (µg)	0.29	0.024	Phosphorus (P) (mg)	24	0.72
Vitamin E, added (mg)	0	–	Potassium (K) (mg)	153	4.073
Tocopherol, β (mg)	0.01	0.002	Sodium (Na) (mg)	1	0.1
Tocopherol, γ (mg)	0.08	0.01	Zinc (Zn) (mg)	0.14	0.013
Tocopherol, δ (mg)	0.01	0.005	Copper (Cu) (mg)	0.048	0.004
Vitamin D (D2 + D3) (µg)	0	–	Manganese (Mn) (mg)	0.386	0.018
Vitamin D (IU)	0	–	Selenium (Se) (µg)	0.4	–
Vitamin K (phyloquinone) (µg)	2.2	0.29	Fluoride (F) (µg)	4.4	0.4
Anthocyanidins			Flavonols		
Petunidin (mg)	0.1	0.1	Isorhamnetin (mg)	0	–
Delphinidin (mg)	0.3	0.28	Kaempferol (mg)	0.5	0.01
Malvidin (mg)	0	0.01	Myricetin (mg)	0	0.04
Pelargonidin (mg)	24.8	0.69	Quercetin (mg)	1.1	0.04
Peonidin (mg)	0	0.05	Isoflavones		
Cyanidin (mg)	1.7	0.05	Daidzein (mg)	0	0
Flavan-3-ols			Genistein (mg)	0	0
(+)-Catechin (mg)	3.1	0.19	Glycitein (mg)	0	–
(–)-Epigallocatechin (mg)	0.8	0.35	Total isoflavones (mg)	0	0.005
(–)-Epicatechin (mg)	0.4	0.13	Formononetin (mg)	0	–
(–)-Epicatechin 3-gallate (mg)	0.2	0.02	Coumestrol (mg)	0	–
(–)-Epigallocatechin 3-gallate (mg)	0.1	0.06	Proanthocyanidin		
(+)-Gallocatechin (mg)	0	0.005	Proanthocyanidin monomers (mg)	3.7	0.8
Flavanones			Proanthocyanidin dimers (mg)	5.3	1.89
Hesperetin (mg)	0	0	Proanthocyanidin trimers (mg)	4.9	2.27
Naringenin (mg)	0.2	0.25	Proanthocyanidin 4–6mers (mg)	28.1	6.47
Flavones			Proanthocyanidin 7–10mers (mg)	23.9	3.47
Apigenin (mg)	0	0	Proanthocyanidin polymers (>10mers) (mg)	75.8	13.36
Luteolin (mg)	0	0.001			

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