

STRAWBERRY SPECIES

INTRODUCTION TO SPECIES

Numerous species of strawberries are found in the temperate zones of the world. Only a few have contributed directly to the ancestry of the cultivated types, but all are an important component of our natural environment. The strawberry belongs to the family *Rosaceae* in the genus *Fragaria*. Its closest relatives are *Duchesnea* Smith and *Potentilla* L.

Species are found at six ploidy levels in *Fragaria* (Table 1.1; Fig. 1.1). The most widely distributed native species, *Fragaria vesca*, has 14 chromosomes and is considered to be a diploid. The most commonly cultivated strawberry, *Fragaria* × *ananassa*, is an octoploid with 56 chromosomes. Interploid crosses are often quite difficult, but species with the same ploidy level can often be successfully crossed. In fact, *F.* × *ananassa* is a hybrid of two New World species, *Fragaria chiloensis* (L.) Duch. and *Fragaria virginiana* Duch. (see below).

There are 13 diploid and 12 polyploid species of *Fragaria* now recognized (Table 1.1). Although a large number of the strawberry species are perfect flowered, several have separate genders. Some are dioecious and are composed of pistillate plants that produce no viable pollen and function only as females, and some are staminate male plants that produce no fruit and serve only as a source of pollen (Fig. 1.2). The perfect-flowered types vary in their out-crossing rates from self-incompatible to compatible (Table 1.1). Isozyme inheritance data have indicated that California *F. vesca* is predominantly a selfing species (Arulsekhar and Bringham, 1981), although occasional females are found in European populations (Staudt, 1989; Irkaeva *et al.*, 1993; Irkaeva and Ankudinova, 1994). Ahokas (1995) has identified at least two different self-incompatible genotypes of *Fragaria viridis* in Finland.

F. vesca has the largest native range of all the species, encompassing most of Europe, Asia and the Americas (Fig. 1.1). The rest of the species are more restricted in ecogeography, being clustered primarily in Euro-Siberia, northern

Table 1.1. Wild strawberries of the world and their fruiting characteristics.
(Adapted from Staudt, 2008 and Liston *et al.*, 2014.)

Ploidy	Species	Breeding system	Distribution
2x	<i>F. bucharica</i> Losinsk.	Hermaphrodite – SI	West Himalaya
	<i>F. chinensis</i> Losinsk.	Hermaphrodite – SI	China
	<i>F. daltoniana</i> J. Gay	Hermaphrodite – SC	Nepal, adjacent China
	<i>F. nubicola</i> Lindl.	Hermaphrodite – SI	Himalayas
	<i>F. hayatai</i> Makino	Hermaphrodite – SC?	Taiwan
	<i>F. iinumae</i> Makino	Hermaphrodite – SC	Japan
	<i>F. mandshurica</i> Staudt	Hermaphrodite – SI	North-east Asia
	<i>F. nilgerrensis</i> Schltdl. ex J. Gay	Hermaphrodite – SC	South-east Asia
	<i>F. nipponica</i> Makino	Hermaphrodite – SI	Japan
	<i>F. pentaphylla</i> Losinsk.	Hermaphrodite – SI	China
	<i>F. vesca</i> L.	Gynodioecious or Hermaphrodite – SC	North America/ Europe to Siberia
	<i>F. viridis</i> Duchesne	Hermaphrodite – SI	West Eurasia
	<i>F. x bifera</i>	Hermaphrodite	France, Germany
	<i>F. corymbosa</i> Losinsk.	Dioecious	China
4x	<i>F. gracilis</i> Losinsk.	Dioecious	China
	<i>F. moupinensis</i> Cardot	Dioecious	China
	<i>F. orientalis</i> Losinsk.	Dioecious	North-east Asia
	<i>F. tibetica</i> Staudt & Dickoré	Dioecious	China
	<i>F. x bringhurstii</i> Staudt	Dioecious	California
5x, 6x	<i>F. moschata</i> Duchesne	Dioecious	West Eurasia
8x	<i>F. chiloensis</i> Duchesne	Subdioecious	Alaska – California, Hawaii, Chile, Argentina
	<i>F. virginiana</i> Duchesne	Subdioecious	North America
	<i>F. x ananassa</i> Duchesne	Subdioecious(modern cultivars hermaphrodite)	Cultivated worldwide; native in north-west North America
	<i>F. iturupensis</i> Staudt	Subdioecious	Iturup Island
10x	<i>F. cascadiensis</i> Hummer	Subdioecious	Oregon, USA

SI = self-incompatible; SC = self-compatible.

China and Manchuria, Indo-South China, Japan and the Americas. Japan is particularly species rich, with at least four endemic species radiating across its islands. The cultivated strawberry *F. x ananassa* is grown in almost all arable zones of the world, although its native range is restricted to the Pacific Northwest of North America.

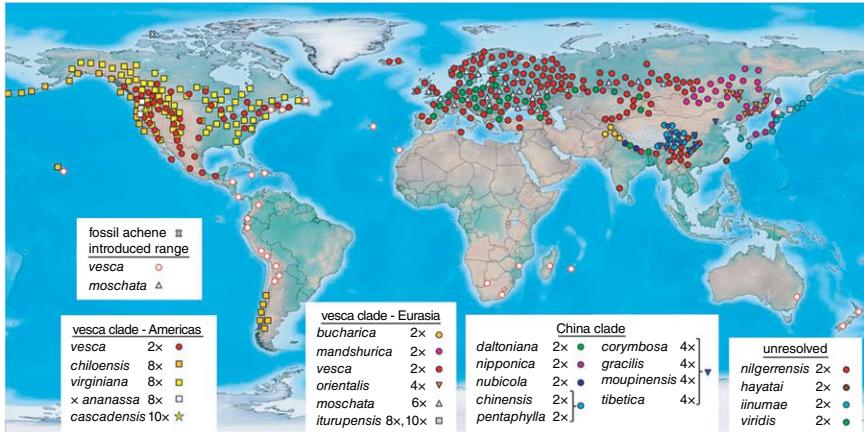


Fig. 1.1. Geographic distribution of *Fragaria* species based on their clade and ploidy. (From Liston *et al.*, 2014.)

Varying degrees of reproductive isolation exist within and among ploidy levels (Bors and Sullivan, 2005; Nosrati *et al.*, 2011a); however, several diploid and polyploid species of *Fragaria* grow sympatrically and produce interspecific hybrids. Hybrids of diploid *F. vesca* and *F. viridis* are found in Europe that have been named *Fragaria* \times *bifera* (Staudt *et al.*, 2003). Pentaploid hybrids have been found in California of *F. vesca* \times *F. chiloensis* (Bringhurst and Senanayake, 1966) and in north-east China between *Fragaria mandshurica* \times *Fragaria orientalis* (Lei *et al.*, 2005). In Europe, both 5x and 7x individuals of *F. vesca* \times *Fragaria moschata* have been reported (Nosrati *et al.*, 2011b), as well as a single 9x individual of *F. vesca* \times *F. chiloensis* in California (Bringhurst and Senanayake, 1966). A large zone of introgression exists in north-western North America between *F. chiloensis* and *F. virginiana* (Luby *et al.*, 1992; Salamone *et al.*, 2013).

INHERITANCE OF GENDER IN STRAWBERRIES

The genus *Fragaria* displays a number of sexual systems, including gynodioecy (females and hermaphrodites), subdioecy (females, males, and hermaphrodites), and dioecy (females and males) (Table 1.1). *F. chiloensis* is almost completely dioecious (Hancock and Bringhurst, 1980). *F. virginiana* populations commonly contain female, male and hermaphroditic individuals; a range in fertility can be found in hermaphrodites, from self-infertility to complete fruit set (Stahler *et al.*, 1990, 1995; Luby and Stahler, 1993). Most commercial strawberries are now strict hermaphrodites, with sexual dimorphism having been bred out.

Ahmadi and Bringhurst (1991) originally suggested that sex in the octoploids was regulated at a single locus where female (F) is dominant to



Fig. 1.2. Morphological diversity of *Fragaria*: (A) staminate flower of *F. chiloensis*; (B) pistillate flower of *F. chiloensis*; (C) sympodial stolons of *F. chiloensis*, with sterile node (red arrow) alternating with fertile node (yellow arrow); (D) flower of *F. iinumae* with seven petals – six to nine petals are characteristic of this species; (E) *F. iinumae* with achenes in shallow pits on the receptacle, also found in the octoploid clade – note the glaucous leaflets, a characteristic shared with *F. virginiana*; (F) *F. vesca* with achenes raised above the surface of the receptacle; (G) tetraploid *F. moupinensis* (back) and diploid *F. pentaphylla* (front) – note that *F. moupinensis* is larger and the central leaflet overlaps the two lateral leaflets; (H) elongated mature receptacle of *F. daltoniana*, one of the most distinctive species of the China clade, with small, coriaceous leaves; and (I) *F. viridis* with characteristic reflexed calyx and mature receptacle that detaches from the calyx with an audible ‘click’. (From Liston *et al.*, 2014.)

hermaphrodite (H), which is dominant to male (M). However, through genetic mapping Spigler *et al.* (2008, 2010) determined that the sex phenotype in octoploid strawberries is actually more complex and is determined by two linked loci, with sterility alleles at each. In their model, the male sterility allele (‘A’ for androecial function) is dominant to an allele conferring male fertility (‘a’), and

at the female-function locus, a female fertility allele ('G' for gynoecia function) is dominant to an allele conferring female sterility ('g'). *F. chiloensis* is almost completely dioecious (Hancock and Bringhurst, 1980) and sex determination is a classic ZW system in which males (staminate) are the homogametic sex (ZZ), while females (pistillate) are the heterogametic sex (ZW) (Charlesworth and Charlesworth, 1978; Tennessen *et al.*, 2016). In the gynodioecious *F. vesca* ssp. *bracteata*, there are at least two unlinked loci carrying male sterility alleles, one being homozygous and the other heterozygous on chromosome IV (Tennessen *et al.*, 2013; Ashman *et al.*, 2015). In *F. orientalis* and *F. moschata*, Staudt (1967a,b) found tetrasomic inheritance for sex and he described the alleles for sex as male suppressor Su^M (F) dominant to male inducer Su^+ (H) and to the female suppressor Su^F (M). Su^F was dominant to Su^+ .

The sexual determining regions (SDR) of the octoploids have now been sequenced and mapped in four geographically distinct octoploid taxa: *F. virginiana* ssp. *virginiana*, *F. virginiana* ssp. *platyptala*, *Fragaria cascadiensis* and *F. chiloensis* (Spigler *et al.*, 2008, 2010, 2011; Goldberg *et al.*, 2010; Tennessen *et al.*, 2018). The SDR cassette contains two putatively functional sex-determining genes that moved at least three times by likely transposition, as evidenced by the size of their flanking sequence, which increased with each 'jump' (Tennessen *et al.*, 2018). The SDR of *F. virginiana* ssp. *virginiana*, *F. virginiana* ssp. *platyptala* and *F. chiloensis* are found on a unique section of a chromosome from the same homoeologous group, but from a different subgenome. *F. cascadiensis* male function maps to the same subgenome as in *F. virginiana* ssp. *platyptala* but at a different chromosomal position (Wei *et al.*, 2017b).

Tennessen *et al.* (2013, 2014) used targeted-sequence capture to map the sex determination regions in *F. vesca* ssp. *bracteata*. They identified locations affecting sexual phenotype on two chromosome regions, one on LG4 and another on LG6. The dominant allele (R) on LG6 appears to restore fertility in the absence of a male sterile allele at the LG4 locus. The *F. vesca* locus contains a high density of pentatricopeptide repeat genes, a class commonly involved in restoration of fertility caused by cytoplasmic male sterility. They also found evidence of a third unmapped locus influencing sex phenotype. The gene on LG6 in *F. vesca* is on the same chromosome as the one regulating sex in *F. chiloensis* but at a different position. However, these two genes are likely not homologous, as the one in *F. chiloensis* is dominant while the one in *F. vesca* is recessive.

DESCRIPTION AND LOCATION OF STRAWBERRY SPECIES

Diploids ($2n = 2x = 14$)

Fragaria bucharica Losinsk.

This species is similar to *Fragaria nubicola* except it has sympodial rather than monopodial runners (Staudt, 2006; Hummer *et al.*, 2011). Two subspecies are recognized based on the size of their bractlets: *F. bucharica* ssp. *bucharica*

(larger) and *F. bucharica* ssp. *darvasica* (smaller). *Fragaria nubicola* can be crossed with *F. mandshurica*, *F. vesca* and *F. viridis*, resulting in mostly heterotic plants with the morphological characters of *F. bucharica*. Crosses with *Fragaria nipponica* produce dwarf plants. *F. bucharica* is distributed from Tadjikistan to Afghanistan, Pakistan and Himachal Pradesh in India.

Fragaria chinensis Losinsk.

This species is a slender plant about 8–15 cm in height with monopodial branching runners (Lei *et al.*, 2014). Its leaves are trifoliate, elliptic or obovate and nearly sessile. Its runners and peduncles are glabrous or covered with sparse appressed hairs. There are two to six flowers per inflorescence with a calyx that is wide lanceolate to triangular. Its fruits are pale red to red and mostly flavourless, with light yellow to brown seeds that are deeply sunken in the fruit. *F. chinensis* is native to western and south-western China.

Fragaria vesca L.

The wood or alpine strawberry is cultivated to a limited extent in North America and Europe. It has thin, light-green, sharply serrated leaves borne on slender petioles (Fig. 1.3). The branching of its stolons is sympodial. The terminal tooth of the terminal leaflet is usually longer than the adjacent lateral teeth and the calyx is reflexed. The plant is erect and 15–30 cm tall. Flowers are bisexual, approximately 1.3 cm wide; inflorescences are about the same length or taller than the leaf petioles. Most plants are short day, but everbearing types exist (*F. vesca* f. *semperflorens*). Fruits are long ovate, bright red in colour



Fig. 1.3. Duchesne's drawing of *Fragaria vesca*. Cytogenetic studies suggest that this species may be a diploid progenitor of the octoploid strawberries. (From Darrow, 1966.)

and highly aromatic. The fruit has very soft flesh and raised or superficial seeds. Runnerless and white-fruited forms exist.

There are four subspecies found in the group (Staudt, 1962, 1999): (i) *F. vesca* ssp. *vesca* – woods of Europe and Asia; (ii) ssp. *americana* (Porter) Staudt – woods of eastern North America to British Columbia; (iii) ssp. *bracteata* (Heller) Staudt – woods of western North America; and (iv) ssp. *californica* (Chamisse and Schlechtendal) Staudt – California. Several ecotypes have been described within ssp. *californica* including headland scrub, coastal forest and Sierran forest (Table 1.2). All of these subspecies are hermaphroditic and self-fertile, except for ssp. *bracteata* which has both hermaphrodites and occasional females (Staudt, 1989).

Fragaria viridis Duch.

This is a slender, upright species with dark-green leaves with smaller serrations than *F. vesca* (Fig. 1.4). It is native to Europe and central Asia, and found in open grassland hills, steppes, at the edge of forests and among brush. It produces only a few nodeless runners with monopodial branching. Flower numbers per inflorescence are smaller than *F. vesca*, but it has perfect flowers that are larger than *F. vesca*. The petals overlap and are often yellowish-green when opening. Fruit is small but larger than *F. vesca*, firm, green to pink in colour, and aromatic. The scapes lie along the ground when the berries are ripe. Seeds are set in pits. The calyx is clasping and hard to separate. *F. viridis* can be distinguished from *F. vesca* by its phosphoglucose isomerase isozyme pattern (Arulsekhar and Bringhurst, 1981).

Fragaria daltoniana J. Gay

This species is vigorous, with petiolulate leaves that have few teeth along the margins. Runners are slender and sympodial branching; flowers are solitary and self-compatible (Bors and Sullivan, 1998). Fruit range from ovate to cylindrical, are relatively long (2–2.5 cm), bright red, spongy and tasteless. It has shiny, coriaceous leaves. Staudt (2006) suggests that it can be crossed with *Fragaria iinumae*, *Fragaria nilgerrensis*, and *F. nipponica*, producing morphologically intermediate hybrids. It is distributed in the Himalayas from India to Myanmar at elevations of 3000–4500 m.

Fragaria nilgerrensis Schlecht.

This species is vigorous and spreading with pubescent, dark-green and heavily veined leaves. The petioles and peduncles are covered with long, stout hairs. The leaflets are petiolate, round to ovate, with small serrations, dull green and very pubescent. Branching of stolons is sympodial. It produces a small inflorescence with three or four large bisexual flowers. The flowers have a pink blush. The fruit are small, subglobose, pale-pink, tasteless to unpleasant and have many small, sunken seeds. Staudt (1989) describes it as having a banana-like flavour. The subspecies *F. nilgerrensis* ssp. *hayatai* from Taiwan has anthocyanin in all parts of the plant, including the berries.

Table 1.2. Ecotypes of *F. vesca* and *F. chiloensis* found in California. (From Hancock and Bringhurst, 1979a, b.)

Species	Environment	Mean rainfall (mm year ⁻¹)	Mean temperature (°C)		Soil characteristics			
			January	July	Type	% carbon	Salinity	
							ppm	pH
<i>F. vesca</i>	Headland scrub	686	10.1	15.9	Silt loam	2.8	497	6.0
	Coastal forest	1160	8.9	16.7	Silt loam	5.9	326	6.3
	Sierran forest	1453	6.5	17.2	Silt loam	5.5	205	5.6
<i>F. chiloensis</i>	Dunes	476	10.4	10.5	Sand	0.3	663	6.7
	Coastal strand	1837	7.7	8.1	Sand	0.3	652	6.7
	Headland scrub	482	9.5	10.3	Silt loam	2.8	497	6.0
	Woodland meadows	1416	7.9	8.2	Sandy loam	2.8	390	5.4



Fig. 1.4. Duchesne's drawing of *Fragaria viridis*. (From Darrow, 1966.)

Fragaria nubicola Lindl. ex Lacaita

This species closely resembles *F. viridis*. It is around 4–10 cm in height and its leaves are obovate with very sharp teeth (Lei *et al.*, 2014). Appressed hairs cover its petioles, runners and peduncles. Its stolons are filiform and monopodial branching. Fruits are globose or elliptic with an appressed, persistent calyx. It is found in Tibet at elevations of 1500–4000 m.

Fragaria pentaphylla Losinsk.

This species has penniform, thick leaves, reflexed sepals and elongated calyculs at fruit maturity. They are self-incompatible (Bors and Sullivan, 1998) and the fruit is ovoid–globose. It is 6–15 cm height with monopodial branching runners; the leaves have five leaflets and the central one is elliptic with large serrations and long petioles, nearly glabrous above and purplish-red beneath (Lei *et al.*, 2014). Often there are 2–3 auriculate leaves on petioles. The petioles and runners are covered with spreading hairs, while the peduncles have few hairs. There are both white and red coloured fruited forms. The white fruits are elliptic, slightly aromatic, and tasteless with sunken seeds and reflexed calyx. The red fruits are smaller ovate, and very acid. *F. pentaphylla* has strong leaf-spot resistance (Lei *et al.*, 2014). This species is found in grassy mountain slopes at elevations of 1000–2000 m in Shanxi, Guanshu and Sichuan.

Fragaria mandshurica Staudt

This species closely resembles the autotetraploid *F. orientalis*, except that the flowers are smaller, and the leaves and teeth are less coarse than *F. orientalis* (Staudt, 1989). It is 15–25 cm in height and its runners are sympodial branching. Its leaves are covered with spreading hairs, while its peduncles have mostly appressed hairs. The fruits are red, conical and highly aromatic and contain seeds that are green and raised. Some accessions of *F. mandshurica* rebloom in autumn (Lei *et al.*, 2014). Its distribution is in north-east China and inner Mongolia.

Fragaria iinumae Makino

This species is restricted to the alpine mountains of central and northern Japan. It is a vigorous, erect plant with slender filiform runners with sympodial branching. Leaflets are subglaucous in colour, broadly obovate or cuneate-orbicular, rounded at the apex, petiolate with margins that are coarsely denticulate. They are glabrous above with appressed to ascending long pubescence beneath especially on the nerves. Only a few scapes are produced that are one- to three-flowered. Flowers are 15–25 mm across, have more than five petals and are self-incompatible (Bors and Sullivan, 1998). The fruit is elongate, 8 mm across \times 1.5 cm long with a small calyx and sunken achenes. The fruit are spongy and nearly tasteless. *F. iinumae* appears to be deciduous, as no leaves are visible during the winter. The glaucous leaf of *F. iinumae* is unique to the rest of the diploids.

Fragaria nipponica Lindl.

This is found in the mountains of Japan. It is thought to be closely allied to *Fragaria yezoensis* (Ohwi, 1965). Terminal leaflets are elliptic to broadly ovate with ovate or subdeltoid teeth, pale-green colour and appressed pubescence especially on nerves beneath. Stolons are monopodial. Scapes are 2–2.5 cm across and have one to four flowers. The fruit is globose to ovoid (1.5–3 cm across) with an unpleasant taste, and its achenes are within pits. Staudt (1989) suggests that there is an undescribed species in the Himalayas that is very similar to *F. nipponica*.

Tetraploids ($2n = 4x = 28$)*Fragaria gracilis* Losinsk.

This is an extremely slender, short plant, only 3–10 cm in height with filiform and monopodial branching runners. Leaves are trifoliate, obovate and nearly sessile. Its petioles, runners and peduncles have sparse, spreading hairs. Its stolons are monopodial. There are only one to two flowers per inflorescence. Its fruit are red, small, subglobose or elliptic and tasteless with red, very small seeds that are deeply sunken. It does not do well in hot summer temperatures (Lei *et al.*, 2014). *F. gracilis* is found on grassy mountain slopes, ditches and in forests of Shanxi, Guanchu, Qihai, Henan, Hubei, Sichuan, Yunnan and Tibet.

Fragaria orientalis Losinsk.

This is a small, upright plant (10–20 cm) with long, slender runners that are sympodial branching. It is found in forests and open mountain slopes. Its leaves are ovate, light green, nearly sessile with deeply serrate margins. Its stolons are sympodial branching. There are a few large flowers (2.5–3 cm) on the inflorescence. Female plants often rebloom in autumn (Lei *et al.*, 2014). Fruit is

large, obovoid and only slightly aromatic. Seeds are sunken. Distribution is in north-east China.

Fragaria corymbosa Losinsk.

This plant is approximately 10–15 cm in height (Lei *et al.*, 2014). Leaves are pinnately quinquefoliolate or trifoliate, obovate, with a cuneate apex. Its petioles are covered with long, thin spreading hairs. Runners are filiform and monopodial branching, with spreading hairs. Flowers have overlapping petals and filaments are longer than pistils. Fruit are red, ovate, tasteless and slightly acid with deeply sunk seeds and pinkish-white flesh. It is not high-temperature resistant in summer. Distribution is in west and central China.

Fragaria moupinensis (French.) Cardot

The plants and fruit of this species are very similar to *F. nilgerrensis*. The leaves are trifoliate, serrate, elongated oval, with the lower leaflets being smaller. Petioles, runners and peduncles are covered with thickly spreading hairs (Lei *et al.*, 2014). The inflorescence is longer than the leaf petioles and has only two to four flowers. Runners are short monopodial branching. The fruit are orange-red coloured, oval-globose, globose or elliptic, with deeply set achenes, and the flesh is spongy and nearly tasteless. Distribution is in south-west China.

Fragaria tibetica Staudt & Dickoré

This species is approximately 5–15 cm tall and its leaves are pinnately quinquefoliolate or trifoliate and nearly sessile, elliptic with a cuneate apex (Lei *et al.*, 2014). Petioles, runners and peduncles are covered with appressed or ascending hairs. Runners are monopodial branching. There are few flowers per inflorescence, most often two. Fruit are orange-red to light red, oval-globose, globose or elliptic. Seeds are sunken on the shaded side of fruit but not on the sunny side of fruit. Distribution is in south-west China.

Hexaploids ($2n = 6x = 42$)

Fragaria moschata Duch.

The musky strawberry is a dioecious, tall, vigorous plant that produces few runners. It is native to central Europe, and grows in forests, under shrubs and in tall grass. Leaves are large, dark green, rugose, rhombic, prominently veined and pubescent. The flowers are large (20–25 cm in diameter) and the inflorescence emerges above the foliage, but due to the weight of the ripe berries the scapes lie along the ground. The calyx is usually reflexed. Its stolons are sympodial branching. The fruit is light red to dull-brownish to purplish-red, soft, irregular-globose to ovoid and has a strong vinous flavour. The fruit is slightly larger than that of *F. vesca* and bears raised achenes. The calyx is strongly reflexed. Both white and red, perfect-flowered forms are cultivated to a limited extent under the name hautboy or hautbois.

Octoploids ($2n = 8x = 56$)

Fragaria chiloensis (L.) Duch.

The beach or Chilean strawberry was once extensively cultivated in western South America and France but is now only grown to a limited extent (see Chapter 2, this volume). Plants are low-spreading and vigorous with prolific runnering (Fig. 1.5), and they tend to be evergreen. Flowers are large, 20–35 mm in diameter. Leaves are generally thick, strongly reticulate-veiny beneath, dark green and very glossy. Runners are robust and bright red. Native forms have fruit that is dull to bright red in colour, with white flesh and mild to pungent flavour. Achenes are reddish-brown to dark brown. Many of the cultivated forms are albino. Fruit is round to oblate with raised or sunken achenes. Fruit size in the cultigens can be in excess of 10 g, but most native forms average 1–3 g.

Wild populations of *F. chiloensis* are either dioecious, gynodioecious or perfect flowered depending on geographical location. North American *F. chiloensis* are primarily dioecious, with staminate plants being about 10% more common than pistillate (Hancock and Bringhurst, 1979b, 1980). In some cases, apparent males are polygamodioecious and bear a few early fruits. Highly fertile hermaphrodites have been found in California at Año Nuevo and Pigeon Point, Alaska, and in the northern islands off the coast of British Columbia. In Chile, *F. chiloensis* is largely gynodioecious as all wild plants are either pistillate or hermaphroditic (Lavín, 1997). Plants in Hawaii are all hermaphroditic.

There are four subspecies of *F. chiloensis* recognized (Staudt, 1989): (i) ssp. *lucida* (E. Vilmorin ex Gay) Staudt – coast of Pacific Ocean from Queen Charlotte



Fig. 1.5. Duchesne's drawing of *Fragaria chiloensis*. This species is one of the progenitors of the cultivated species *Fragaria* × *ananassa*. (From Darrow, 1966.)

Island to San Luis Obispo, California; (ii) *ssp. pacifica* Staudt – coast of Pacific Ocean from Aleutian Islands to San Francisco, California; (iii) *ssp. sandwicensis* (Degener and Degener) – Hawaii; and (iv) *ssp. chiloensis* (L.) Duch. – beaches and mountains of South America. Two forms of this subspecies are recognized, the cultivated *f. chiloensis* and the native *f. patagonica*.

It is believed that the aboriginal people of Chile (Mapuche and Picunche) were the domesticators of *F. chiloensis* *ssp. chiloensis* *f. chiloensis* about 1000 years ago and they grew them in small garden plots in coastal areas between latitudes 35°S and 39°S (see Chapter 2, this volume). Consistent with a domestication bottleneck, intersimple sequence repeat (ISSR) genetic diversity in *f. chiloensis* (Percentage of polymorphic bands (P) = 48%, Nei's genetic index (h) = 0.12, Shannon's information index (S) = 0.19) was found to be half of that in *f. patagonica* (P = 90%, h = 0.25, S = 0.38) (Carrasco *et al.*, 2007).

Recent morphometric and random amplified polymorphic DNA (RAPD) analyses of interspecific variation in *F. chiloensis* have indicated that *ssp. lucida* and *pacifica* might intergrade too much to be considered separate subspecies, but *ssp. sandwicensis* and *chiloensis* are distinct (Catling and Porebski, 1998). The major characteristics used to separate the subspecies were hair length, leaflet size, plant colour, petal number and whether the hairs on the leaf stalk were ascending or spreading. Hair orientation was the only reliable way to distinguish *ssp. lucida* from *pacifica*.

Several ecotypes of *F. chiloensis* have been identified in both North and South America. Distinct dune, coastal-strand, headland-scrub and woodland-meadow types are found in California (Table 1.2). They are distinguished primarily by flower number, leaf width, leaf biomass, runner width and resistance to salt and drought stress. The woodland-meadow types may be stabilized hybrid derivatives of *F. chiloensis* × *F. virginiana* (Hancock and Bringhurst, 1979b). At least two distinct native races have been described in Chile: a coastal type with dark, more glossy, green leaves, and a higher-elevation form with duller leaves and a blue casting, much like *F. virginiana* *ssp. glauca* (Cameron *et al.*, 1993). In a morphometric analysis of Chilean *F. chiloensis*, del Pozo and Lavin (2005) identified four cluster groups among wild accessions, although they did not specify any climatic or regional patterns to the variability. The most diagnostic characteristics were leaflet size, plant size, weight of fruit and fruit size. Interestingly, white forms of native *F. chiloensis* were discovered that clustered very closely to the white, much larger-fruited domesticated forms (Fig. 1.6).

Native hybridizations between *F. vesca* and *F. chiloensis* in coastal California have resulted in persistent 5x, 6x and 9x colonies (Fig. 1.7) (Bringhurst and Senanayake, 1966). These have been named *Fragaria* × *bringhurstii* after their discoverer R.S. Bringhurst (Staudt, 1989). Their leaves are intermediate between *F. chiloensis* and *F. vesca* with regard to thickness, colour, profile, pubescence and the appearance of the upper leaf surface. They are mostly sterile at $2n = 35, 42$ or 63 , but small percentages of aneuploid gametes are produced that are interfertile with octoploid material.

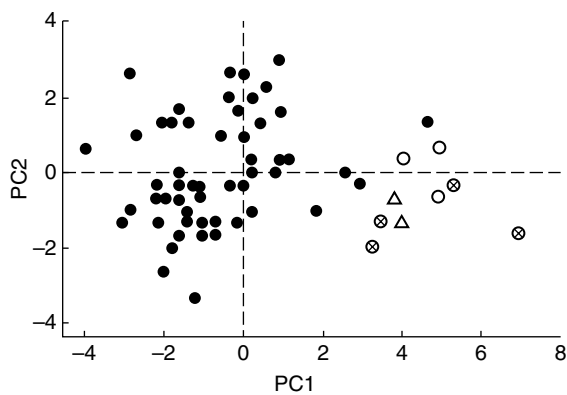


Fig. 1.6. Distribution of 61 Chilean accessions of strawberry on the first and second principal components (PC1 and PC2) of a multivariate analysis of morphological traits. Symbols represent accessions of: wild *Fragaria chiloensis* f. *patagonica* with red fruit (●); wild *F. chiloensis* f. *patagonica* with white fruit (△); cultivated *F. chiloensis* f. *chiloensis* (○), and cultivated *F. x ananassa* (⊗). Note that the white forms of the wild forms cluster closely with domesticated *F. chiloensis*. (Adapted from Lavín, 1997, and del Pozo, Muñoz, Lavín and Maureira, unpublished.)

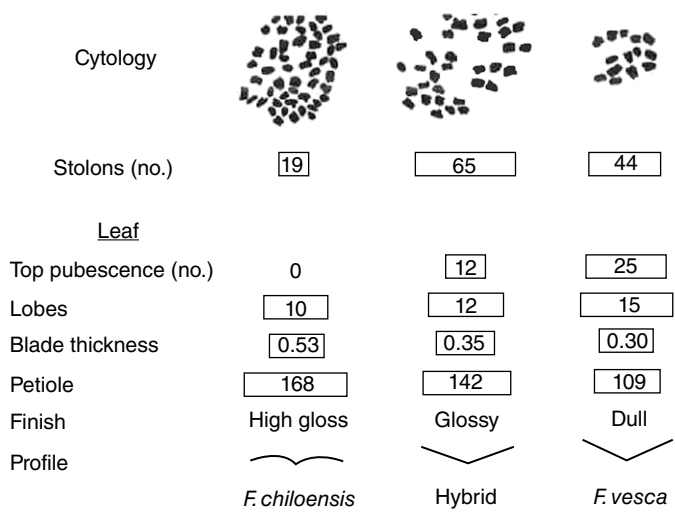


Fig. 1.7. The morphological and cytogenetic traits distinguishing *F. chiloensis*, *F. vesca* and their pentaploid hybrid at Point Sur, California. (Adapted from Bringhurst and Khan, 1963.)

Fragaria virginiana Duch.

The scarlet or Virginia strawberry is found in meadows throughout central and eastern North America. Plants are slender, tall and profusely running (Fig. 1.8). Leaves are coarsely toothed and obovate to oblong. The terminal



Fig. 1.8. Duchesne's drawing of *Fragaria virginiana*. This species is the North American progenitor of the cultivated strawberry, *F. × ananassa*. (From Darrow, 1966.)

tooth of the terminal leaflet is usually shorter than the adjacent lateral teeth. The inflorescence is variable, basal to high branching and flowers are small to large (0.6–2.5 cm) and dioecious. The fruit is soft and round, up to 3 cm in diameter (although most fruit is much smaller). It is light red with white flesh, aromatic and has deeply embedded seeds. *F. virginiana* can be distinguished from *F. chiloensis* by a number of morphological traits (Table 1.3).

Populations of *F. virginiana* vary from being completely dioecious to trioecious. In western populations of *F. virginiana*, all three sexes are found in similar proportions, whereas in eastern populations, only hermaphrodites and females are observed, again in relatively equal proportions (Staudt, 1968; Luby and Stahler, 1993). Levels of fertility in hermaphrodites are highly variable, with large ranges of fertility being found in natural populations from pure males to pure hermaphrodites (Hancock and Bringham, 1979a, 1980; Stahler, 1990). In general, females are more fertile than hermaphrodites (Dale *et al.*, 1992). Environment probably plays a role in the fertility of hermaphrodites (Stahler, 1990; Dale *et al.*, 1992), but most of the control is genetic. The level of fertility in hermaphrodites appears to be polygenic as large ranges of fertility are generated in crosses of native males with cultivated hermaphrodites (Scott *et al.*, 1962) and fruit set in native hermaphrodites can be greatly enhanced through recurrent selection (Luby *et al.*, 1995).

F. virginiana has undergone considerable genetic differentiation like the other octoploid species, *F. chiloensis*. Staudt (1962) described four subspecies: (i) ssp. *glauca* (Wats.) Staudt – southern Rocky Mountains to north-west Canada and central Alaska; (ii) ssp. *platypetala* (Rydb.) Staudt – Rocky Mountains from

Table 1.3. The characteristics that separate *F. chiloensis* from *F. virginiana*. (From Darrow, 1966.)

Character	<i>F. chiloensis</i>	<i>F. virginiana</i>
Leaves	Thick, leathery	Thin
	Deep set stomata	Shallow set stomata
	Strongly netted	Not strongly netted
	Glossy	Dull
	Dark green	Bluish to light green
	Evergreen	Deciduous
	Short teeth	Coarse teeth
Petioles	Thick	Slender
	Not channelled	Broadly channelled
Runners	Robust	Slender
	Red	Green
	Persistent	Ephemeral
Crown	Thick	Less thick
Flowers	Large	Small
	Large stamens	Small stamens
Fruit	Dull red	Scarlet to crimson
	Seeds slightly sunken	Seeds sunken in pits
	Late ripening	Early ripening
	Large	Small
	Firm	Soft

Wyoming to Colorado, west to Sierra Nevada and Cascades Mountains; (iii) ssp. *grayana* (E. Vilmorin ex Gay) Staudt – meadows and forest margins from New York to Alabama, Louisiana and Texas; and (iv) ssp. *virginiana* Duch. – meadows and forest margins from eastern USA, Newfoundland and Yukon Territory. Staudt felt that ssp. *virginiana* was more common in the north and ssp. *grayana* more common in the south.

The western subspecies have yielded considerable taxonomic debate. Darrow (1966) considered the western types of *E. virginiana* to be a separate species *E. ovalis*, but Staudt (1962) did not give species rank to this material because of the lack of barriers to hybridization and the intermediacy of its characters. The separation of ssp. *platypetala* and ssp. *glauca* has also been questioned. Welsh *et al.* (1987) suggested that the two subspecies completely intergrade and probably should be referred to as a single taxon var. *glauca*. Others have followed this designation (Scoggan, 1978) or have not attempted to recognize infraspecific taxa (Dorn, 1984). What was formerly recognized as a distinct species, *E. multicipita*, was recently reduced to *E. virginiana* ssp. *glauca* f. *multicipita* when it was discovered that its unique morphology was caused by a phytoplasma (Catling, 1995).

Whereas *E. virginiana* ssp. *virginiana* and ssp. *glauca* appear to be largely distinct across their range, strawberries in the Black Hills and eastern front ranges

of the Rocky Mountains may be introgressive swarms between *ssp. glauca* and *ssp. virginiana* (Luby *et al.*, 1992; Hokanson *et al.*, 1993; Sakin *et al.*, 1997). In a multivariate analysis of *E. virginiana* and *E. chiloensis* populations across the northern USA, Harrison *et al.* (1997b) found that Black Hill populations are intermediate between collections of eastern *ssp. virginiana* and western *ssp. glauca* for morphological traits, and when analysed with RAPD markers, the Black Hill populations were part of a large cluster group incorporating both *ssp. virginiana* and *ssp. glauca* (Fig. 1.9). The Black Hill populations probably represent relicts of the late Pleistocene when the Great Plains were mainly a boreal forest that provided a continuous habitat for hybridization between eastern and western forms of *E. virginiana*.

Natural hybrids of *E. virginiana* × *E. chiloensis* exist where native habitats of the two species overlap in British Columbia, Washington, Oregon and Northern California. Staudt (1999) has designated these hybrids as *E. × ananassa ssp. cunefolia* (Nutt ex Howell). The *E. chiloensis* populations noted on woodland-meadow sites by Jensen and Hancock (1981) probably represent stabilized hybrid derivatives of this cross. Hybrid populations of *E. chiloensis* × *E. virginiana* are common from Vancouver Island along the coast to Fort Bragg, California, and Staudt (1989) has indicated that ‘the further one goes from the coastal area the more the *E. chiloensis* characters decrease. Plants with somewhat thinner leaves but some other characters of *E. chiloensis* are combined in *ssp. platypetala* of *E. virginiana* ... considered to be the final link of introgression of *E. chiloensis* into *E. virginiana ssp. glauca*.’ Luby *et al.* (1992) present evidence of interaction between these two species in the mountains of northern Idaho and western Montana, where individuals of *E. virginiana* have thick, roundish leaves and thick runners reminiscent of *E. chiloensis* even though they are more than 400 km from the Pacific Ocean.

In the recent study by Harrison *et al.* (1997b), variation patterns in the morphological traits suggested that *E. virginiana ssp. platypetala* is distinct from *E. chiloensis ssp. lucida* in the Pacific Northwest (Fig. 1.9). However, in the RAPD analysis, the two groups were combined even though they remained distinct from all the eastern *E. virginiana*. It is possible that the RAPD markers are selectively neutral traits that reflect ancient patterns of gene flow between *E. chiloensis* and *E. virginiana* in early post-Pleistocene times, whereas the morphological traits were moulded through selection as the genus *Fragaria* faced new environmental challenges.

Fragaria × *ananassa* L.

This is now the most important strawberry cultivated worldwide, however, its domestication was not based on natural hybrids between *E. chiloensis* and *E. virginiana*, but instead on accidental hybrids that appeared in European gardens in the mid-1700s (see Chapter 2, this volume). From a horticultural point of view, many of the traits distinguishing the two species are complementary (Table 1.3), and it is not surprising that hybrid-derived populations came to

Decaploids ($10n = 10x = 70$)

Fragaria iturupensis Staudt

This species is found solely on Iturup Island, north-east of Japan (Staudt, 1989; Hummer *et al.*, 2011). Staudt's original chromosome counts of *F. iturupensis* indicated that it was octoploid, but a later collection after the original plant was lost found it to be decaploid. (Hummer *et al.*, 2009). It has obovate, subglaucous leaves that are bluish, much like *F. iinumae*. The petiole is covered with patulate hairs. The flowers are hermaphroditic, 16–20 mm wide with five petals. There are two to four flowers to an inflorescence. The fruit is similar to *F. vesca*, but larger. Stolons are branched with no secondary runners from axils of primary bracts. Berries are subspherical, bright red and shiny with reflexed calyxes and superficial achenes.

Fragaria cascadenis Hummer

Other than its decaploid chromosome number, *F. cascadenis* has a morphology similar to the octoploid *F. virginiana* ssp. *platypetala* (Staudt, 1999; Hummer, 2012). It can only be accurately distinguished by its hairy adaxial leaf surfaces and comma-shaped achenes. *F. virginiana* ssp. *platypetala* of the Oregon Cascades has no hairs on the upper leaf surface, and achenes are dome shaped. It is only known in a narrow distribution range in the western Oregon Cascades at elevations from 1000 to 3800 m. Many have studied strawberries from this region without realizing a wild polyploid *Fragaria* species was there with more than 56 chromosomes (Darrow, 1966; Harrison *et al.*, 1997b; Hokanson *et al.*, 1993, 2006). Hancock *et al.* (2001) even unknowingly included the decaploid cytotype CFRA 110 (PI 551527) in their core selection of native octoploid germplasm.

EVOLUTIONARY RELATIONSHIPS

A much clearer understanding of the phylogeny of *Fragaria* has emerged in the last decade as a number of molecular phylogenies have been published (Liston *et al.*, 2014; Sobczyk, 2018). There are two major clades with nine species each (Rousseau-Gueutin *et al.*, 2009; Njuguna *et al.*, 2013). One is named 'vesca' representing the closely related diploids *F. bucharica*, *F. mandshurica* and *F. vesca*; the tetraploid *F. orientalis*; the hexaploid *F. moschata*; the octoploids *F. chiloensis* and *F. virginiana*; and the decaploids *F. iturupensis* and *F. cascadenis*. The other is named 'China' representing four diploid species (*F. chinensis*, *F. daltoniana*, *F. nubicola*, *F. pentaphylla*) and four tetraploid species (*F. corymbosa*, *F. gracilis*, *F. moupinensis*, *F. tibetica*) endemic to China and adjacent Himalayan countries, and one diploid species endemic to Japan (*F. nipponica*). Unfortunately, the placement of *F. iinumae*, *F. hayatai*, *F. nilgerrensis* and *F. viridis* was left poorly resolved, as was the parental ancestry of most of the polyploids.

Although there appear to be some barriers to interfertility among the diploid strawberries, they can all be crossed to some extent, and meiosis in the hybrids is regular, even in cases where the interspecific hybrids are sterile (Federova, 1946; Staudt, 1959; Fadeeva, 1966). This suggests that they may share the same genome, with only cryptic structural differences. Iwatsubo and Naruhashi (1989) found that the chromosomes of *F. nipponica* and *F. vesca* are very similar in morphology, although *F. iinumae* had some distinguishing features. It seems likely that *F. vesca* is ancestral to all the diploids, as its geographical range overlaps or touches almost all the other diploid species and it has been successfully crossed with most of them, including *F. nilgerrensis*, which is sexually isolated from all the other species tested (Fadeeva, 1966).

Based on levels of interfertility, there are at least three overlapping groups of species (Bors and Sullivan, 1998): (i) *F. vesca*, *F. nubicola*, *F. pentaphylla* and *F. viridis*; (ii) *F. vesca*, *F. daltoniana*, *F. pentaphylla* and *F. nilgerrensis*; and (iii) *F. pentaphylla*, *F. gracilis* and *F. nipponica*. No fertile seeds were recovered when *F. iinumae* was crossed with Group 1 and Group 2 species, but Bors and Sullivan (1998) did not attempt to cross it with Group 3 species.

Polyploidy in *Fragaria* probably arose through the unification of $2n$ gametes, as several investigators have noted that unreduced gametes are relatively common in *Fragaria* (Scott, 1951; Islam, 1960; Bringhurst and Gill, 1970; Dickinson *et al.*, 2007). Staudt (1984) observed restitution in microsporogenesis of an F_1 hybrid of *F. virginiana* \times *F. chiloensis*. In a study of native populations of *F. chiloensis* and *F. vesca*, Bringhurst and Senanayake (1966) found frequencies of giant pollen grains to be approximately 1% of the total. Over 10% of the natural hybrids generated between these two species were the result of unreduced gametes.

Although there may not be sufficient differentiation among the diploids to warrant the designation of separate genomes (Staudt, 1959), cytogenetic studies have indicated that there are distinct sets of chromosomes associating in the hexaploid and octoploid species (Federova, 1946; Senanayake and Bringhurst, 1967). Lerceteau-Köhler (2003), studying segregation ratios of AFLP markers in a full-sib family, found that 92% (727 out of 789) had simplex ratios and 8% (62 out of 789) fitted a multiplex ratio. This suggests that inheritance in the octoploid strawberries is mixed, being mostly disomic but not completely.

Cytogenetic studies indicated that at least two pairs of genomes are represented in the octoploid species. When they are crossed with the diploids *F. vesca* or *F. viridis*, bivalent or multivalent numbers approaching 14 are commonly observed in pentaploid hybrids, suggesting that there is pairing between one set of diploid and octoploid chromosomes, and another set of octoploid chromosomes (Ichijima, 1926, 1930; Federova, 1946; Bringhurst and Khan, 1963; Senanayake and Bringhurst, 1967). An additional set of chromosomes is left as largely univalents, either due to non-homology with the other sets or competition with a homologous set of chromosomes from the diploid. Similar

results have commonly been obtained whether *E. chiloensis*, *E. virginiana* or *E. × ananassa* was used as the octoploid parent, although a few studies have reported much higher numbers of bivalents (21–28) in diploid × *E. × ananassa* crosses (Yarnell, 1931; Ellis, 1962).

Based on the cytogenetic studies, three genome formulas were suggested for the octoploids: AAAABBCC (Federova, 1946), AAA'A'BBBB (Senanayake and Bringhurst, 1967) and AAA'A'BBB'B' (Fig. 1.10; Bringhurst, 1990). It seems likely that species similar to *E. vesca* and *E. viridis* are in the background of all the octoploid strawberries, as chromosomes from both pair regularly with those of *E. chiloensis*, *E. virginiana* and *E. × ananassa*. Federova suggested that the *A* genome came from an ancestor of *E. orientalis* other than *E. vesca*, the *B* from *E. nipponica* and the *C* from *E. vesca*. After examining the pairing relationships of octoploids crossed with 2x and 4x *E. vesca*, Senanayake and Bringhurst suggested that the genomic formula should be AAA'A'BBBB, as higher bivalent numbers were observed in hexaploid than pentaploid hybrids. This indicated that the chromosome of *E. vesca* had at least partial homology with another set of octoploid chromosomes. Their guess was that the *A* genome was contributed by either *E. vesca* or *E. viridis*, and they had no idea about the origin of the *A'* and *B* genomes. Bringhurst (1990) later suggested that the genome formula should be AAA'A'BBB'B' to reflect his contention that the octoploids are completely diploidized with strict disomic inheritance. Noguchi *et al.* (1997) produced hybrids between *E. iinumae* and *E. × ananassa* that were highly fertile after chromosome doubling, suggesting that *E. iinumae* contributed a genome to the octoploids. Liu *et al.* (2016) using genomic *in situ* hybridization (GISH), found that octoploid-derived gametes carried seven chromosomes with hybridization

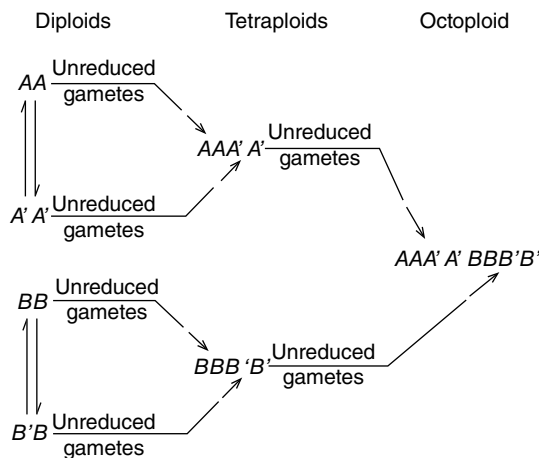


Fig. 1.10. Genomic origin of the octoploid strawberry species proposed by Bringhurst (1990). Different letters represent highly divergent species, while those distinguished with a prime originated from much closer relatives.

affinities to *F. vesca*, while the remaining 21 chromosomes displayed varying affinities to *F. iinumae*.

The first phylogenetic studies utilizing the sequences of nuclear low-copy genes indicated that one of the octoploid subgenomes was closely related to *F. vesca* or *F. mandshurica*, and a second subgenome donor was *F. iinumae* (Rousseau-Gueutin *et al.*, 2009; DiMeglio *et al.*, 2014; Sargent *et al.*, 2016), together forming a AAA'A'BBB'B' genome structure. More recently, Tennesen *et al.* (2014), using sequenced regions anchored in the *F. vesca* map, came up with a more complex subgenome compliment of 2Av,2Bi,2B1,2B2. The Av genome was hypothesized to have come from a diploid *F. vesca* ancestor, the Bi from a diploid *F. iinumae* ancestor, and the B1, B2 ancestor from an *F. iinumae*-like autotetraploid. The divergence between homeologous chromosomes appeared to have been greatly augmented by interchromosomal rearrangements. Kamneva *et al.* (2017) using 'haploSNPs' found that one or more diploid ancestors, possibly related to *F. viridis*, *F. bucharica* or *F. mandshurica*, formed a hexaploid with *F. iinumae* (2Bi, 2B1, 2B2), which then introgressed with a diploid *F. vesca*-like species (2Av). Using sequences of 24 single-copy or low-copy nuclear genes, Yang and Davis (2017) found that at least five diploid ancestors contributed to the subgenomes of octoploids (*F. vesca*, *F. iinumae*, *F. bucharica*, *F. viridis*, and at least one additional allele contributor of unknown identity) and that the composition of the subgenomes was complex and not derived from a single ancestral source.

Edger *et al.* (2019) examined the species origin of the octoploid species by generating a near-complete chromosome scale assembly for the cultivated octoploid strawberry (*F. × ananassa* cv. Camarosa) and comparing it with 31 sequenced and de novo assembled transcriptomes of every described diploid *Fragaria* species, including 19,302 nuclear genes in the genome. Their analysis revealed that four species are in the ancestry of the octoploid strawberry: *F. iinumae*, *F. nipponica*, *F. viridis* and *F. vesca* ssp. *bracheata*. Because the range of *F. viridis* overlaps with that of the hexaploid *F. moschata*, they hypothesized that these were the evolutionary intermediates between the diploids and the wild octoploid species. This conclusion has been questioned based on methodological issues (Edger *et al.*, 2020; Liston *et al.*, 2020).

Edger *et al.* (2019) did not propose a genome formula for the octoploid strawberry but based on earlier crossability studies, it could be represented by Bringhurst's (1990) proposal of AAA'A'BBCC. *F. vesca* (AA) and *F. viridis* (A'A') can be crossed with limited fertility so they warrant a similar letter designation. *F. iinumae* (BB) and *F. nipponica* (CC) cannot be crossed with any other diploid species so warrant separate letter designations.

Hardigan *et al.* (2019) employed whole-genome shotgun genotyping of interspecific segregating populations to identify 1.9 million subgenome variants spanning 3394 cM in *F. chiloensis* ssp. *lucida*, and 1.6 million subgenome variants spanning 2017 cM in *F. × ananassa*. Through comparative genetic mapping of these variants, they were able to show that the genomes of the

wild octoploids are effectively diploidized as predicted by Bringhurst (1990) and completely collinear. This genetic structure has allowed for ‘unimpeded gene flow’ during the domestication and interspecific hybridization of the strawberry.

In comparisons of the nuclear and organelle genomes of the octoploids, it appears that *F. vesca* ssp. *bracteata* was the chloroplast donor of the octoploid strawberries, while both *F. vesca* ssp. *bracteata* and *F. iinumae* were the sources of the mitochondrial genomes, which subsequently recombined (Mahoney *et al.*, 2010; Njuguna *et al.*, 2013; Govindarajulu *et al.* 2015). Little is known about the origin of *F. iturupensis*, except it shares the same plastid donor as *F. chiloensis* and *F. virginiana*. A plastid genome phylogeny generated by Dillenberger (2018) found that the octoploid *F. chiloensis* is monophyletic, while all other polyploid taxa are para- or polyphyletic. *F. cascadiensis* has biparental plastid inheritance and has four different plastid donors.

The tetraploid *F. orientalis* and hexaploid *F. moschata* likely represent a polyploid series (Harrison *et al.*, 1997a; Njuguna *et al.*, 2013). Based on the molecular studies of Lin and Davis (2000), Rousseau-Gueutin *et al.* (2009) and DiMeglio *et al.* (2014), *F. orientalis* appeared to be an allopolyploid derived from *F. vesca* and *F. mandshurica*, and *F. moschata* contains the additional genome of *F. viridis*. Based on the work of Edger *et al.* (2019), *F. orientalis* is more likely derived from *F. vesca* and *F. nipponica*. *F. moschata* crosses readily with *F. viridis* (Schiemann, 1937), *F. nubicola* (Ellis, 1958), *F. nipponica* (Lilienfeld, 1933), *F. orientalis* (Federova, 1946), and with difficulty with *F. vesca* (Mangelsdorf and East, 1927).

In the older studies on crossability, *F. orientalis* and *F. viridis* were shown to cross relatively easily and the resulting hybrids were partially fertile (Federova, 1946). Hybrids of *F. orientalis* and $2x$ *F. vesca* are much more difficult to make, although Staudt (1952) was able to produce a fertile hexaploid hybrid between them, and Bors and Sullivan (1998) found the cross of $4x$ *F. vesca* and *F. orientalis* to be relatively easy to make. Schiemann (1937) described plants that looked like *F. orientalis* that were derived from a pentaploid F_2 population of *F. vesca* \times *F. moschata*.

The diploid–tetraploid relationships previously proposed in the ‘China’ clade by Staudt (2008) based on geographical and morphological similarities (*F. pentaphylla* > *F. tibetica*, *F. chinensis* > *F. gracilis*/*F. corymbosa*, *F. nubicola* > *F. moupinensis*) has not been supported by recent molecular phylogenetic studies (Kamneva *et al.*, 2017; Yang and Davis, 2017). It appears that *F. corymbosa*, *F. gracilis* and *F. moupinensis* all share *F. pentaphylla* and *F. chinensis* as parent, and *F. tibetica* is most likely derived from *F. pentaphylla* and *F. nubicola*.

Dominance of subgenomes in octoploid strawberries

The octoploid genome sequence provided by Edger *et al.* (2019) along with gene expression data show that the last species to enter into the octoploid

species, *F. vesca*, is the dominant subgenome 'with significantly greater gene content, gene expression abundance, and biased exchanges between homoeologous chromosomes, as compared with the other subgenomes'. Their data fits the 'subgenome-dominance theory' which predicts that genome-wide expression disparity can arise when the merged genomes differ in their transposable element (TE) complement and in their level of TE-mediated repression of gene expression (Bertioli, 2019). Edger and his group found that *F. vesca* has 20% fewer transposable elements, has retained 20% more genes and has generally higher gene expression. The metabolic pathways that give rise to strawberry flavour, colour and fragrance are largely controlled by this dominant subgenome.

Origin of the North American octoploid strawberries

The phylogenetic study of Edger *et al.* (2019) combined with the geographic distributions of extant species supports a North American origin for the octoploid strawberry with *F. vesca* ssp. *brachea* being the last diploid to be added in the formation of the ancestral octoploid strawberry. It is likely that *F. chiloensis* and *F. virginiana* are extreme forms of the same biological species, which emerged in Beringia and subsequently evolved differential adaptations to coastal and mountain habitats of North America. The north-eastern Asia distribution of *F. iturupensis* suggests that it may have been part of the genomic pool that originated in north-east Asia before spreading across the Bering Strait to north-western North America. The rise of the octoploid clade is estimated to have occurred 0.37–2.05 million years ago (Njuguna *et al.*, 2013).

While *F. chiloensis* and *F. virginiana* are completely interfertile, there are significant morphological distinctions between them. *F. chiloensis* has thick, dark-green, coriaceous leaves and large achenes, whereas *F. virginiana* has thin, bluish-green leaves and smaller achenes (Staudt, 1999). Substantial separation of *F. virginiana* and *F. chiloensis* has been observed in cluster analysis of morphological characters, simple sequence repeats and RAPDs (Fig. 1.9; Harrison *et al.*, 1997b; Hokanson *et al.*, 2006). Yang and Davis in their phylogenetic study also found substantial divergence, finding a number of well-supported clades comprised of sequences exclusively from *F. chiloensis* and *F. virginiana*.

The origin of Hawaiian and Chilean *F. chiloensis* is also obscure, but presumably they were introduced from North America via bird migrations. Dillenberger *et al.* (2018) found *F. chiloensis* from Oregon and Northern California to be sisters to a Chilean sample of *F. chiloensis*, but only a handful of *F. chiloensis* clones were analysed. It is likely that multiple introductions were made into Chile as the habitats of South American *F. chiloensis* have an extensive range from beaches and headlands to montane forests at 1900 m elevation (Darrow, 1966; Cameron *et al.*, 1991, 1993). Glaucous forms of octoploids

may also have been introduced, as at high elevations in Chile leaf colour and thickness resemble *F. virginiana* ssp. *glauca* (Cameron *et al.*, 1993).

Origin of decaploid species

Because of the current sympatry between the octoploid *F. virginiana* ssp. *platypetala*, diploid *F. vesca* ssp. *bracteata* and the decaploid *F. cascaden-sis* in the Cascade Mountains of Oregon, it was originally hypothesized that *F. cascaden-sis* originated from hybrid polyploid speciation between the two octoploid and diploid congeners (Hummer, 2012). However, Wei *et al.* (2017a) discovered its origin was more likely due to an ancient hybrid speciation in Beringia. In a phylogenetic analysis of linkage-mapped chromosomes from targeted sequences, they found that the additional subgenome of *F. cascaden-sis* was derived from a *F. iinumae*-like diploid progenitor rather than *F. vesca* ssp. *bracteata*. The *F. cascaden-sis* found in the Oregon Cascade Mountains may be a remnant of a more widespread species that survived in a Willamette Valley refugium during the last glacial maximum (Dillenberger, 2018). Whether *F. cascaden-sis* and the other decaploid *F. iturupensis* have a common ancestor or evolved independently is unknown. They could have both evolved in Beringia and then moved southwards in different directions along the Pacific Ocean and became isolated (Wei *et al.*, 2017a).

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