2

History of Strawberry Domestication

It seems likely that our species, *Homo sapiens*, has always gathered and consumed strawberries from the wild. Who can walk by a strawberry patch in a forest or field without gathering these succulent berries? In fact, the ease with which strawberries can be collected from the wild may actually have delayed their cultivation until almost modern times. Although our important grain crops were domesticated over 10,000 years ago (Hancock, 2014), the first strawberry species were domesticated in the last 2000 years, and the major strawberry of commerce, *Fragaria* × *ananassa*, was born only 250 years ago.

DOMESTICATION OF OLD WORLD SPECIES

The strawberry was probably grown in Roman and Greek gardens, but there is only limited reference to its cultivation in early writings (Darrow, 1966). Ovid and Virgil mentioned the strawberry in poems, and Pliny (AD 23–79) lists its fruit 'Fraga' (fragrant) as a natural product of Italy. It seems likely that the Romans cultivated indigenous strawberries, as they spent considerable funds importing a wide array of fruits for their country estates including apples, apricots, cherries, citrons, figs, grapes, peaches, plums and pears (Wilhelm and Sagen, 1974).

The first references to strawberry cultivation in Europe appear in the French literature of the 1300s. Most notably, it is known that King Charles V had over 1000 strawberries planted in the royal gardens of the Louvre in Paris, and strawberries were grown in four blocks of the gardens of the Dukes of Burgundy (Darrow, 1966). The mother stock for these gardens was most likely collected from the wild, and then propagated by moving runners from established blocks to vacant soil. The popularity of the strawberry steadily grew during the Middle Ages, in spite of a warning from the noted abbess and mystic St Hildegard von Bingen in the 12th century that the strawberry was unhealthy because its fruit were found near the ground in stale air (Bühler, 1922).

It is known that *Fragaria vesca*, the wood strawberry or *fraise des bois*, was widely planted in gardens all across Europe by the 1500s. Records are common in Renaissance herbals, and after about 1530 there is a clear distinction made between wild and garden strawberries (Sauer, 1993). The wood strawberry was grown not only for private consumption, but for market as well. In fact, the strawberry may have got its name from the activities of street vendors who strung the berries on straws of grass or hay to take to market (Darrow, 1966; Wilhelm and Sagen, 1974). Another possible origin of the name relates to its ripening at the same time as hay, as *streaw* is the Anglo-Saxon word for hay. Most likely, strawberries were named after the way the runners 'strew' or scatter around the mother.

The first printed illustration of the strawberry is found in the *Herbarius Latinus Moguntiae* published in 1484 by Peter Schöffer, a partner of Johann Gutenberg (Leyel, 1926). The inclusion of the strawberry meant that it was considered important to healthful living. The first colour illustration of the strawberry (Fig. 2.1) was published in 1485 in the German edition of Schöffer's book titled *Herbarius zu Teutsch* or *Gart der Gesundheit*, meaning literally 'Garden of Good Health'. This book 'occupied a place unsurpassed in German natural history for more than a half century' (Wilhelm and Sagen, 1974). In fact, the strawberry was grown widely in apothecary gardens all across Europe. All parts of the plants were used in medicinal teas, syrups, tinctures and ointments. Strawberry concoctions were used for skin irritations and bruises, bad breath, throat infections, kidney stones, broken bones and many other injuries.

Several different forms of *F. vesca* were identified by botanists in the 1500s, including albino types and everbearing ones from the Alps (*F. vesca* 'Semperflorens'). Some of the earliest cultivars were everbearing including 'Fraisier de Bargemont' from France, 'Haarbeer' and 'Brösling' ('Pressling') from Germany and 'Capiton' from Belgium. Most of these varieties were likely selected from the wild, except 'Capiton', which may have been derived from 'Haarbeer' (Wilhelm and Sagen, 1974). Fruit of all these varieties was pale coloured and only the early developing fruit had large size. Much redder 'Capiton' plants with improved fruit size began to appear in the 16th century and they supplanted the white forms. Much like today, fruit from these early varieties were served with cream, soaked in wine or covered with powdered sugar. Strawberry jelly appeared in the 1600s (Wilhelm and Sagan, 1974).

The musky flavoured *Fragaria moschata* (also known as hautbois or hautboy strawberry) was also planted in gardens by the late 15th century, together with the green strawberry, *Fragaria viridis*. *F. viridis* was used solely as an ornamental throughout Europe, whereas *F. moschata* was utilized for its fruit by the English, Germans and Russians. The French largely scorned it (Duchesne, 1766). Domestication of the hautboy strawberry probably began in the 16th century (Sauer, 1993) and the earliest cultivars, such as 'Fraisier à Bouquet', appeared in the 18th century. The origin of the musky strawberries was initially clouded by Philip Miller in 1735 when he improperly suggested

Fig. 2.1. Earliest colour illustration of the strawberry, printed by Peter Schöffer in 1485.

in his influential series *The Gardeners Dictionary* that they came from the New World, but in fact they were of European origin (Wilhelm and Sagen, 1974). The name 'hautboy' was apparently an English spelling of the French *haut bois* (high [fruiting] woods [strawberry]).

Hautboy fruit varied from red to rose-violet and were borne on trusses extending above the leaves. Their flavour has been described as a mixture of honey and musk (Wilhelm and Sagen, 1974). Hautboy strawberries initially fell into disrepute, as the earliest types were dioecious, leading to poor production when

only one gender was planted, but the great French botanist Duchesne (1766) discovered that interplanting pistillate plants with good pollen producers of other *F. moschata* or *Fragaria virginiana* yielded good crops. Regardless of this, perfect-flowered types were soon developed.

By the 1600s, the culture of the native European strawberries was widely practised and well refined. Many of our modern practices had already been developed including frequent establishment of beds to maintain high plant vigour, the use of raised beds in areas with poor drainage and the application of mulch to protect against winter cold. Fruit size was maximized by early planting dates, optimal plant spacing, elimination of the first flower trusses and removal of all but the first three or four flowers in a cluster. Europeans had become expert strawberry growers and the stage was set for the rapid acceptance of a new, highly promising horticultural type from the New World, *F. virginiana*.

DOMESTICATION OF THE SCARLET STRAWBERRY, *F. VIRGINIANA*

The wood strawberry, *F. vesca*, dominated strawberry cultivation in Europe for centuries, until *F. virginiana* from Canada and Virginia began to replace it in the 1600s. All of the clones that found their way to Europe were wild in origin, as the aboriginal peoples of North America did little gardening with strawberries. They enjoyed the fruit both fresh and in cornmeal bread (Wilhelm and Sagen, 1974; Sauer, 1993) but the natural abundance of the strawberry had generated little stimulus for domestication in the New World.

The exact particulars of the entry of *F. virginiana* into Europe are unknown, but it had certainly arrived in both France and England by the late 1500s, and new importations occurred regularly over the next 150 years. Jacques Cartier, the discoverer of the St Lawrence River of Canada in 1534, was probably the first to bring *F. virginiana* to the Old World. There are no specific records of its introduction by him, but Cartier made numerous mentions of it in his diary and he was known to have introduced other Canadian plants (Wilhelm and Sagen, 1974). The first published reference to the strawberry of Canada was in the garden catalogue of Robins, the botanist to Henri IV of France. He and his brother first reported it in 1624, but it is likely that they planted it long before then, as they were active importers of plants from throughout the world.

The Canada strawberry, then known primarily as *Fragaria americana* but now called *F. virginiana*, rapidly spread to gardens across France and all of Europe (Wilhelm and Sagen, 1974). It was incorporated in 1636 into the huge Jardin Royal des Herbes Mèdecinales of Guy de La Brosse, physician to Louis XIII. In 1633 it had appeared in a catalogue of Canadian exotics written by Giovanni Battista Ferrari, a professor of Hebrew at the Collegio Romano in Rome. The noted apothecary Jean Hermans was growing the Canada strawberry in his garden in Brussels by 1652, and numerous English herbalists and

horticulturalists were raising it by the early 1600s, including John Tradescant and John Parkinson. At least nine different accessions of *F. virginiana* were being grown in Europe by 1650.

Although the first strawberries imported from Canada were botanically interesting and intriguing horticultural curiosities, most produced little fruit, were green where the fruit were shaded and frequently produced excessive runners. Not until strawberries from Virginia became widely distributed did *F. virginiana* really make an impact on the horticultural industry. What became known as the 'Scarlet strawberry' was favoured for its large fruit size, high yields and deep red colour. They were particularly enjoyed in jam, because of their persistent colour, acid flavour, high aroma and retention of shape (Darrow, 1966).

It is not clear when the first Scarlet strawberries arrived in Europe, but in the garden of de La Brosse there was an item called *F. americana* magno fruto rubro, which may have been a large-fruited, scarlet type. The surviving colonists from Plymouth may also have brought back Scarlet strawberries when they returned in 1586. Regardless, during the late 1500s and 1600s, all kinds of native plants of North America appeared in the gardens of Europe, making multiple introductions of the Scarlet strawberry likely.

The early cultivar development of *F. virginiana* was primarily conducted by growers who found raising seed imported from North America often resulted in horticulturally important variations. The numbers of varieties available increased dramatically from three to about 26, over a period of a few decades at the turn of the 17th century (Darrow, 1966). Some of the most important early cultivars were 'Oblong Scarlet', 'Grove End Scarlet', 'Duke of Kent's Scarlet', 'Knight's Large Scarlet', 'Wilmot's Late Scarlet', 'Morrisana Scarlet', 'Common Scarlet', the 'Australian Scarlet' and 'Hudson Bay Scarlet'. They came from all over the New World including Nova Scotia, Virginia and New York. The early improvements were modest, however, and generally did not yield any substantial advancements from the best of the earlier imported types such as 'Large Early Scarlet'.

Garden culture of strawberries began in North America in the middle of the 17th century with varieties imported from England. Early garden calendars listed three types of strawberries: (i) the hautboy (*F. moschata*); (ii) the Chili (*Fragaria chiloensis*, originally from Chile); and (iii) the Redwood (*F. vesca* from Europe) (Fletcher, 1917). Little cultivation of *F. virginiana* was undertaken until the importation of 'Large Early Scarlet' in the late 1700s, even though native strawberry populations abounded and 'Large Early Scarlet' had actually been sent to England a century earlier from the wilds of North America.

The first native American clone of *F. virginiana* to be propagated for sale in North America in 1791 was called 'Hudson'. It was very vigorous and had soft, scarlet fruit with high flavour. It was cultivated well into the 1800s and can probably be considered the first important American strawberry (Hedrick, 1925). The first commercial strawberry plantings were established around

Boston, New York, Philadelphia and Baltimore in the early 1800s. Until that time, most commercial strawberries had been gathered from the extensive wild populations that were springing up in conjunction with the clearing of forests and the abandonment of worn-out agricultural sites.

'Red Wood', an English variety of *F. virginiana*, was probably the most important variety grown in the early part of the 18th century in North America, along with a number of Scarlet varieties (Fletcher, 1917). 'Red Wood' was thought to be inferior in flavour to the older Scarlet varieties but had a longer season of production. Other popular cultivars during the first half of the 1800s were 'White Wood' (a white-fruited type), 'Early Hudson', 'Old Scarlet', 'Crimson Cone', 'Large Early Scarlet', 'Hudson Bay Scarlet', 'Methven Scarlet', 'Ross Phoenix' and 'Early Virginia'. All of these except for 'Ross Phoenix' and 'Hudson Bay Scarlet' were imported from England.

DOMESTICATION OF *F. CHILOENSIS* IN THE NEW WORLD

The cultivated strawberry of South America, *F. chiloensis*, has a long and rich history (Hancock *et al*., 1999; Lavín and Maureira, 2000). It was utilized well over 1000 years ago by the indigenous Mapuches between the rivers Biobio and Tolten in south-central Chile, and by the more northern Picunches tribe between the rivers Itata and Biobio. The Picunches had contact with the northern agrarian Inca invaders and were probably the first to transport elite plants from the wild to their home gardens. The Mapuches were primarily hunters and gatherers but learned about agriculture from the Picunches.

The indigenous Chileans used strawberry fruits fresh, dried, as a fermented juice or as medicinal infusions against indigestion, diarrhoea and bleeding (de Moesbach, 1992). The Mapuches made many kinds of fermented juices, but the one from the *llahuen* or *lahueñe* small red-fruited wild strawberry was their favourite, called *lahueñe mushca* (Labarca, 1994).

Most evidence indicates that the primary domesticants were the larger white-fruited forms, called *kallén* or *quellghen* by the Mapuches. Albino-fruited types are rare in nature but have been found at three southern locations. Some red-fruited forms may also have been domesticated but reports of their existence are sketchy. Darrow (1957) described Chilean large red-fruited forms from around Santiago in the middle of the 20th century, although there are no earlier reports of cultivated *lahueñe*. Wild red-fruited forms were abundant from Santiago southward, so the pressure to cultivate them was probably minimal. It is reported, however, that the Mapuches planted small plots of the wild red forms in open spaces in the forests as a trap for the Spanish soldiers. When the soldiers dropped their arms to pick the fruit, the fierce Indians attacked and killed them (Gonzalez de Nájera, 1866).

Strawberry cultivation by the Mapuches was mostly limited to garden plots. After the conquest by the Spaniards, larger commercial plantings of

1–2 ha began to appear in the coastal areas from north of the Itata River to Chiloé Island. These traditional plantings of *F. chiloensis* flourished until the 1950s, when they began to be mixed with Northern Hemisphere cultivars of *F.* × *ananassa.* Cultivation of *F. chiloensis* has now largely disappeared, but small plantings can still be found along the traditional area of cultivation from Iloca on the coast of Curicó province to Chiloé Island (Hancock *et al.*, 1999). Recently, there has been a burst of interest in redeveloping the commercial *F. chiloensis* industry in Chile, particularly around the white-fruited forms (Retamales *et al.*, 2005; Céspedes, 2018; Morales-Quintana and Ramos, 2019).

SPREAD OF *F. CHILOENSIS* OUTSIDE CHILE

During their period of exploration and conquest in the mid- to late 1500s, the Spanish spread *F. chiloensis* throughout north-western South America. Major industries developed around Cuzco (Peru), Bogotá (Colombia) and Ambato (Ecuador) (Popenoe, 1921, 1926; Darrow, 1957). The source of these plants is not known; however, the variability among the preserved land races suggests that they had multiple origins (Hancock *et al.*, 1999). The land races may have been spread from several Chilean locations or seedling volunteers may have been moved from their original sites to new locations.

The largest hectarage of cultivated *F. chiloensis* in South America was grown at Huachi-Grande, Ecuador, near Ambato (Darrow, 1953). There were probably 500–700 ha from at least the late 1700s until 1970 (Hancock *et al.*, 1997; Finn *et al.*, 1998). Father Velasco wrote in 1789 that the *frutilla* was three times the size of the European strawberry and 'it is produced throughout the entire year, and though it is common in several provinces, in no other is it so abundant, nor so excellent as in that of Ambato' (Popenoe, 1921). The English botanist Richard Spruce visited Ambato in the mid-1800s and proclaimed that the strawberry grown in abundance in the nearby village of Huachi was of exceptional quality. Wilson Popenoe (1921) declared that 'It is the custom in Ecuador to throw the fruits into boxes: they are then carried six or seven miles on mule-back to the city of Ambato, where they are sorted by hand, for shipment by train to Quito or Guayaquil. There is probably no other strawberry in the world which could tolerate this sort of handling.' In an expedition to Huachi-Grande in 1997, Finn, Hancock and Heider (1998) were able to locate a field that had been visited by both Popenoe (1921) and Darrow (1953), and they brought back samples to North America for breeding (Fig. 2.2).

One of the Chilean clones even found its way into Europe in the 1700s compliments of a French spy Captain Amédée Frézier (Darrow, 1966; Wilhelm and Sagen, 1974). Frézier was struck by the large-fruited strawberry grown around Concepción, Chile, during his mapping of Spanish fortifications from

Fig. 2.2. Fruit and flowers picked from the ancient land race of *F. chiloensis* still grown in Hauchi-Grande, Ecuador. (From Finn *et al.*, 1998.)

1714 to 1716. He selected some of the largest-fruiting types and took them back with him to Marseilles in 1716 (Fig. 2.3). Five of these plants survived and one of them was given to Antoine de Jussieu, the director of the Jardin de Plantes in Paris, where clones of *F. virginiana* were already growing.

Reports on this remarkable new introduction spread widely and within a few years plants were located in botanical gardens all across Europe. Unfortunately, early reports on the Chilean strawberry were negative, as the plants were largely barren. Frézier had inadvertently brought back staminate plants that needed a pollinator. French horticulturalists solved the problem when they discovered that the 'Chili' would produce fruit when pollinated by *F. moschata* or *F. virginiana.*

The Chilean strawberry reached its highest acclaim in Brittany, where it came to be known as the Fraise de Plougastel, after one of the major cities of production. The Chili thrived in the cool maritime climate of Brittany, which was similar to its original home environment. By the mid-1800s, there was probably more cultivation of *F. chiloensis* in France than in its native land, as 200 ha were grown in Brest and over 1000 ha in all of Brittany (Wilhelm and Sagen, 1974). The clones originally grown in Brittany had much more impressive size than the Scarlet types when effectively pollinated (primaries the size of walnuts), but their fruit were paler in colour (whitish-red), seedier and fainter of flavour. Over time, improved hermaphroditic selections of *F. chiloensis* were identified with greater self-fertility, but they still needed a pollinator to reach maximal production.

The strawberry of Chile never became popular in Europe outside of Brittany. Difficulties with its fertility probably played a role, but climatic factors may have been more important. The Chilean was difficult to grow in the harsher inland climates and had to be protected from winter cold. Under most

Fig. 2.3. A woodcut of the original *Fraise du Chili* or *Frutilla* clone of Chilean *Fragaria chiloensis* brought to France by A. Frézier in 1716. The picture comes from Frézier's book *A Voyage to the South Seas and along the Coasts of Chile and Peru in the Years 1712, 1713 and 1714*. (From Darrow, 1966.)

continental conditions, the '... fruit was poor coloured, and poor textured and often had a mawkish flavour' (Darrow, 1966). Soil-borne pathogens were also a limiting factor, and the Chili grew vigorously only on well-drained sandy soils (Wilhelm and Sagen, 1974).

ORIGIN OF THE DESSERT STRAWBERRY, *F.* × *ANANASSA*

Unusual seedlings began to appear in Brittany and in gardens elsewhere with unique combinations of fruit and morphological characteristics. Although the origin of these seedlings was initially clouded, Duchesne (Fig. 2.4) determined in 1766 that they were hybrids of *F. chiloensis* × *F. virginiana* and he named them *F.* × *ananassa* to denote the perfume of the fruit that smelled like pineapple (*Ananas*). It is not clear from the literature where the first hybrids of the pineapple, or pine, strawberry appeared, but they must have arisen early in the commercial fields of Brittany, and in botanical gardens all across Europe such as the Trianon, the Royal Garden at Versailles where Duchesne studied. The first hybrid cultivars were disseminated from the Netherlands, perhaps because the Dutch were such active seed merchants and had imported early hybrids, but it is also possible that they had recognized unique types in their own gardens. The first description of a variety that matched *F.* × *ananassa* was by Philip Miller in the 1759 edition of *The Gardeners Dictionary*, although he was not sure of its origin (Fig. 2.5).

Duchesne referred to these early cultivars of *F.* × *ananassa* as 'Quoimios' in his 1771 supplement to *L'Histoire Naturelle des Fraisiers* (Darrow, 1966). Two were pale fruited like the Chili but were improved in other ways. One from Haarlem, the Netherlands, was a partial hermaphrodite that was best used as a pollinator because it bloomed during the same late season as the female Chili and its early developing flowers were barren. One called 'Quoimio de

Fig. 2.4. The great French botanist Antoine Nicholas Duchesne, who first recognized the hybrid nature of the garden strawberry *Fragaria* × *ananassa*. (From Darrow, 1966.)

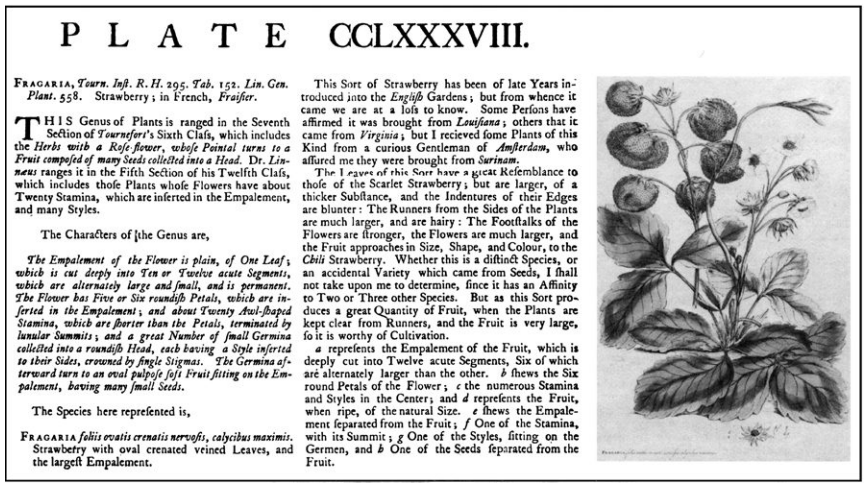

PLATE CCLXXXVIII.

FRAGARIA, *Tourn. Inſt. R. H.* 295. *Tab.* 152. *Lin. Gen. Plant.* 558. Strawberry; in French, *Fraiſier.*

THIS Genus of Plants is ranged in the Seventh Section of *Tournefort's* Sixth Claſs, which includes the *Herbs with a Roſe flower, whoſe Pointal turns to a Fruit compoſed of many Seeds collected into a Head.* Dr. *Linnæus* ranges it in the Fifth Section of his Twelfth Claſs, which includes thoſe Plants whoſe Flowers have about Twenty Stamina, which are inſerted in the Empalement, and many Styles.

The Characters of the Genus are,

The Empalement of the Flower is plain, of One Leaf; which is cut deeply into Ten or Twelve acute Segments, which are alternately large and ſmall, and is permanent. The Flower has Five or Six roundiſh Petals, which are inſerted in the Empalement; and about Twenty Awl-ſhaped Stamina, which are ſhorter than the Petals, terminated by lunular Summits; and a great Number of ſmall Germina collected into a roundiſh Head, each having a Style inſerted to their Sides, crowned by ſingle Stigmas. The Germina afterward turn to an oval pulpoſe ſoft Fruit ſitting on the Empalement, having many ſmall Seeds.

The Species here repreſented is,

FRAGARIA *foliis ovatis crenatis nervoſis, calycibus maximis.* Strawberry with oval crenated veined Leaves, and the largeſt Empalement.

This Sort of Strawberry has been of late Years introduced into the *Engliſh* Gardens; but from whence it came we are at a loſs to know. Some Perſons have affirmed it was brought from *Louiſiana*; others that it came from *Virginia*; but I recieved ſome Plants of this Kind from a curious Gentleman of *Amſterdam*, who aſſured me they were brought from *Surinam*.

The Leaves of this Sort have a great Reſemblance to thoſe of the Scarlet Strawberry; but are larger, of a thicker Subſtance, and the Indentures of their Edges are blunter: The Runners from the Sides of the Plants are much larger, and are hairy: The Footſtalks of the Flowers are ſtronger, the Flowers are much larger, and the Fruit approaches in Size, Shape, and Colour, to the *Chili* Strawberry. Whether this is a diſtinct Species, or an accidental Variety which came from Seeds, I ſhall not take upon me to determine, ſince it has an Affinity to Two or Three other Species. But as this Sort produces a great Quantity of Fruit, when the Plants are kept clear from Runners, and the Fruit is very large, ſo it is worthy of Cultivation.

a repreſents the Empalement of the Fruit, which is deeply cut into Twelve acute Segments, Six of which are alternately larger than the other. *b* ſhews the Six round Petals of the Flower; *c* the numerous Stamina and Styles in the Center; and *d* repreſents the Fruit, when ripe, of the natural Size. *e* ſhews the Empalement ſeparated from the Fruit; *f* One of the Stamina, with its Summit; *g* One of the Styles, ſitting on the Germen, and *h* One of the Seeds ſeparated from the Fruit.

Fig. 2.5. The first European description of *Fragaria* × *ananassa* made by Philip Miller in his 1759 edition of *The Gardeners Dictionary*. (From Otterbacher and Skirvin, 1978.)

Bath' had smaller berries than the Chilean but was superior in vigour and size. Three other early varieties had much redder fruit than the Chili, including the 'Carolina' with cherry red fruit, 'Quimio de Cantorbéri', which had deep coloured flesh, and 'Clagny Quoimio', a scarlet-coloured type, which Duchesne thought was a backcross of *F. virginiana* × 'Quoimio de Haarlem'.

BREEDING IN EUROPE FROM 1800 TO 2000

At first, only chance hybrids of *F. chiloensis* and *F. virginiana* were evaluated by horticulturalists. Steady genetic progress was made over the years but yields and fruit quality still left something to be desired. Formal strawberry breeding was initiated in England in 1817 by Thomas A. Knight (Pearl, 1928; Darrow, 1966; Wilhelm and Sagen, 1974). He was one of the first systematic breeders of any crop, and he used clones of both *F. virginiana* and *F. chiloensis* in his crosses. He produced the famous 'Downton' and 'Elton' cultivars, noted for their large fruit, vigour and hardiness. Michael Keen, a market gardener near London, also became interested in strawberry improvement at about this time and developed 'Keen's Imperial', whose offspring 'Keen's Seedling' (Fig. 2.6) is in the background of many modern cultivars. The berries of 'Keen's Seedling' were a sensation as they were sometimes 2 in. in diameter, deep red in colour and particularly good flavoured. The plants were prolific and bore their fruit well above the ground. This variety dominated strawberry acreage for close to a century (Table 2.1) and the Royal Horticultural Society awarded this remarkable berry its silver cup in 1821.

Fig. 2.6. The strawberry 'Keen's Seedling', which was a sensation in England in the late 1800s. It is in the pedigree of many modern cultivars. (From Darrow, 1966.)

Numerous excellent varieties followed the success of 'Keen's Seedling' in Europe in the first half of the 18th century and were grown for decades (Darrow, 1966). Among the most elite were J. William's 'Pitmaston Black', a Mr Myatt's 'British Queen' (1840), J. Salter's 'Jucunda' (1854) and J. Bradley's 'Sir Joseph Paxton' (1862). 'Pitmaston Black' and 'British Queen' were dominant in the mid-1800s and were grown in England as late as 1914. 'Jucunta' was a major variety in both Europe and the USA until the 1920s and was still planted to some extent in the 1960s. 'Sir Joseph Paxton' was the leading variety in England until the 1930s and in France for another decade. Particularly noteworthy characteristics of these cultivars were the high flavour of the 'Pitmaston Black' and 'British Queen', the productivity, lateness, high flavour and capping ease of 'Jucunda', and the brilliant, glossy red colour and firmness of 'Sir Joseph Paxton'.

Several excellent French varieties were released during the mid-1800s including J. Jamin's 'Vicomptesse Héricart de Thury' (1845) and M. Lebreton's

Table 2.1. Dominant *Fragaria* × *ananassa* cultivars in Europe before 2000. (From Darrow, 1966; Brooks and Olmo, 1997; Hancock, 1996; David Simpson and Bruno Mezzetti, personal communications.)

Cultivar	Year of release	Place developed	Notable characteristics
'Downton'	1817	England	Large, oblong fruit
'Keen's Seedling'	1821	England	Very large fruit, deep rich red colour, juicy and vigorous with upright fruit
'Elton'	1828	England	Lateness, beautiful fruit, vigour and hardiness
'British Queen'	1840	England	Excellent flavour
'Vicomptesse Héricart de Thury'	1849	France	Excellent flavour, glossy red colour and firmness
'Jucunda'	1854	England	Productivity, firmness, red flesh colour, lateness and easy capping ability
'Marguerite'	1859	France	Huge fruit size and acid flesh
'Sir Joseph Paxton'	1862	England	Brilliant, firm and glossy red fruit
'Nobel'	1884	England	Large, attractive fruit, productivity and broad adaptation
'Royal Sovereign'	1892	England	Large, bright scarlet, firm and high-flavoured fruit
'Deutsch Evern'	1902	Germany	Early, long conical fruit
'Madame Moutot'	1910	France	Productivity, very large fruit and broad adaptation
'Surprise des Halles'	1910	France	Earliness and productivity
'Oberschlesien'	1919	Germany	Productivity and broad adaptation
'Auchincruive Climax'	1947	Scotland	Productivity and high fruit quality
'Cambridge Favourite'	1947	England	Long picking season, excellent dessert and canning quality
'Cambridge Vigour'	1947	England	Large, firm fruit and drought tolerance
'Senga Sengana'	1954	Germany	Hardiness, broad adaptation, productivity, deep red colour and excellent processing quality
'Talisman'	1955	Scotland	Similar to 'Auchincruive Climax', but highly resistant to red stele root rot
'Redgauntlet'	1956	Scotland	Maintenance of size throughout season, bruise resistance and resistant to red stele
'Domanil'	1960	Belgium	Late and productive, aromatic
'Gorella'	1960	Netherlands	Early, very large fruit, healthy foliage
'Belrubi'	1962	France	Early with extended season
'Zefyr'	1965	Denmark	Early
'Elvira'	1967	Netherlands	Early, resistant to crown rot
'Ostara'	1969	Netherlands	Productive

Continued

Table 2.1. Continued.

Cultivar	Year of release	Place developed	Notable characteristics
'Bogotá'	1971	Netherlands	Late fruiting, productive
'Gariguette'	1976	France	Attractive fruit, excellent flavour
'Korona'	1977	Netherlands	Large fruit
'Elsanta'	1981	Netherlands	Productivity, fruit quality
'Addie'	1982	Italy	Early, large, productive
'Dana'	1982	Italy	Very large, resistant to Verticillium wilt
'Pandora'	1983	England	Very large, very late, resistant to mildew
'Rapella'	1983	Netherlands	Everbearing, productive
'Rhapsody'	1987	Scotland	Late, resistant to red stele and Verticillium wilt
'Pegasus'	1990	England	Productive, resistant to Verticillium wilt and red stele
'Tudla'	1992	Spain	Early, large elongated berry
'Evita'	1993	England	Day-neutral, productive, resistant to powdery mildew and Verticillium wilt
'Marmolada'	1994	Italy	Large and sweet, long shelf life
'Tango'	1994	England	Day-neutral, resistant to red stele and Verticillium wilt
'Bolero'	1996	England	Day-neutral, high fruit quality
'Darselect'	1996	France	Large, sweet and firm
'Florence'	1997	England	Late, large, resistant to *Verticillium* wilt and mildew
'Everest'	1999	England	Day-neutral, large fruit and very productive

'Marguerite' (1858) (Darrow, 1966). 'Héricart de Thury' had excellent flavour and glossy red, firm berries that made it the most important preserve berry for 100 years. 'Marguerite' did not achieve the long-term status of 'Héricart de Thury' but was widely admired for its exceptionally large berries, said to average 15–20 g with 40–45 g primaries.

Thomas Laxton of England was the most active breeder during the late part of the 18th century and released a number of important varieties including 'Noble' (1884) and 'Royal Sovereign' (1892). These two varieties were grown on both sides of the Atlantic Ocean and were popular until the middle of the 20th century. 'Noble' was known for its earliness, cold hardiness and disease resistance. 'Royal Sovereign' was popular because of its earliness, productivity, flavour, attractiveness and hardiness. The American variety 'Sharpless' was in the ancestry of both these cultivars.

Some of the most popular releases in the early 20th century were C. Moutot's 'Madame Moutot' (France, 1910), Bottner's 'Deutsch Evern' (Germany, 1902), O. Schindler's 'Oberschlesien' (Germany, 1919) and Guyot of Dijon's 'Surprise des Halles' (France, 1929). 'Madame Moutot' was popular

in France and other European countries until the late 1960s due to its size and productiveness. 'Deutsch Evern' was the standard early variety in northern Europe for decades and was still grown to some extent in 1960 (Darrow, 1966). It was noted for its productivity and long, conical, light-red fruit. 'Oberschlesien' was widely planted in Germany until 1945 for its high yield and adaptability. 'Surprise des Halles' was the most popular cultivar in France in the mid-1960s because of its earliness, fruit quality and productivity.

In the middle of the 20th century, a number of particularly active breeding programmes emerged in Scotland, England, Germany and the Netherlands. In Scotland, R. Reid developed a series of varieties resistant to red stele, utilizing American 'Aberdeen' as a source of resistance. His variety 'Auchincruive Climax' (1947) dominated acreage in Great Britain and northern Europe until its demise due to June yellows in the mid-1950s. He then released 'Redgauntlet' (1956) and 'Talisman' (1955), which served as suitable replacements. In England, D. Boyle produced a large series of varieties with the prefix 'Cambridge'. 'Cambridge Favourite' (1953) became the most important of the group and dominated the acreage in Great Britain by the 1960s. It is still planted somewhat today, due to its productivity, firmness, shippability and capping ease. In Germany, R. von Sengbusch produced a 'Senga' series, of which 'Senga Sengana' (1954) became paramount. 'Senga Sengana' was widely planted for its processing quality and is still important in Poland and other eastern European countries. In the Netherlands, H. Kronenberg and L. Wassenaar released several cultivars, of which 'Gorella' (1960) made the greatest impact. It was noted for its size, bright-red glossy skin and red flesh.

BREEDING OUTSIDE EUROPE FROM 1800 TO 2000

The greatest concentration of breeding activity outside of Europe until the modern period was in the USA, although the Japanese produced two important varieties: Dr H. Fukuba's 'Fukuba' (1899), noted for its large size and high flavour (Darrow, 1966), and K. Tamari's 'Kogyoku' (1940), respected for its vigour, earliness and fruit size (Mochizuki, 1995). 'Fukuba' was the most important variety in forcing culture until the early 1970s. 'Kogyoku' was one of the leading field-grown cultivars after World War II, until it lost importance to the American import 'Donner' in the 1950s (Darrow, 1966).

Charles Hovey, of Cambridge, Massachusetts, produced the first important North American cultivar 'Hovey', by crossing the European pine strawberry 'Mulberry' with a native clone of *F. virginiana* in 1836 (Fig. 2.7). It was the first variety of any fruit to come from an artificial cross in America and for some time made the strawberry the major pomological product in the country (Table 2.2; Hedrick, 1925).

'Hovey' often proved to have low fruit set, the basis of which led to considerable horticultural debate (Fletcher, 1917). It had been known in Europe

Fig. 2.7. The 'Hovey' strawberry. (From Wilhelm and Sagen, 1974.)

since 1760 that strawberries could have separate genders, but Americans were not aware of this work and for a decade from 1840 to 1850 debate raged among horticultural societies as to the nature of 'Hovey's' unproductiveness. Hovey himself originally asserted that his cultivar was perfect, but eventually had to recant under pressure from Nicholas Longworth of Cincinnati, Ohio.

The release of 'Hovey' stimulated a great deal of interest in strawberries throughout the country and numerous private individuals began making crosses and growing seedlings. The variety that had the largest immediate impact was 'Wilson' (1851), developed by James Wilson in New York. It played an important role in expanding the North American strawberry industry from a few thousand hectares to hundreds of thousands. It produced large, dependable crops even under indifferent care and its flowers were bisexual, eliminating the need for a pollinator. The fruit of 'Wilson' were larger and more attractive than that of its predecessors and were firm enough to ship long distances. Unfortunately, its flavour was very sour but its other strengths led to the liberal use of the sugar bowl.

Several important cultivars were developed in the late 1800s and early 1900s to meet the need of the burgeoning strawberry industry (Darrow, 1937, 1966). Some of the most successful were W. Parmalee's 'Crescent' (Conneticut, 1876), J. Sharpless's 'Sharpless' (Pennsylvania, 1872), Neunan's 'Neunan' (South Carolina, 1868), M. Ewell's 'Marshall' (Massachusetts, 1890), C. Loftus's

Table 2.2. Dominant *Fragaria* × *ananassa* cultivars in North America before 2000. (From Darrow, 1966; Hancock, 1996; Brooks and Olmo, 1997.)

Cultivar	Year of release	Place developed	Notable characteristics
'Hovey'	1836	Massachusetts	First variety of fruit developed in North America, better adapted than English varieties
'Wilson'	1851	New York	Productivity, firmness, deep red colour, hardiness and broad adaptability
'Sharpless'	1872	Pennsylvania	Pollinator of 'Wilson'
'Crescent'	1876	Connecticut	Productivity, earliness, hardiness and broad adaptability
'Ettersburg 80'	1880	California	Drought resistant, dessert and jam quality, hardiness
'Aroma'	1889	Kansas	Large, firm and attractive fruit, productivity, well adapted to clay and silt soils, resistance to leaf spot and leaf scorch
'Marshall'	1890	Massachusetts	Adaptation to mild climates, large fruit size, excellent flavour, high freezing quality and drought tolerance
'Nich Ohmer'	1898	Ohio	Productivity, large, firm, glossy-crimson berries
'Pan American'	1898	New York	First widely successful everbearer
'Dunlap'	1900	Illinois	Extreme hardiness, high flavour and deep red colour
'Missionary'	1900	Virginia	Low chilling requirement
'Klondike'	1901	Louisiana	Tolerance to heat, deep red colour and vigour
'Howard 17' ('Premier')	1915	Massachusetts	Excellent parent, resistance to leaf diseases, early flower bud initiation, multiple crowns, deep red colour and productivity
'Blakemore'	1929	Maryland	Outstanding shipper, resistant to leaf diseases, scarlet colour and productivity
'Robinson'	1932	Michigan	Large size, productivity, colour and tolerance to virus diseases
'Catskill'	1933	New York	Large fruit size and productivity
'Fairfax'	1933	Maryland	Outstanding flavour, resistance to leaf diseases, low acid fruit
'Gem'	1933	Michigan	Dependable everbearer
'Tennessee Beauty'	1933	Tennessee	Productivity, firm and glossy red fruit, tolerance to virus diseases, capping ease

Continued

Table 2.2. Continued.

Cultivar	Year of release	Place developed	Notable characteristics
'Sparkle'	1943	New Jersey	Productivity, attractiveness, high flavour and resistance to red stele
'Albritton'	1945	North Carolina	Late, large, uniform, attractive and firm fruit with excellent flavour, freezing quality
'Lassen'	1945	California	Low chilling requirement, large fruit and productivity
'Shasta'	1945	California	Large, firm and attractive berries
'Pocahontas'	1946	Maryland	Large attractive fruit, good frozen quality
'Northwest'	1949	Washington	Lateness, productivity and tolerance to virus
'Surecrop'	1950	Maryland	Resistance to many diseases (red stele, leaf spot, leaf scorch and Verticillium wilt), vigorous and drought resistant
'Midway'	1951	Maryland	Productivity, deep red colour, freezing quality and resistance to red stele
'Florida 90'	1952	Florida	Long, large and early berries, high flavour and productivity
'Jerseybelle'	1955	New Jersey	Vigorous, very large fruit
'Tioga'	1955	California	Large, attractive, firm fruit, high productivity
'Headliner'	1957	Louisiana	Early ripening, large fruit, productivity and resistance to leaf spot
'Redcoat'	1957	Ontario	Very winter hardy
'Goldsmith'	1958	California	Productivity, large, firm, glossy, attractive berries, good shipping quality
'Daybreak'	1961	Louisiana	Productivity, excellent flavour
'Sunrise'	1964	Maryland	Resistant to red stele, Verticillium wilt, leaf scorch and mildew
'Hood'	1965	Oregon	Excellent flavour, processing quality, caps easily, multiple resistances to leaf and root fungal diseases
'Veestar'	1967	Ontario	Very early
'Raritan'	1968	New Jersey	Productivity
'Redchief'	1968	Maryland	Good processing quality, resistant to red stele and Verticillium wilt
'Guardian'	1969	Maryland	Resistant to leaf scorch, mildew, red stele and Verticillium wilt
'Apollo'	1970	North Carolina	Late, multiple leaf disease resistances
'Atlas'	1970	North Carolina	Freezing quality, resistant to red stele

Continued

Table 2.2. Continued.

Cultivar	Year of release	Place developed	Notable characteristics
'Shuksan'	1970	Washington	Good processing quality, resistant to red stele, Verticillium wilt and *Botrytis* infection
'Honeoye'	1971	Maryland	Productive
'Totem'	1971	British Columbia	Good for processing, resistant to red stele, Verticillium wilt and *Botrytis* infection
'Bounty'	1972	Nova Scotia	Vigorous and productive
'Pajaro'	1973	California	Productive
'Tangi'	1973	Louisiana	Vigorous, resistant to leaf spot and scorch
'Cardinal'	1974	Arkansas	Concentrated ripening, processing quality
'Benton'	1975	Oregon	High vigour, adapted to high-pH soils
'Earliglow'	1975	Maryland	Excellent flavour, resistant to multiple leaf and root diseases and botrytis fruit rot
'Aiko'	1976	California	Particularly long fruiting season
'Lateglow'	1976	Maryland	Late, resistant to red stele and Verticillium wilt
'Micmac'	1976	Nova Scotia	Productive, very winter hardy
'Douglas'	1979	California	Productive
'Chandler'	1980	California	Large, firm and productive
'Dover'	1980	Florida	Resistant to *Colletotrichum* infection and anthracnose crown rot
'Allstar'	1981	Maryland	Productive, resistant to red stele, leaf scorch and powdery mildew
'Kent'	1981	Nova Scotia	Productive, very winter hardy
'Tribute'	1981	Maryland	Day-neutral
'Selva'	1983	California	Day-neutral, productive
'Annapolis'	1984	Nova Scotia	Productive, resistant to Verticillium wilt
'Blomidon'	1984	Nova Scotia	Productive
'Glooscap'	1984	Nova Scotia	Productive
'Governor Simcoe'	1984	Ontario	Vigorous, large brightly coloured fruit
'Jewel'	1985	Nova Scotia	Productive, flavourful and drought tolerant
'Oso Grande'	1987	California	Productive, very large firm fruit
'Cavendish'	1990	Nova Scotia	Flavourful, resistant to red stele and Verticillium wilt
'Chambly'	1990	Quebec	Very winter hardy, resistant to several leaf diseases and red stele

Continued

Table 2.2. Continued.

Cultivar	Year of release	Place developed	Notable characteristics
'Diamonte'	1991	California	Day-neutral, large firm fruit, high productivity
'Seascape'	1991	California	Day-neutral, productive, bright red internal and external colour
'Camarosa'	1992	California	Very large and firm, productive, vigorous
'Sweet Charlie'	1992	Florida	Productive, flavourful, resistant to *Colletotrichum* infection
'Aromas'	1994	California	Productive, day-neutral, resistant to *Phytophthora cactorum*, anthracnose crown rot and powdery mildew
'Delmarvel'	1994	Maryland	Resistant to multiple leaf diseases and red stele
'Mohawk'	1994	Maryland	Very early, resistant to multiple leaf diseases and red stele
'Noreaster'	1994	New Jersey	Resistant to red stele and most leaf diseases
'Winona'	1995	Minnesota	Late, winter hardy, resistant to common leaf diseases, red stele and black root rot
'Mira'	1996	Nova Scotia	Resistant to common leaf diseases and red stele
'Gaviota'	1998	California	Productive, large firm fruit, resistant to powdery mildew and anthracnose crown rot
'Brunswick'	1999	Nova Scotia	Productive, brightly coloured berries

'Banner' (California, about 1890), E. Cruse's 'Aroma' (Kansas, 1892), J. Beaver's 'Nich Ohmer' (Ohio, 1898) and S. Cooper's 'Pan American' (New York, 1898). 'Neunan' was a seedling of 'Wilson' and became the standard in the south-eastern USA in the late 1800s because it was a little less dark and a touch firmer than 'Wilson' in hot climates. 'Crescent' and 'Sharpless' were second and third to 'Wilson' in popularity from 1880 to 1900. 'Wilson' was pistillate and 'Sharpless' was commonly used as its pollinator. 'Marshall' was only a modest success in the east where it was bred, but it became a major variety in the Pacific Northwest and California from 1905 to almost 1960, because of its high flavour and how well it could be frozen and preserved. 'Pan American' was notable as the first really successful everbearing variety. Although it was widely planted in gardens, its greatest importance was as a parent and was a major source of the everbearing trait until Powers and Bringhurst utilized native populations of *F. virginiana* ssp. *glauca*

(see Chapter 8, this volume). 'Nich Ohmer' was not successful in its state of origin, Ohio, due to its low vigour, susceptibility to leaf spot and its small, only fair-flavoured fruit, but it was widely grown in California in the 1920s and 1930s because of its long fruiting season. It is in the genetic background of most successful California cultivars.

'Banner' ('Sweet Briar') was discovered in an abandoned strawberry patch by C. Loftus on his farm in Sweet Briar, California (Wilhelm and Sagen, 1974). Its early importance was limited due to insufficient runner production, but it rapidly grew in prominence in the Central Valley from 1904 until the mid-1930s, when it was found that it could be successfully propagated in northern California. The berries of the 'Banner' strawberry were large, regularly conical in shape, bright red and had a wonderful taste and fragrance. It may have been a seedling or runner descendant of 'Marshall'.

Some of the most important varieties developed in the early part of the 20th century (Darrow, 1966) were Rev. J. Reasoner's 'Dunlap' (Illinois, 1900), N. Gohn's 'Missionary' (Virginia, 1900), R. Cloud's 'Klondike' (Louisiana, 1901), A. and E. Howard's 'Howard 17' or 'Premier' (Massachusetts, 1915) and J. Kuhn's 'Aberdeen' (New Jersey, 1923). 'Dunlap' dominated acreage in the northern states and Canada for the first 50 years of the century, because of its extreme hardiness. It was used widely as a parent in everbearing breeding, even though it was a short-day type. 'Missionary' was also important for about 50 years, as one of the first really good low-chilling varieties, performing well even in the semi-tropics of Florida. It was also an excellent parent in breeding of warm-climate types. 'Howard 17' ('Premier') was a major eastern cultivar for at least 40 years both as a commercial cultivar and breeding parent. It is found in the ancestry of most North American and many European cultivars, and it was particularly noted for its resistance to leaf diseases and viruses, formation of many crowns, frost-hardy flowers and high productivity. 'Aberdeen' was grown in the 1930s in New Jersey and the east but may have found its greatest importance as a breeding source for red stele resistance in both European and North American cultivars.

The most active breeder around the turn of the century was probably Albert Etter of California who developed dozens of varieties utilizing native *F. chiloensis* clones (Wilhelm and Sagen, 1974; Fishman, 1987). His most successful variety was 'Ettersburg 80' (1910), which was widely grown in California, Europe, New Zealand and Australia. Renamed as 'Huxley', it was still popular in England as late as 1953. 'Ettersburg 80' was extremely drought resistant, of outstanding dessert and jam quality due to its solid bright red colour and was unusually hardy for a California type. Other outstanding Etter varieties were 'Ettersburg 121', 'Fendalcino' and 'Rose Ettersburg'. Although his releases were very successful as cultivars, they may have had their greatest impact as breeding parents. Almost all California cultivars (and many others) have an Ettersburg variety in their background (Darrow, 1937, 1966; Sjulin and Dale, 1987).

In the 1930s and early 1940s, several new cultivars became important across the USA including the great US Department of Agriculture (USDA) breeder G. Darrow's 'Blakemore' (USDA-MD, 1929) and 'Fairfax' (USDA-MD/NC, 1933), G. Slate's 'Catskill' (New York, 1933), K. Keplinger's 'Gem' (Michigan, 1933), J. Haley's 'Robinson' (Michigan, 1940) and E. Henry's 'Tennessee Beauty' (Tennessee, 1943). 'Blakemore' became the major southern variety in the mid-1930s until the early 1960s because of its earliness, firm, bright-red berries, suitability for freezing and preserving, and disease resistance. 'Blakemore' was used extensively in breeding, finding its way into the ancestry of a diverse array of cultivars grown in all parts of the USA. 'Tennessee Beauty' became dominant in the upper south from 1940 to the 1960s due to its high productivity, tolerance to virus and good freezing quality. 'Gem' (also called 'Superperfection' and 'Brilliant') was the most important everbearer from 1940 to the modern period. 'Fairfax' was widely planted in the middle of the century from southern New England to Maryland and westward to Kansas. It was particularly noted for its outstanding flavour but may have been more important as a breeding parent, finding its way into the pedigree of numerous European, USA, Canadian and even Japanese cultivars.

In the late 1940s and early 1950s, several more cultivars achieved importance including J. Clarke's 'Sparkle' or 'Paymaster' (New Jersey, 1943), E. Morrow's 'Albritton' (North Carolina, 1945), H. Thomas and E. Goldsmith's 'Lassen' and 'Shasta' (California, 1945), D. Scott and G. Darrow's 'Pocahontas' (Maryland, 1946) and C. Schwartze's 'Northwest' (Washington, 1949). 'Sparkle' dominated in the north-east and mid-west in the 1950s and 1960s, due to its high flavour, attractive appearance and resistance to red stele. 'Northwest' was the most planted variety in the USA in the 1960s, even though all of the acreage was in Oregon and Washington (Darrow, 1966). It was particularly noted for its lateness and tolerance to virus diseases. 'Shasta' was widely grown in the central coast of California in the 1950s and 1960s because of its large size, firmness and long season. 'Lassen', grown extensively in southern California about the same period, was prized for its short rest period and high productivity. 'Pocahontas' was widely grown in the lower mid-west and south in the 1960s and 1970s, and even became important in Italy in the late 1970s. It was known for its productivity, large, attractive, firm berries and good freezing quality.

The middle decades of the 20th century saw the release of D. Scott's 'Surecrop' (Maryland, 1950) and 'Midway' (Maryland, 1960), R. Bringhurst and V. Voth's 'Tioga' (California, 1955), P. Hawthorne's 'Headliner' (Louisiana, 1957) and 'Dabreak' (Louisiana, 1961), L. Spangelo's 'Redcoat' (Ontario, 1957), H. Thomas and E. Goldsmith's 'Goldsmith' (California, 1958) and A. Brook's 'Florida 90' (Florida, 1952). 'Surecrop', which was important in the upper south and lower mid-west during the 1960s and 1970s, was noted for its high disease tolerance both to leaf and soil pests. 'Midway' replaced 'Robinson' in the 1960s in the mid-western USA, primarily because of its firmer berries

and resistance to red stele. 'Redcoat' dominated eastern Canada in the 1960s and 1970s. It was known for its high yield, appearance, earliness and shipping qualities. 'Headliner' and subsequently 'Daybreak' became important in the south in the 1960s and 1970s, replacing the earlier varieties, due to their larger size, higher productivity and an earlier season. 'Tioga' replaced 'Lassen' in California in the late 1960s because of its greater size, attractiveness, firmness and productivity. 'Florida 90' became popular in Florida in the late 1950s due to its very long, large, early berries and high flavour (Darrow, 1966). 'Goldsmith' was the first important private variety in California, noted for its productivity and shipping quality.

DIVERGENCE OF NORTH AMERICAN BREEDING PROGRAMMES

As previously described, strawberry breeding began in North America by hybridizing F. × *ananassa* cultivars derived from Europe with native genotypes of the founding species of *F. chiloensis* and *F. virginiana* that came from diverse geographic and subspecies origins (Darrow, 1966). Breeding programmes subsequently cropped up all across the continent in a broad range of climates ranging from the cold temperate climates of the eastern seaboard to the mild Mediterranean ones of coastal California. Over time, considerable genetic differentiation occurred among the various breeding programmes through hybridization and selection. The wild progenitor ecotypes would have provided an almost unlimited source of genes to generate unique regional group structures (Hancock and Luby, 1993).

Over 50 years ago, Darrow (1966) identified a series of 18 traits that separated *F. chiloensis* from *F. virginiana* and then rated five eastern varieties for the proportion of their phenotype that appeared to be based on *F. chiloensis*. According to his rating system, 'Fairfax' expressed 57% of the characteristics of *F. chiloensis*; 'Earlidawn', 28%; 'Blackmore', 31%; 'Howard 17', 31%; and 'Missionary', 27%. From these values he suggested that his eastern breeding programme had been selecting for more *F. virginiana* characteristics than *F. chiloensis* characteristics. He further asserted that 'Fairfax' with the most *F. chiloensis* characteristics would be more broadly adapted than the others and that 'greater use of *F. chiloensis* in breeding for superior varieties seems indicated' (Darrow, 1966).

Much more recently, Hardigan *et al.* (2018) analysed genome-wide DNA profiles of 1300 octoploid individuals, including wild species, historic varieties (1814–present) and the University of California germplasm collection. They evaluated 16,492 polymorphic and subgenome-specific markers. They found that the cultivars bred for California were substantially differentiated from the temperate-climate cultivars developed in eastern North America and they did indeed carry a much higher proportion of genes from *F. chiloensis*. Selection

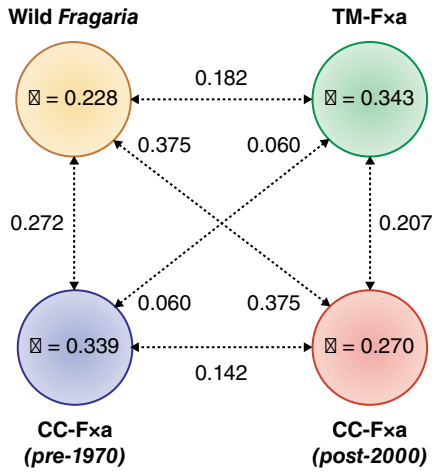

Fig. 2.8. Population divergence [Weir and Hill *F*-statistic (F) arrow labels] of wild progenitor species (South American *F. chiloensis* and *F. virginiana*), temperate *F.* × *ananassa* (TM-F×a), California coastal (CC-F×a) pre-1970, and CC-F×a post-2000. Internal values reflect average marker diversity (π) within the populations. (From Hardigan *et al.*, 2018.)

over the last 20–30 years in California had restructured genetic diversity similar to the restructuring that occurred during the first 200 years of breeding, and coastal *F.* × *ananassa* has diverged further from the temperate *F.* × *ananassa* than the latter from their wild progenitors (Fig. 2.8). They also showed that introgression of the day-neutral flowering trait from non-ancestral *F. virginiana* ssp. *glauca* into coastal California led to a transition to a different gene source of late-season flowering.

AMERICANIZATION OF EUROPEAN BREEDING PROGRAMMES

As previously described, strawberry breeding began in Europe in the early 1800s, with a collection of New World representatives of *F. chiloensis* and *F. virginiana*. In the mid-1800s, the early hybrid cultivars from Europe found their way across the Atlantic and were used by the first North American breeders to initiate their programmes. Over the next 100 years, the European and North American breeding programmes tended to operate in isolation with only limited germplasm exchange. However, this separation dramatically changed in the 1960s, when European breeders began to widely employ improved North American cultivars from California in their breeding programmes.

The appearance of US germplasm in European breeding programmes has been documented in a couple of recent studies using diagnostic DNA markers.

Gil-Ariza *et al*. (2009) used simple sequence repeat (SSR) markers derived from expressed sequence tags to determine similarity relationships of 92 mostly US and European cultivars from the mid-1800s to present. They identified three clusters: (i) a clade of 26 old accessions (most of them released before 1969) of European or American origin with little California genetics incorporated; (ii) a clade of 44 later-released accessions from both continents represented by 'Camarosa' and carrying a goodly proportion of genetics from the Strawberry Breeding & Research programme at the University of California, Davis (Cal-Davis); and (iii) a clade of 22 cultivars from different breeding periods represented by 'Selva' and also carrying a strong contribution of genes from Cal-Davis.

Horvath *et al*. (2011) employed 23 SSR markers to examine diversity patterns and population substructuring in 57 European cultivars dating from the late 1800s to modern times and 29 others developed outside Europe (mostly North American) from the early 1900s to the present. They observed 'a progressive abandonment in European breeding efforts of old European cultivars towards mainly North American ones' and a distinct separation between old European cultivars developed before 1960 and those bred more recently. They found a clustering of cultivars into four groups: (i) mostly old European cultivars; (ii) mixtures of American and modern European cultivars grown across the continent; (iii) mixtures of mostly American cultivars from California and modern cultivars grown in southern Europe; and (iv) an 'intermediate' group of cultivars introgressed with *F. chiloensis* and *F. moschata*. They warned that the older European material needs to be protected and maintained so that potentially valuable genes from the infancy of strawberry breeding in Europe are not lost.

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