Our Southern Strawberry Heritage: *Fragaria chiloensis* of Chile

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The strawberry genus, *Fragaria,* is a polyploid series composed of nine diploids, three tetraploids, one pentaploid, one hexaploid, and four octoploids (Hancock and Luby, 1993). The primary species of international commerce is the octoploid *F.* ×*ananassa* Duch. (2x = 8n = 56), a hybrid of *F. chiloensis* L. and *F. virginiana* Duch. Native populations of *F. chiloensis* are found on the beaches and mountains of central and southern Chile, Hawaii, and in a narrow band along the coast of western North America from the middle of California to the Aleutian Islands. Wild *F. virginiana* is native to the woodlands and meadows of much of the United States and Canada.

The evolutionary origin of the octoploid strawberry species is clouded. Cytogenetic data indicate that they are complex hybrids with the genomic constitution AAA'A'BBB'B' (Bringhurst, 1990). The A genome donor has been identified as *F. vesca* L., but the other genomic contributors remain obscure. Although *F. chiloensis* and *F. virginiana* are restricted to the western hemisphere, the octoploids probably originated in the eastern hemisphere, as *F. vesca* is the only other species found in the United States and Canada. The point of origin is unclear, but the range of *F. chiloensis* extends north and west along the Aleutian Islands, almost to the Kuril Islands, where the only Asian octoploid, *F. iturupensis* Staudt, is found (Staudt, 1973). This suggests that the original octoploid arose in East Asia and then spread across the Bering Strait to North America. The ancestral octoploid species must have differentiated into *F. chiloensis* and *F. virginiana* as they moved south and developed differential adaptations to coastal and mountain habitats (Luby et al., 1992). In fact, the two species are completely interfertile and no significant differences between them have been identified in chloroplast DNA (Harrison et al., 1997a). Randomly amplified polymorphic DNA data suggest that they have remained relatively isolated, but the interspecific fertility and proximity of these groups have allowed for occasional introgression (Harrison et al., 1997b).

The origin of Chilean and Hawaiian *F. chiloensis* is just as obscure, but presumably they were introduced from North America via bird migrations. Interestingly, the single Chilean species *F. chiloensis* has evolved multiple ecotypes that fill the habitats of both North American species, *F. chiloensis and F. virginiana.* At high elevations in Chile, plants occur that have the glaucous, thin leaves characteristic of *F. virginiana* ssp. *glauca* (Wats.) Staudt in the Rocky Mountains. On the beach in Chile, forms of *F. chiloensis* ssp. *chiloensis* f. *patagonica* Staudt can be found that resemble both the glossy, thick-leaved *F. chiloensis* ssp. *pacifica* Staudt found in the coastal fog belt of California and the more delicate *F. chiloensis* ssp. *lucida* (E. Vilm.) found on the coast of the Pacific Northwest (Cameron et al., 1991; Darrow, 1966; Lavín, 1997).

DOMESTICATION OF THE CHILEAN STRAWBERRY

The cultivated strawberry of South America, *Fragaria chiloensis* ssp. *chiloensis* f. *chiloensis* Staudt, has a long and rich history. 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 (Aldunate, 1989).

The Picunches grew mainly corn (*Zea mays* L.), quinoa (*Chenopodium quinoa* Willd.), dry beans (*Phaseolus vulgaris* L. and *P. lunatus* L.), squashes (*Cucurbita maxima Duchesne* ex Lam.), oca (*Oxalis tuberosa* Molina), pepper (*Capsicum annuum* L.), madi [*Madia chilensis* (Nutt.) Reiche], and mango (*Mangifera indica* L.) (Montaldo, 1988). Strawberry fruits were used by the native Chileans fresh, dried, as a fermented juice or as medicinal infusions against indigestion, diarrhea, and bleeding (De Moesbach, 1992). The Mapuches made many other kinds of fermented juices, but their favorite was the one from the "llahuen" or "lahueñe" (small, red-fruited wild strawberry) that was called "lahueñe mushca" (Labarca, 1994).

Most evidence indicates that the primary domesticants were the larger, white-fruited forms, called "kellén" or "quellghen" by the Mapuches. Albino-fruited types are rare in nature, but have been found at three southern locations. When subjected to a multivariate analysis, these forms were more closely associated with the cultivated white types than with the native wild red ones (de Pozo et al., unpublished; Lavín, 1997).

Some red-fruited forms may also have been domesticated, but reports of their existence are sketchy. Darrow (1957a) described large, red-fruited forms being grown around Santiago, Chile, in the middle of this century, but 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. However, the Mapuches reportedly 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 fierce Indians attacked and killed them (Gonzalez de Nájera, 1866).

Strawberry cultivation by the native Chileans was mostly limited to garden plots. During the Spanish colonial period, larger semi-commercial plantings of 1 to 2 ha began to appear in the coastal areas from north of the Itata River to Chiloé Island. From the second half of the 19th century to the first half of the 20th, *F. chiloensis* was grown on farms of several hectares located at least in Buchupureo, Cobquecura, along the Gulf of Arauco, Cañete, Lake Lanalhue, Lake Lleulleu, Lake Budi, Puerto Saavedra, Nueva Imperial, Trovolhue Carahue, Corral, and probably the Island of Chiloé. The fruit grown in most of these areas was transported by mules to city markets, in trips that lasted up to 4 d (Fernando Coloma, personal communication).

At Renca, immediately north of Santiago, there were numerous small strawberry plots (1–2 ha) from the very beginning of the colonial period until after the independence of Chile in 1818 (Gay, 1865; Peri, 1992; Rosales, 1995). These plantings were probably initiated from the wild strawberries that existed in the area when the Spaniards arrived (Bibar, 1966). The fruits were sold at mule-back in Santiago, but it was very common for people to travel from Santiago across the Calicanto Bridge to pick fruit (the first strawberry U-pick!) (Rosales, 1995).

Gay (1865) states that European cultivars of *F.* ×*ananassa* began

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to be grown in Chile around 1830, but only sparingly. The two types of strawberries were clearly distinguished, with the European types being called "fresas" (transliteration from the French "fraisier") and the Chilean types being called "frutillas" from the Spanish "little fruits" (although the word "frutilla" is a Chilean invention) (Medina, 1917).

In the first half of this century, a large canning industry based on *F. chiloensis* arose around Nueva Imperial (Rodrigo Infante, personal communication) and a smaller one near Corral, expanding the southern industry to hundreds of hectares (Nuñez, 1993). The traditional plantings of *F. chiloensis* flourished until the 1950s, when they began to be mixed with European cultivars of *F.* ×*ananassa* and ultimately lost dominance. In the last 30 years, California cultivars of *F.*×*ananassa* have replaced the European cultivars and are grown in large plantings around Santiago and to a lesser extent near San Fernando, Curicó, and Parral. While cultivation of *F. chiloensis* has diminished, small plantings can still be found along the traditional area of cultivation from Iloca on the coast of Curicó province to Chiloe Island. "Quellghen" types have been collected in the last 10 years by A. Lavín and coworkers at Iloca, Carrizal, Pelluhue, Curanipe, Buchupureo, Cobquecura, Cañete, Purén, and Carahue, by R. Hepp at Concepción, and by R.S. Bringhurst at Purén. They appear to represent numerous different land races, as they display substantial variability in their leaf morphology, habit, taste, aroma, and color (Lavín et al., 1997).

SPREAD OF STRAWBERRY CULTURE OUTSIDE OF CHILE

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

The largest area of cultivated *F. chiloensis* in South America was grown near Ambato at Huachi-Grande, Ecuador. There were probably 500 to 700 ha from at least the late 1700s until 1970 (Finn et al., 1998; Hancock et al., 1997). According to Popenoe (1921), 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." 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. Popenoe (1921) himself 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."

CONTRIBUTION OF THE CHILEAN STRAWBERRY TO THE MODERN STRAWBERRY

One of the Chilean clones even found its way into Europe in the 1700s, compliments of the French spy, Captain Amédée Frézier (Darrow, 1966; Wilhelm and Sagen, 1972). While gathering information about Spanish fortifications along the coast of Chile, Frézier was struck by the large-fruited strawberries grown by the native peoples at Concepción. *F. chiloensis* was initially a great disappointment in Europe, as Frézier had inadvertently brought back only female plants that required a pollinizer. It was redeemed, however, by the discovery that it produced fruits if interplanted with the European native *F. moschata* or *F. virginiana* that had been introduced from the New World. *F. chiloensis* became the major species of commerce in France, and Brittany became the European center of production.

Over time, strawberry seedlings began to appear in European gardens with exceptionally large-sized fruit with red flesh in comparison with the white pulp of *F. chiloensis*. While the origin of these seedlings was initially clouded, Antoine Nicholas Duchesne determined in 1766 that they were hybrids of *F. chiloensis* x *F. virginiana*, which he named *Fragaria* ×*ananassa* (Darrow, 1966). The strawberry industry relied on these chance hybrids for decades, until Thomas A. Knight began the first formal strawberry breeding project in England in 1817 (Darrow, 1966).

Since the early formative years of *F.* ×*ananassa*, native clones of *F. chiloensis* have been used only sparingly in strawberry breeding programs (Dale and Sjulin, 1990; Hancock, et al., 1993; Sjulin and Dale, 1987), although several important horticultural characteristics have been captured from them, including unique disease and pest resistances, large fruit size, and a high photosynthetic rate (Bringhurst and Voth, 1984; Cameron and Hartley, 1990; Hancock and Luby, 1995; Hancock et al., 1989, 1990; Luby et al., 1991). Almost all of the wild *F. chiloensis* clones that have been used in breeding have come from North America (Hancock and Luby, 1995; Sjulin and Dale, 1987), even though South American populations of *F. chiloensis* have long been recognized as having larger fruit size and better firmness than North American populations (Bringhurst and Voth, 1960; Darrow, 1953; Popenoe, 1921), and were genetically improved over 1000 years of selection by the Chilean Mapuches.

A Huachi-Grande clone, apparently collected by Popenoe, is the only representative of South American *F. chiloensis* that has entered a North American pedigree in this century. It was used as a parent by George Waldo in Oregon, and is in the background of most of the varieties now grown in the Pacific Northwest (Sjulin and Dale, 1987; Waldo, 1953). The great U.S. Dept. of Agriculture (USDA) breeder, George Darrow, traveled to Ecuador, Perú, and Colombia in 1951 to bring elite clones of *F. chiloensis* back to the United States for varietal improvement (Darrow, 1953, 1957a, 1957b), but, unfortunately, his early F_1 and backcross populations of *F.* ×*ananassa* x *F. chiloensis* did not prove well adapted to the seasonal temperature extremes of the eastern United States and were soon dropped from his breeding program.

PRESENT STATUS OF CHILEAN STRAWBERRY CULTURE AND GERMPLASM COLLECTIONS

The introduction into South America of European cultivars in the 1950s and California cultivars in the 1960s have put most native land races of *F. chiloensis* perilously close to extinction. In Ecuador, we found that what was once 500 to 700 ha of Huachi-Grande has been reduced to ≈5 ha (Finn et al., 1998; Hancock, et al., 1997). In Chile, only a few hectares remain of the Chilean strawberry that was collected near Concepción by Frézier, and only scattered small acreages exist anywhere else. Most of the native land races are contaminated by hybridization and introgression with native clones. Reports from Perú and Colombia suggest that the native cultivars have almost disappeared there as well, although some still exist due to some demand at specialty markets near Cuzco and Bogotá.

In the last 10 years, renewed interest has developed in evaluating the strawberry of South America. Scott Cameron of the Univ. of Washington has led two expeditions to Chile to collect primarily native germplasm with the help of the Chilean scientists Carlos Muñoz and Arturo Lavín from the Instituto de Investigaciones Agropecuarias (INIA) (Cameron et al., 1991, 1993; Lavín et al., 1993). Most recently, a Japanese group from the National Research Institute of Vegetables, Ornamental Plants, and Tea, led by Tatsuya Mochizuki with the cooperation of scientists from the Chilean Instituto de Investigaciones Agropecuarias, collected strawberries in Chile (Mochizuki et al., 1996). Numerous valuable traits have been identified in replicated trials of this material, including large fruit size, high flower number, resistance to salinity and drought, low nutrient needs, and high photosynthetic rates (Lavín, 1997). However, only a small fraction of the white- to pink-fruited land races of *F. chiloensis* are still being cultivated in South America, and none of the old red land races described by Darrow have been evaluated . Evaluations of domesticated *F. chiloensis* have been limited to a handful of the white to pink forms collected by Lavín in Chile (Lavín, 1997).

A number of South American land races are available for trial from

the national Clonal Germplasm Repository at Corvallis, Ore., but, except for the recently collected Chilean and Ecuadorian material, the existing passport information is limited mostly to collection site. In several cases, it is not clear whether the maintained clones are properly labeled, particularly those attributed to Darrow. The cultivated races have received only modest attention, even though they are far superior in size to the wild types (del Pozo et al., unpublished data; Lavín, 1997), and are easily hybridized with *F.* ×*ananassa*, and the F_1 hybrids generally have fruit size far superior to the midparent value (Bringhurst and Voth, 1960; Hancock, et al., unpublished data). In fact, land races of *F. chiloensis* compared favorably with many of the *F.* ×ananassa cultivars currently grown on small farms in Chile (del Pozo et al., unpublished data; Lavín, 1997).

We should collect as many of the land races as possible before they become completely extinct. Losing the genetic improvement made by the indigenous Chilenos and later spread by the Spanish colonists would be a crime. The wild populations of *F. chiloensis* in Chile are also threatened by development (Cameron et al., 1993), but a representative sample of wild Chilean *F. chiloensis* is probably contained in the germplasm collections of Lavín and Cameron. This material has been extensively evaluated for its fruiting and vegetative characteristics, although little information is available on pest and disease resistances.

THE FUTURE

South American *F. chiloensis* has much to offer to plant breeders in both North and South America (Hancock and Luby, 1993; Hancock et al., 1993). The marvelous work of the Picunches and Mapuches probably can be built upon through the systematic selection and crossing of elite native and cultivated races of *F. chiloensis.* We believe that large, red-fruited types can be developed with higher yields and improved fruit firmness. There should be a ready market, as pure *F. chiloensis* fetches three to four times the price of common strawberries in central Chile and Ecuador. Cultivars of *F.* ×*ananassa* may also be improved by hybridization with superior clones of *F. chiloensis.* In South America, the hybridization of locally adapted races of *F. chiloensis* with *F.* ×*ananassa* could improve the regional adaptations of the cultivars originally developed in North America. The flavor and aroma of both North and South American varieties of *F.* ×*ananassa* may also be improved by crossing them with elite clones of *F. chiloensis.* At the very least, the genes of the Chilean strawberry should be injected into *F.* ×*ananassa* to expand its genetic base; this might yield unexpected epistatic interactions of horticultural importance. Complete reconstruction of *F.* ×*ananassa,* using systematically selected clones of *F. chiloensis* and *F. virginiana,* may even prove useful (Hancock et al. 1993).

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