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Reconstruction of the Strawberry, *Fragaria ×ananassa*, Using Genotypes of *F. virginiana* and *F. chiloensis*

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***Abstract*. The germplasm base of strawberries is restricted. The major cultivated strawberry species, *Fragaria ×ananassa*, originated ≈250 years ago when South American *F. chiloensis* subsp. *chiloensis* forma *chiloensis* and North American *F. virginiana* subsp. *virginiana* accidentally hybridized in European gardens. Since that time, only a handful of native clones have been used by breeders. As a novel way to expand the germplasm base of the strawberry, we preselected native clones of *F. virginiana* and *F. chiloensis* for a wide range of horticulturally important characteristics and then reconstructed *F. ×ananassa* by crossing superior clones of each. Before crossing between species, we undertook one round of selection within species to maximize diversity. Reconstruction appeared to be an effective method of strawberry improvement, because superior families and individuals were identified that had outstanding vigor, high productivity, seed set, fruit color, and firmness. None of the fruit were of commercial size, but one reconstruction family, FVC 11 [(*F. virginiana* Frederick 9 × LH 50-4) × (*F. chiloensis* Scotts Creek × 2 MAR 1A)], had individuals with fruit weights of almost 20 g.**

The founding genetic base of the commercial strawberry, *Fragaria ×ananassa* Duchesne in Lamarck, is limited. It originated ≈250 years ago when a few clones of South American *F. chiloensis chiloensis* (L.) Miller subsp. *chiloensis* forma *chiloensis* and North American *F. virginiana* Miller subsp. *virginiana* accidentally hybridized in European gardens (Darrow, 1966). The systematic breeding of strawberries was started in England in 1817 by Thomas A. Knight using only a small number of native and cultivated clones. North American genetic improvement was initiated in the mid-1800s with a restricted group of European *F. ×ananassa* cultivars, South American *F. chiloensis*, and North American *F. virginiana* genotypes. This germplasm base played the predominant role in public and private breeding programs for the next 100 years.

Although impressive breeding progress was made using this narrow germplasm base, other horticulturally useful genes are likely available in native populations of *Fragaria*, because both octoploid species have extensive geographical ranges that encompass a broad range of biotic and abiotic stresses (Hancock et al., 2004; Staudt, 1999). Contained within the wild germplasm is a wide range of interesting flavors and aromas, unusual resistance to heat, drought and salinity, almost a continuum of photoperiod sensitivities, and tolerance to a wide variety of diseases and pests (Hancock, 1999; Hancock et al., 1990; Luby et al., 1991).

To date, almost all the novel native genes that have been incorporated into cultivated material have come through back-crossing (Hancock, 1999; Hancock et al., 1993a). At least eight wild clones have been introgressed into *F. ×ananassa* since the 1920s (Sjulin and Dale, 1987) bringing in such traits as day-neutrality, red stele and strawberry aphid resistance, drought and salinity tolerance, and winter-hardiness (Barritt and Shanks, 1980; Bringhurst and Voth, 1984; Daubeny, 1990; Galletta et al., 1989).

Back-crossing from wild genotypes has allowed for the rapid incorporation of a few genes into the genetic background of *F. ×ananassa*. However, only a limited number of native clones have been used in this manner, leaving much genetic diversity untapped. Also, potentially useful diversity at non-selected genes has likely been lost when back-crossing and tightly linked deleterious genes can be carried into late generations. These two disadvantages are compounded when only a single non-selected native clone is used rather than a group of elite selections from a broad screen of native material.

An alternate strategy for germplasm enhancement would be to pre-select native clones of *F. virginiana* and *F. chiloensis* for a wide range of horticulturally important characteristics and then reconstruct *F. ×ananassa* by hybridizing superior clones of each. Hancock et al. (1993a) suggested a multiple stage process of reconstruction (Fig. 1): 1) select elite clones of *F. chiloensis* and *F. virginiana* from published reports and personal experience; 2) intercross the elite selections within species and select the superior progeny; 3) intercross these elite selections again within species and select the most promising genotypes; 4) reconstruct *F. ×ananassa* by making interspecies crosses among the elites of *F. virginiana* and *F. chiloensis*; and 5) select superior genotypes of reconstructed *F. ×ananassa* that can be used in further breeding and/or varietal release.

There are several advantages to using the reconstruction approach. The most obvious is that genetic diversity will be greatly expanded within the *F. ×ananassa* gene pool. This will not only afford breeders with an expanded germplasm base, but unique epistatic interactions might appear that are of horticultural use. If sufficiently large populations of native material are screened, a breeder should be able to select for a wide group of positive characteristics with the minimum level of deleterious combinations. This method may also produce higher levels of genetic heterozygosity than conventional back-crossing methods, because the starting material will be more diverse than the typical breeding populations.

Of course, there are several potential disadvantages to the "reconstruction" approach. When a high number of traits are being selected simultaneously, numerous linked genes with negative impacts are often carried in the breeding population (Galletta et al., 1989). In back-crossing strategies, deleterious

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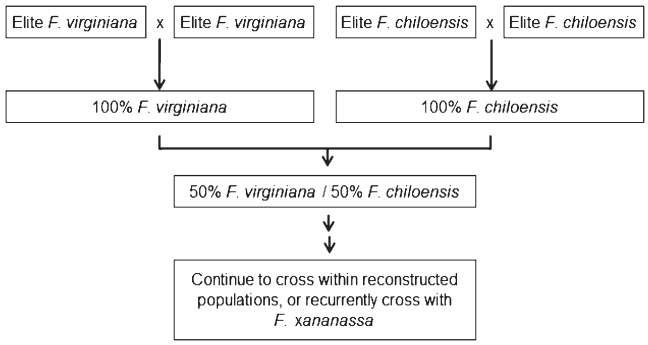

Fig. 1. Breeding scheme to reconstruct *Fragaria ×ananassa* using native clones of *F. virginiana* and *F. chiloensis*.

Fig. 2. Fruit of FVC 11-3 from the cross of *F. virginiana* (Frederick 9 × LH 50-4) × *F. chiloensis* (Scotts Creek × 2 MAR 1A).

associations are less of a problem, simply because fewer genes are being selected. However, *F. chiloensis* and *F. virginiana* have been interbred on numerous occasions without any reports of chromosomal, physiological, or morphological abnormalities (Darrow, 1966, Luby et al., 2008). The existence of separate sexes in the wild species (dioecy) might also present a problem, although sex can be controlled through the selection of hermaphroditic parents or by incorporating the trait in later stages when existing hermaphroditic *F. ×ananassa* are used. The genetics of sex in the octoploid strawberries is regulated by a single locus or closely linked ones in which female is dominant to hermaphrodite, which is dominant to male (Ahmadi and Bringhurst, 1991; Spigler et al., 2008).

We recently undertook a study to test how well native clones of *F. chiloensis* and *F. virginiana* combine genetically. We intercrossed 15 genotypes of the two species that had high vigor, good yields, and resistance to common foliar diseases as well as large, attractive fruit that were unusually firm for wild clones (Luby et al., 2008). The progeny were planted in Minnesota and Ontario and evaluated for disease resistance, winterhardiness, spring bloom date, fruit set, seed set, fruit size, and photoperiod sensitivity. We found that substantial breeding progress could be made by reconstructing *F. ×ananassa* if care is taken to select elite, complimentary genotypes of *F. virginiana* and *F. chiloensis*.

We report on another reconstruction effort that differed from the previous effort in two major ways: 1) we used a broader germplasm base that included elite clones of Chilean germplasm that were horticulturally superior to the *F. chiloensis* previously studied; and 2) we performed a round of improvement within species before making the interspecific crosses to maximize levels of genetic diversity. We did not sib the best performing interspecies F_1 hybrids as previously suggested in Hancock et al. (1993a), because we felt few deleterious genes would actually segregate out in a single generation of inbreeding an octoploid. This approach yielded superior reconstructed *F. ×ananassa* with very broad adaptations, high yields, excellent fruit quality, and near commercial-sized fruit.

Materials and Methods

Previous germplasm evaluations. A large number of studies have collected and evaluated wild germplasm. Members of our group have examined over 600 genotypes of *F. virginiana* ssp. *glauca* from the northern Rocky Mountains (Hokanson et al., 1993; Luby et al., 1992; Sakin et al., 1997) and nearly 2100 genotypes of *F. virginiana* ssp. *virginiana* from the central United States and Ontario along with a few representatives from Alaska, Alberta, New York, Pennsylvania, and western North Carolina (Dale et al., 1993; Luby and Stahler, 1993; Stahler et al., 1995). These clones have been evaluated for a wide range of traits, including photoperiod sensitivity, fruit size, sex, female fertility, disease resistance, nematode resistance, and environmental adaptations (Hancock et al., 1993b; Lewers et al., 2007; Pinkerton and Finn, 2005; Serçe and Hancock, 2005a, 2005b; Serçe et al., 2002).

We have also evaluated over 1000 wild genotypes of *F. chiloensis* from California for morphological variation and physiological tolerances (Hancock and Bringhurst, 1979, 1989; Jensen and Hancock, 1982). Others have screened more than 100 genotypes of *F. chiloensis* from Chile for phenotypic variation (Cameron et al., 1991; Gambardella et al., 2005; Lavín et al., 2005), physiological tolerances (Lavín, 1997), and fruit flavor characteristics (Carrasco et al., 2005; Nishizawa et al., 2005). Over 4000 *F. chiloensis* clones from the Pacific Northwest have been screened for resistance to aphids (Crock et al., 1982; Shanks and Barritt, 1974), black vine weevils (Doss and Shanks, 1987; Shanks et al., 1984), spider mites (Shanks and Moore, 1995; Shanks et al., 1995), nematodes (Pinkerton and Finn, 2005), foliar diseases (Luffman and Macdonald, 1993), physiological characteristics (Cameron and Hartley, 1990), and variation in reproductive traits (Dale et al., 1993; Luby et al., 1991; Luffman and Macdonald, 1993).

Recently, we selected an elite group of 38 wild strawberry accessions that appeared to be horticulturally superior and represented a wide range of the natural diversity found in *F. chiloensis* and *F. virginiana* (Hancock et al., 2001a, 2001b, 2001c). These genotypes were evaluated in five different states in the United States for a number of characteristics, including plant vigor, flower number, flowering date, harvest date, runner density, fruit weight and color, seed set, and foliar disease resistance. A much larger sample of 270 genotypes of wild *F. virginiana* and *F. chiloensis* from the National Clonal Germplasm Repository at Corvallis, OR, was also compared in a greenhouse at Michigan State University (MSU) for 14 morphological, reproductive, and production characteristics (Hancock et al., 2003). All the parents used in the current study were evaluated in these comparisons.

First round of crosses within F. virginiana. We began our reconstruction work by selecting a small group of 16 elite *F. virginiana* clones that we felt represented the range of diversity in the North American material from cool climates (Table 1). Sixty-two families were generated among these at Simcoe, Ontario, in the winter of 1996, including High Falls 22 × LH 10-6, LH 28-1, LH 30-4, LH 39-15, LH 10-1, N8417, RH 18, RH 23, RH 30, and RH 43; Montreal River 10 × LH 10-6, LH 30-4, LH 10-1, N8417, RH 23, and RH 43; LH

Table 1. Characteristics of the wild octoploid *Fragaria* used in the reconstruction crosses.[z]

Species and genotype	PI number	Location	Flowering	Sex	Superior characteristics
F. virginiana					
Eagle 14	612492	Ontario	Weak RM	Partially fertile hermaphrodite	Very large fruit; resistant to root-lesion nematode
Frederick 9	612493	Ontario	RM	Female	Very vigorous; high productivity; red flesh; resistant to mildew and scorch; very resistant to N. root knot nematode
Hemlo 2	None	Ontario	SD	Partially fertile hermaphrodite	Very resistant to mildew and scorch
High Falls 22	None	Ontario	SD	Female	Large fruit and resistant to common foliar diseases
Montreal River 10	612497	Ontario	Very strong RM	Male	Very large fruit resistant to common foliar diseases
LH 10-6	None	Wyoming	RM	Strong hermaphrodite	Flowers tolerant to frost
LH 28-1	None	Montana	RM	Partially fertile hermaphrodite	Large fruit and very high yields
LH 30-4	None	Montana	RM	Partially fertile hermaphrodite	Very large fruit
LH 39-15	None	Montana	RM	Strong hermaphrodite	Very large fruit and very high yields; blossoms tolerant to frost
LH 40-4	None	Montana	RM	Partially fertile hermaphrodite	Good sized fruit and very high yields
LH 50-4	612495	Montana	RM	Strong hermaphrodite	Very cold-hardy; highly vigorous; unusually large fruit; deep red fruit flesh; very resistant to N. root knot nematode
RH 18	None	New York	Weak RM	Strong hermaphrodite	Large fruit and very productive; moderately resistant to mildew
RH 23	612498	Minnesota	RM	Hermaphrodite	Large fruit and good yields; resistant to scorch, leaf spot, and black root rot; moderately resistant to powdery mildew; high cold tolerance
RH 30	612499	Minnesota	RM	Strong hermaphrodite	High flower numbers per truss; deep red flesh; excellent productivity; resistant to scorch, black root rot, and leaf spot; moderately resistant to mildew
RH 43 (N8688)	612500	Alberta	RM	Hermaphrodite	Unusually strong remontant
N8417	612496	Alaska	RM	Hermaphrodite	Very cold-hardy; resistant to black root rot
F. chiloensis					
2 BRA 1A	612316	Chile	SD	Hermaphrodite	Large white fruit; high soluble solids; ancient land race
CA 1541	551736	Peru	SD	Hermaphrodite	Very large reddish fruit; good winter-hardiness; resistant to root lesion nematode; ancient land race
Del Norte	551753	California	SD	Male	Resistant to aphids, two-spotted spider mites, red stele, and leaf spot
Darrow 72	236579	Chile	SD	Hermaphrodite	Large, red fruits, many flowers; ancient land race
HM1	612489	Oregon	SD	Hermaphrodite	High flower number; bright red fruit
Lions Head 3	None	British Columbia	SD	Female	Large fruit
NAH 4	612318	Ecuador	SD	Hermaphrodite	Very large fruit; drought tolerance; resistant to northern root knot nematode, ancient land race
2 MAR 1A	602567	Chile	SD	Hermaphrodite	Very high inflorescent number; reddish fruit; high salt and drought tolerance; low nutrient requirements
RCP 37	551445	California	SD	Male	Resistant to aphids, two-spotted spider mites, red stele, leaf spot; powdery mildew and root lesion nematode
Sable Beach 8	none	British Columbia	SD	Female	Large fruit
Scotts Creek	612490	California	SD	Female	High flower number; bright red fruit; good fruit size; high salt and drought tolerance; low nutrient needs

[z]Photoperiod: RM (remontant) and SD (short-day). The genotypes are represented by the names given by the original collectors.

10-6 × N8417, RH 23, and RH 43; LH 28-1 × Eagle 14; LH 30-4 × Eagle 14, Montreal River 10, Hemlo 2, Frederick 9, and RH 23; LH 39-15 × Eagle 14, Montreal River 10, Hemlo 2, Frederick 9, N8417, RH 23, RH 30, and RH 43; LH 40-4 × Eagle 14, Hemlo 2, and Frederick 9; RH 18 × Eagle 14, Montreal River 10, Hemlo 2, Frederick 9, LH 10-6, LH 28-1, LH 30-4, LH 39-15, and LH 10-1; RH 23 × Eagle 14, Hemlo 2, Frederick 9, and LH 10-1; RH 30 × Eagle 14, Montreal River 10, Hemlo 2, Frederick 9, LH 10-6, LH 28-1, LH 30-4, and LH 10-; and N8417 × Eagle 14, Hemlo 2, Frederick 9, LH 10-6, LH 28-1, LH 30-4, and LH 10-1. These genotypes were the same *F. virginiana* used in the previously published reconstruction study (Luby et al., 2008).

Seeds were germinated and grown to the four-leaf stage and six to 12 individuals from each family were set together in rows in May 1996 at Benton Harbor, MI. The plants were placed at 1.2 × 1.2-m spacing and their runners were trained by cross-cultivation into a 0.6 × 0.6-m square. In the summer of 1997, each genotype was subjectively evaluated for yield, fruit size, firmness, flavor, aroma, and color and the most elite genotypes were selected.

First round of crosses within F. chiloensis. In 1999, we crossed three Chilean landraces (*F. chiloensis* subsp. *chiloensis* f. *chiloensis*) at East Lansing, MI, with superior combinations of high soluble solids, excellent flavor, strong aroma, and large size but poor color and low yields (2 BRA 1A—Chile, CA 1541—Peru, and NAH 4—Ecuador) with another ancient cultivar, Darrow 72, with many large red fruits, and several native clones (*F. chiloensis* subsp. *chiloensis* f. *patagonica*) with high fruit numbers (HM 1—Oregon and 2 MAR 1A—Chile), unusually large fruit size and dark internal color (Scotts Creek—California), or multiple disease resistance (RCP 37—California) (Table 1; Hancock et al., 2005). Of these genotypes, only HM 1 and RCP 37 were used in the previously published reconstruction study (Luby et al., 2008).

Seedlings of each family were germinated in East Lansing, MI, and when they had all produced their first true leaves, 20 to 40 representatives of each family were shipped overnight, unrefrigerated, to Corvallis, OR. On arrival, they were transplanted into a commercial potting mix in 4 × 4 × 4-cm pots in a greenhouse

and grown to the four-leaf stage. In May, individuals from each family were set together in rows in the field at 1.2 × 1.2-m spacing and their runners were trained periodically by cross-cultivation into a 0.6 × 0.6-m square. In 2001, the plants were subjectively evaluated weekly during the next harvest season for yield, fruit size, firmness, flavor, and color and the most elite genotypes were selected (Table 2).

In Michigan, 20 to 40 plants of each family were also transplanted into a commercial potting mix in 4 × 4 × 4-cm pots and set in a randomized complete block design in a greenhouse (for full details see, Hancock et al., 2005). All flowers and runners were removed in 2000. In 2001, data were collected on each plant for bloom date, harvest date, crown number, runner number, peduncle length, flower number, fruit weight, skin color, and flesh color and the most elite genotypes were selected (Table 2). To enhance pollination, a camel hair brush was used to mix pollen from all open flowers in the greenhouse on a 3- to 4-d sequence. The results of this study were reported in Hancock et al. (2005).

Second round of crosses between elite F. virginiana *and* F. chiloensis *hybrids.* The elite selections of *F. virginiana* and *F. chiloensis* (Table 2) were intercrossed in 26 combinations in 2005 (Table 3). Seedlings of each family were germinated at MSU and half were shipped to Oregon when they had their first true leaves. These plants were transferred to 4 × 4 × 4-cm pots and grown to the four-leaf stage. In May at Benton Harbor, MI, and Corvallis, OR, the plants were set at 1.2 × 1.2-m spacing and their runners were trained by cross-cultivation into a 0.6 × 0.6-m square. Ten to 76 plants of each family were set adjacent in rows.

In 2006, five random plants were selected in each family at both locations and were given a subjective vigor rating from 1 (low) to 9 (high) based on the relative size of the mother plant and her daughters. These same plants were observed on a weekly basis to determine when the first flowers and ripe fruit appeared. When each of the selected genotypes was in full bloom, the number of flowers was counted on five randomly selected inflorescences from the mother and daughters of each genotype. When ≈50% of the fruit were ripe in each block of plants, the average percentage of ovules set as filled achenes was visually estimated on a random sample of five fruit from each genotype using a scale of 1 to 10 (representing 10% intervals). The weight of those same berries was determined along with the percentage of their surface area that was colored and the depth of color. Firmness was also evaluated on a subjective scale from 1 to 9. In August, leaf disease incidence was estimated on a subjective 1 to 9 scale.

In Michigan, a random sample of five fully ripe fruit was also evaluated for soluble solids, pH, and titratable acidity (TA). Soluble solids (SS) were determined using a handheld refractometer (Westover Model RHB-32; Southwest United Industries, Tulsa, OK). TA was determined from 10 mL of juice diluted to 100 mL with distilled water, titrated with 0.1 N sodium hydroxide (NaOH) to pH 8.2, and expressed as percentage citric acid (mass/mass) on a fresh weight basis.

The data were analyzed using SAS procedures (SAS Institute Inc., 2005). The descriptive statistics were calculated using TABULATE. The data from families grown in Michigan and Oregon were subjected to analysis of variance (ANOVA). ANOVAs were analyzed in two ways. First, combined analyses were performed on the data collected from each location. In this analysis, a random model was used in which all factors (location, replication, family, location × family interaction and error) were considered random. Because location × family interactions were found to be significant for most of the variables, ANOVAs were constructed for each location separately as well. In this analysis, the families were also considered random.

Results and Discussion

Crosses within F. virginiana. Among the intercrossed *F. virginiana* clones, fruit sizes were generally quite small, but it was not unusual to find genotypes with extremely aromatic fruit that were 2 to 3 cm in width (data not shown). In subjective observations, the most useful parents for fruit size appeared to be High Falls 22 and Montreal River 10, whereas RH 30 appeared to produce the highest proportion of progeny with deep red fruit color. The families producing genotypes with the largest fruit sizes were: High Falls 22 × LH 10, High Falls 22 × N8417, LH 39 × Montreal River 10, LH 40 × Eagle 14, Montreal River 10 × N 8417, Montreal River 10 × RH 23, Montreal River 10 × RH 43, RH 30 × Frederick 9, RH 30 × LH 10, RH 18 × LH 28-1, RH 30 × Montreal River 10, RH 30 × LH 30, and RH 10 × Montreal River 10. From these elite families, five hybrids were selected for further use as reconstruction parents (Table 2): RV-1 (Montreal River 10 × RH 23), RV-2 (Montreal River 10 × RH 43), RV-3 (RH 30 × Montreal River 10), RV-4 (RH 30 × LH 30), and RV-5 (High Falls 22 × LH 10). Unfortunately, RV-5 was lost before further crosses were made. All the parents of these genotypes were used in the previously published reconstruction effort (Luby et al., 2008).

In another study investigating the genetics of day neutrality in octoploid strawberries, Serçe and Hancock (2005b) evaluated a number of *F. virginiana* crosses, including Frederick 9 × LH 50-4, Frederick 9 × RH 30,

Table 2. Characteristics of the elite selections from the first round of intraspecific crosses among selections from *F. chiloensis* and *F. virginiana*.

Species and cross	Code	Notable characteristics
Fragaria virginiana		
Montreal River 10 × RH 23	RV-1	Very large fruit size, red flesh
Montreal River 10 × RH 43	RV-2	High yield, red flesh, firm, day-neutral
RH 30 × Montreal River 10	RV-3	High yield, red flesh, firm, day-neutral
RH 30 × LH 30	RV-4	Very large fruit size, red flesh
High Falls 22 × LH 10	RV-5	High yields
RH 30 × LH 50-4	RV-6	High yields, very large fruit size, red flesh
Frederick 9 × LH 50-4	RV-7	High yields, large fruit size
Fragaria chiloensis		
Scotts Creek × 2 MAR 1A	RC-1	High yields, large fruit, red flesh
NAH 4 × 2 BRA 1A	RC-2	High yields, very large fruit
NAH 4 × Darrow 72	RC-3	High yields, very large fruit
Scotts Creek × CA 1541	RC-4	High yields, very large fruit
Scotts Creek × 2 BRA IA	RC-5	High yields, red flesh, high soluble solids
NAH 4 × 2 MAR 1A	RC-6	High yields, very large fruit
Scotts Creek × NAH 4	RC-7	High yields, very large fruit
(Sable Beach 8 × Del Norte) × (Lions Head 3 × Del Norte)	RC-8	Very high yields, large and round fruit, red flesh
Scotts Creek × Darrow 72	RC-9	High yields, very large fruit, red flesh, high soluble solids
HM 1 × NAH 4	RC-10	High yields, very large fruit, red flesh, high soluble solids, long peduncles
Scotts Creek × RCP 37	RC-11	High yields, red flesh, high soluble solids

Table 3. Hybridizations made in the first round of interspecific crosses.

Number	Female parent	Male parent
FVC 1	RC-1	RV-3
FVC 2	RV-2	RC-2
FVC 4	RC-5	RV-6
FVC 5	RC-8	RV-3
FVC 6	RC-7	RV-2
FVC 7	RC-7	RV-3
FVC 8	RC-8	RV-6
FVC 9	RC-7	RV-1
FVC 10	RC-7	RV-6
FVC 11	RV-7	RC-1
FVC 16	RC-8	RV-1
FVC 17	RC-8	RV-2
FVC 18	RC-3	RV-1
FVC 19	RC-10	RV-1
FVC 20	RV-4	RC-6
FVC 21	RC-2	RV-1
FVC 27	RV-2	RC-1
FVC 28	RC-10	RV-3
FVC 30	RC-8	RV-7
FVC 31	RV-6	RC-1
FVC 32	RC-11	RV-3
FVC 33	RV-3	RC-2
FVC 35	RV-1	RC-1
FVC 36	RC-6	RV-2
FVC 40	RV-4	RC-1
FVC 41	RC-11	RV-3

LH 50-4 × RH 30, Eagle 14 × Frederick 9, and Montreal River 10 × Frederick 9 with a large group of additional families of *F.* ×*ananassa* × *F. virginiana*, *F.* ×*ananassa* × *F. chiloensis*, and *F.* ×*ananassa* × *F.* ×*ananassa*. Although this study focused primarily on flowering patterns, the *F. virginiana* families were also subjectively evaluated for fruit size, fruit color, firmness, and flavor. Of these families, two genotypes were selected for further reconstruction work: RV-6 (RH 30 × LH 50-4) and RV-7 (Frederick 9 × LH 50-4) (Table 2). Although RH 30 and Frederick 9 were in the previously reported reconstruction effort (Luby et al., 2008), LH 50-4 was not. LH 50-4 was found to be one of the largest fruited clones of the *F. virginiana* ssp. *glauca* evaluated by Sakin et al. (1997).

Crosses within F. chiloensis. Significant differences were observed across the *F. chiloensis* families for flowering and fruiting season, peduncle length, fruit size, color, and SS and number of fruit, crowns, and runners. This information was previously published in Hancock et al. (2005). NAH 4 and Pigeon Point transmitted the largest fruit size. Scotts Creek and 2 MAR 1A were the best parents for fruit color. HM 1 produced progeny with the highest flower numbers. Progeny of 2 MAR 1A and 2 BRA 1A were the latest fruiting. The cross Scotts Creek × NAH 3 yielded the highest number of selections with large fruit, excellent color, good yields, and high SS.

A number of families were selected as superior in Oregon, including: Scotts Creek × Darrow 72 (very early fruiting, large fruit with deep color), NAH 4 × Darrow 72 (very early, very large fruit), NAH 4 × 2 MAR 1A (very late fruiting, very high flower numbers, long peduncles, and large fruit), HM1 × Darrow 72 (early, high crown numbers), NAH 4 × CA 1541 (very early, large, and very well-colored fruit), NAH 4 × 2 BRA 1A (late fruiting, very high flower numbers, long peduncles, and very large fruit), and Darrow 72 × CA 1541 (very early, high flower numbers, and good fruit color).

The most superior families selected in Michigan were: Scotts Creek × 2 MAR 1A (late fruiting, high flower numbers, many crowns, and dark red fruit color), HM 1 × 2 BRA 1A (late fruiting, high crown numbers, and dark red fruit color), HM 1 × 2 MAR 1A (late fruiting, high crown numbers, high flower numbers, and dark red fruit color), NAH 4 × 2BRA 1A (late fruiting, very high flower numbers, long peduncles, and very large fruit), NAH 4 × 2 MAR 1A (very late fruiting, very high flower numbers, long peduncles, and large fruit), Scotts Creek × 2BRA 1A (late fruiting, high flower numbers, and deep-colored fruit), Scotts Creek × Darrow 72 (very early fruiting, large fruit with deep color), Scotts Creek × NAH 4 (very large, well-colored fruit), NAH 4 × Darrow 72 (very large fruit), and NAH 4 × RCP 37 (early fruiting, large, very dark red fruit).

Of the selections made in Michigan and Oregon, seven *F. chiloensis* hybrids were chosen as reconstruction parents: RC-1 (Scotts Creek × 2 MAR 1A), RC-2 (NAH 4 × BRA 1A), RC-3 (NAH 4 × Darrow 72), RC-4 (Scotts Creek × CA 1541), RC-5 (Scotts Creek × BRA IA), RC-6 (NAH 4 × 2 MAR 1A), and RC-7 (Scotts Creek × NAH 4) (Table 2). Unfortunately, RC-4 was not successfully used as a parent in subsequent crosses. RC-1, RC-2, RC-3, RC-6, and RC-7 were superior performers in both locations. FC-4 was one of the most elite genotypes in Oregon but not Michigan, whereas RC-5 was elite in Michigan but not Oregon. Another hybrid made by Dale and observed during fruiting in the MSU greenhouse was also selected as a reconstruction parent [RC-8 (Sable Beach 8 × Del Norte) × (Lions Head 3 × Del Norte)]. This hybrid had unusually high numbers of deep red, almost round fruit of better than average size for *F. chiloensis*, and its parents were almost disease-free in the field in Ontario (Dale, personal communication). The parents of all these RC selections were not used in the reconstruction effort reported by Luby et al. (2008).

Reconstruction crosses between F. virginiana × F. chiloensis. Twenty-two families were evaluated in Michigan and Oregon (Table 3). The reconstructed *F.* ×*ananassa* were in general broadly adapted. Virtually all the hybrids survived at both locations and most had vigor ratings above 6.0, although the climatic adaptations of the original *F. virginiana* and *F chiloensis* selections were likely quite distinct. Typically, *F. virginiana* is found in habitats with very cold winters and hot summers, whereas *F. chiloensis* is located in climates that are more moderate in summer and winter.

Significant differences were observed between locations for all the traits except berry weight and flesh color (Table 4). Higher mean values were observed in Oregon for flower number, achene set, skin color, leaf disease, flowering date, and ripening date, whereas higher mean values were observed for vigor and firmness in Michigan (Table 5). Significant location × family interactions were also observed for vigor, flower number, skin color, firmness, leaf disease score, and flowering date but not for achene set, berry weight, or flesh color. Most of the intersite differences were likely the result of environmental variation, although vigor and firmness could have been influenced by individual investigator bias.

Although none of the crosses produced genotypes of overall commercial quality, many of the families carried individual characteristics that were at or near cultivar quality (Table 5). Mean family values for vigor were as high as 9.0 in Michigan and 7.8 in Oregon. Highs for mean flower numbers per inflorescence were 13.0 in Oregon and 9.0 in Michigan. Mean fruit set exceeded 85% in both locations. Families were observed with averages of 100% external color and over 80% internal color in Michigan and Oregon. Mean firmness values exceeded 7.0 in some families at both locations. Flowering and fruiting dates varied by as much as 16 and 12 d at the individual sites, and disease ratings varied from 1.8 to 7.8. In Michigan, mean SS were found to be as high as 11.7%, whereas TA was as low as 0.71% citric acid (Table 6). SS/TA ratios varied from 2.93 to 13.57.

Scott and Lawrence (1975) suggested that to get fruit quality back to industry standards is very difficult when using native germplasm, especially with the small, soft-fruited *F. virginiana* (Scott, 1959). Previous studies have found that at least three rounds of back-crossing back to *F.* ×*ananassa* were necessary to recover genotypes meeting commercial standards (Bringhurst and Voth,

Table 4. Mean squares, df, and significance for combined and separate analyses of variance of families obtained from *Fragaria chiloensis* × *F. virginiana* crosses, which were grown in Michigan and Oregon.

Source	df[z]	Vigor	Flower number	Achene set (%)	Berry wt	Skin color (%)	Flesh color (%)	Firmness	Leaf disease score	Bloom date	Ripe date
Combined											
Location (L)	1	19.0*	141.4**	9723**	49.4	7071**	795	98.7**	280.5**	26759**	4845.4**
Rep/L	8	1.7	5.2	766	6.9*	78	1239*	3.2	1.4	70	24.0
Family (F)	23	7.1	11.4	649	27.4**	278	2919**	7.1	17.9	150	63.3*
L × F	22	4.0**	23.7**	796	4.5	235**	805	4.5**	13.6**	99**	24.5
Error	244	1.7	8.7	577	3.1	110	605	1.9	2.6	43	19.9
Michigan											
Family	22	7.9**	7.7**	855**	8.2**	404**	1040**	6.0**	28.3**	65**	47.8**
Error	121	1.8	3.2	1022	1.7	217	345	2.0	3.1	11	16.1
Oregon											
Family	23	2.9**	27.3**	651**	26.0**	109**	2919**	6.0**	3.2**	181**	39.9**
Error	131	1.6	13.9	266	4.4	31	838	1.9	2.0	77	23.0

[z]Presented df are for vigor. df for other variables slightly differ as a result of missing values.
*, **Significant at $P \leq 0.05$ and 0.01, respectively.

1978, Scott and Lawrence, 1975). Although we did not find any progeny in this study that had commercial-sized fruit, one of the families had fruit that averaged 7.6 g in Michigan and 12.8 g in Oregon, and the largest fruited genotype in this family had primary fruit that averaged 19 g in Michigan (Fig. 1). This value far exceeded the weight of its progenitors found in other studies: Frederick 9 (1.9 g), LH 50-4 (2.1 g), Scotts Creek (3.2 g), and 2 MAR 1A (1.8 g) (Hancock et al., 2001c). Clearly, genes for large fruit are carried in small-fruited, native genotypes. The largest fruited families contained genes from the *F. chiloensis* genotypes Scotts Creek, 2 MAR 1A, and Adam Dale's complex hybrid, FC-8 [(Sable Beach × Del Norte) × (Lions Head 3 × Del Norte)] and the *F. virginiana* genotype LH 50-4. 2 MAR 1A is only modest sized by wild standards, but Scotts Creek, Dale's hybrid, and LH 50-4 are unusually large.

Some of the elite families combined a number of superior traits (Tables 5 and 6). FVC 8 {[(RH 30 × LH-50)] × [(Sable Beach 8 × Del Norte) × (Lions Head 3 × Del Norte)]} had unusually high flower numbers, seed set, and berry weight in Oregon and among the darkest flesh at both locations. FVC 10 (RH 30 × LH 50-4) × (Scotts Creek × NAH 4) were unusually large fruited at both locations with very high vigor and had unusually high seed set and firmness in Michigan and dark flesh color in Oregon. FVC 11 (Frederick 9 × LH 50-4) × (Scotts Creek × 2 MAR 1A) had exceptionally large fruit at both locations and unusually high seed set in Oregon. FVC 16 had very high vigor in Michigan and unusual flower numbers and fruit weight in Oregon. FVC 17 was very well colored and had high fruit numbers and large fruit weights in Michigan and Oregon and a high seed set in Oregon. FVC 18 had unusual vigor at both locations, high SS in Michigan, and high fruit numbers in Oregon. FVC 30 had very high vigor and low fruit acidity in Michigan and unusually high averages for seed set, fruit weight, and skin color in Oregon. FVC 9 (Montreal River 10 × RH 23) × (Scotts Creek × NAH 4) had unusually large fruit and deep flesh color in Michigan and exceptionally well-colored skin in Oregon.

All but one of these populations was represented in the individual selections made in Michigan and Oregon (Table 7). The only one missing was FVC 9. Overall, 13 elite genotypes were selected in Michigan and 12 in Oregon. Representatives of three families were selected in both locations, RVC 8, RVC 10, and RVC 30. Genotypes from FVC 10 and 16 were only selected in Oregon, whereas FVC 17, 18, and 28 were only selected in Michigan.

The genotypes selected offer a wide combination of subspecies, geographic locations, and adaptations. Probably the most diverse is FVC 11, which is composed of four subspecies from four distinct geographical regions, including [*F. chiloensis* ssp. *pacifica* (Scotts Creek from California), *F. chiloensis* ssp. *patagonica* (2 MAR 1A from Chile), *F. virginiana* ssp. *virginiana* (Frederick 9 from Ontario), and *F. virginiana* ssp. *glauca* (LH

Table 5. Values of several horticulturally important traits of families obtained from *Fragaria chiloensis* × *F. virginiana* crosses, which were grown in Michigan and Oregon.

Source	Vigor	Flower number	Achene set (%)	Berry wt (g)	Skin color (%)	Flesh color (%)	Firmness[x]	Leaf disease score[y]	First flower date[z]	First ripe date[z]
Combined locations										
FVC 1	6.7	7.8	63	2.8	86	48	6.0	3.7	119	160
FVC 2	6.2	7.6	58	2.1	94	51	6.2	4.6	121	156
FVC 4	6.8	7.2	71	3.8	94	59	5.9	4.2	116	156
FVC 5	8.1	9.2	71	3.3	94	69	5.3	4.0	119	156
FVC 6	6.4	7.8	69	2.6	76	32	5.9	3.6	125	164
FVC 7	6.7	7.3						5.9	117	150
FVC 8	8.1	9.4	66	5.0	92	83	7.0	3.5	113	155
FVC 9	6.5	7.1	68	3.4	92	75	4.4	6.4	118	158
FVC 10	7.9	8.6	75	5.9	91	82	4.7	5.7	117	156
FVC 11		7.0	72	10.5	80	52	5.4	4.8	120	159
FVC 16	7.4	10.2	66	3.3	98	60	4.9	3.7	118	156
FVC 17	6.6	7.7	75	4.4	94	44	7.1	3.5	120	156
FVC 18	8.4	8.1	57	2.8	92	57	5.0	4.9	115	158
FVC 19	7.0	8.5	74	2.2	94	39	5.9	4.5	125	162
FVC 20	6.8	9.7	80	1.5	95	21	6.6	6.8	124	162
FVC 21	6.3	7.2	47	1.6	82	70	4.8	3.5	119	160
FVC 28	6.3	7.1	86	2.3	92	45	4.7	6.9	118	158
FVC 30	7.6	8.1	72	4.0	88	67	6.7	2.9	115	156
FVC 33	7.0	6.7	80	2.7				3.5	122	163
FVC 35	7.2	8.1	76	2.8	95	57	2.9	4.8	117	157
FVC 36	6.8	6.5	67	2.5	89	43	5.5	4.6	124	159
FVC 40	6.1	8.0	71	1.9	84	16	6.0	5.4	122	158
FVC 41	7.4	7.8	85	2.7	97	63	4.0	5.7	120	156
Mean	6.9	7.8	71	3.3	91	53	5.5	4.7	119	158
SE	0.1	0.2	1.6	0.2	0.8	1.9	0.1	0.1	0.7	0.4
Michigan										
FVC 1	7.3	9.0	60	2.5	80	48	6.8	2.7	130	163
FVC 2	7.2	8.6	42	1.5	92	58	7.6	3.4	125	159
FVC 4	7.1	6.3	74	3.2	91	47	7.1	2.9	129	161
FVC 5	8.9	8.2	57	1.9	88	63	5.4	1.8	127	162
FVC 6	7.0	8.9	64	2.3	66	26	7.0	1.8	131	168
FVC 7	6.6	6.4						6.4	127	158
FVC 8	8.6	5.5	50	3.9	88	80	7.8	1.3	125	160
FVC 9	6.0	7.6	80	5.2	77	82	5.7	6.7	128	167
FVC 10	8.2	7.1	86	5.3	60	60	9.0	5.4	130	158
FVC 11		5.9	53	7.6	65	58	6.3	3.8	130	166
FVC 16	8.0	7.5	52	2.5	97	65	5.4	1.0	124	158
FVC 17	7.2	7.9	63	3.5	91	46	7.0	1.0	130	164
FVC 18	9.0	6.2	68	2.7	83	62	4.4	3.4	127	161
FVC 19	7.0	8.3	54	2	87	63	7.7	4.3	130	168
FVC 20	7.0	8.1	73	1.5	95	40	6.2	7.0	131	166
FVC 21	7.6	8.6	28	1.4	73	53	5.3	2.1	128	165
FVC 28	6.1	7.2	84	1.8	87	51	5.9	7.8	128	164
FVC 30	8.6	5.9	61	2.6	76	57	7.0	0.8	130	162
FVC 33	7.2	8.1	84	2.5				3.0	128	169
FVC 35	7.4	5.9	87	2.3	100	75	2.0	3.9	130	170
FVC 40	6.0	7.5	55	1.7	73	24	6.2	5.8	130	162
FVC 41	7.1	6.3	92	2.3	93	70	5.5	4.8	131	167
Mean	7.2	7.3	63	2.6	84	53	6.4	3.7	129	164
SE	0.1	0.2	3.1	0.2	1.6	2.2	0.2	0.2	0.4	0.5
Oregon										
FVC 1	6.1	6.7	69	3.4	94	48	4.9	4.8	108	155
FVC 2	5.2	6.6	78	2.8	96	43	4.8	5.8	116	154
FVC 4	6.4	8.3	68	4.4	97	70	4.8	5.7	101	152
FVC 5	7.3	10.2	82	4.5	100	73	5.2	6.1	111	151
FVC 6	5.8	6.5	76	3.1	90	39	4.3	5.4	117	158
FVC 7	6.8	8.2	58	3.0	98	55	5.8	5.4	108	149
FVC 8	7.6	13.2	88	6.4	96	86	6.0	5.6	101	150
FVC 9	6.8	6.7	64	2.8	97	72	4.0	6.0	108	155
FVC 10	7.6	100	72	6.0	97	86	3.8	6.0	103	155
FVC 11	6.2	8.0	87	12.8	92	47	4.8	5.8	110	151
FVC 16	6.8	13.0	80	4.2	98	55	4.4	6.4	113	154
FVC 17	6.0	7.4	86	5.1	97	42	7.2	6.0	110	149
FVC 18	7.8	10.0	46	3.0	100	52	5.8	6.4	104	155
FVC 19	7.0	8.8	87	2.4	99	24	4.8	4.6	120	158
FVC 20	6.6	11.4	86	1.5	94	2	7.0	6.6	116	158
FVC 21	5.0	5.8	76	1.7	95	95	4.0	4.8	109	157
FVC 28	6.5	7.1	89	2.8	97	41	3.7	5.9	108	153
FVC 30	6.6	10.4	84	5.3	100	77	6.4	5.0	99	150

(*Continued on next page*)

Table 5. (*Continued*) Values of several horticulturally important traits of families obtained from *Fragaria chiloensis* × *F. virginiana* crosses, which were grown in Michigan and Oregon.

Source	Vigor	Flower number	Achene set (%)	Berry wt (g)	Skin color (%)	Flesh color (%)	Firmness[x]	Leaf disease score[y]	First flower date[z]	First ripe date[z]
FVC 33	6.8	5.4	79	2.8	99	58	3.5	4.0	116	157
FVC 35	7.0	10.4	71	3.0	93	50	3.2	5.6	105	150
FVC 36	6.7	5.9	75	2.9	97	38	4.4	6.4	116	154
FVC 40	6.2	8.4	87	2.2	95	8	5.8	5.0	113	154
FVC 41	7.6	9.3	83	2.8	98	61	3.6	6.5	110	153
Mean	6.7	8.4	77	3.8	96	52	4.8	5.7	110	153
SE	0.1	0.3	1.5	0.2	0.6	2.9	0.1	0.1	0.8	0.4

[z]Subjective evaluation of 1 (firmest) to 9 (softest).
[y]Subjective evaluation of 1 (the least susceptible) to 9 (the most susceptible).
[x]Days from 1 Jan.

Table 6. Values of soluble solids, pH and acidity of families obtained from *Fragaria chiloensis* × *F. virginiana* crosses, which were grown in Michigan.

Source	Soluble solids (SS)	pH	Titratable acidity (TA)	SS/TA
FVC 1	10.6	3.35	0.78	13.57
FVC 2	10.6	3.34	2.07	5.11
FVC 4	10.8	3.53	1.25	8.61
FVC 5	10.1	3.25	0.67	15.17
FVC 6	10.8	3.39	0.58	18.74
FVC 8	9.5	3.32	0.78	12.16
FVC 9	9.9	3.42	0.86	11.54
FVC 10	5.7	3.36	0.88	6.50
FVC 11	7.7	3.24	1.47	5.25
FVC 16	9.9	3.33	0.60	16.63
FVC 17	10.5	3.24	0.99	10.58
FVC 18	11.7	3.35	0.84	13.95
FVC 19	7.8	3.39	1.30	6.00
FVC 20	9.8	3.55	0.71	13.79
FVC 21	11.6	3.45	0.63	18.30
FVC 28	11.4	3.49	1.34	8.48
FVC 30	9.3	3.40	0.82	11.35
FVC 31	10.3	3.46	1.18	8.74
FVC 32	9.3	3.20	3.18	2.93
FVC 33	10.7	3.37	0.72	14.92
FVC 35	11.3	3.55	0.97	11.69
FVC 35	10.2	3.33	1.05	9.71
FVC 36	9.5	3.43	0.97	9.76
FVC 40	12.2	3.51	0.95	12.88
Mean	10.3	3.38	0.99	10.38
SD	0.19	0.02	0.06	3.30
Analysis of variance				
Family	5.6	0.05**	154.6*	0.38
Error	3.6	0.02	76.5	0.37

*, **Significant at 5% and 1%, respectively.

Table 7. Elite FVC selections made in Michigan and Oregon from the elite *Fragaria virginiana* and *F. chiloensis* gene pools.

Family	Number of selections: Oregon	Number of selections: Michigan	Key characteristics of selections
FVC 8	1	4	High yields, strong vigor, high flower numbers, very large fruit, excellent internal color, remontant
FVC 10	2	0	High yields, strong vigor, high flower numbers, very large fruit, excellent internal color, very firm
FVC 11	5	4	High yields, extremely large fruit, long peduncles
FVC 16	1	0	High yields, strong vigor, high flower numbers, large fruit
FVC 17	0	1	High yields, very high flower numbers, large fruit, little foliar disease
FVC 18	0	1	High yields, strong vigor, high flower numbers, large fruit, high soluble solids, strongly remontant
FVC 28	0	1	High yields, very vigorous, upright peduncles, only modest-sized fruit
FVC 30	4	2	High yields, very large fruit, well-colored flesh, very little foliar disease

50-4 from Montana)] (Figure 2). The original parents carried a broad range of adaptations, including cold-hardiness (LH 50-4), powdery mildew [*Sphaerotheca macularis* (Wallr.: Lind)], and leaf scorch resistance [*Diplocarpon earlianum* (Ellis & Everh.) F. A. Wolf] (Frederick 9), high drought and salt tolerance (Scotts Creek and 2 MAR 1A), and a high photosynthetic rate (2 MAR 1A) (Hancock et al., 2001a).

Conclusions

Like in the study of Luby et al. (2008), the reconstruction of *F.* ×*ananassa* by crossing elite genotypes of *F. chiloensis* and *F. virginiana* appears to be an effective strategy for strawberry improvement. Families and individuals were identified that had outstanding vigor, high productivity, seed set, fruit color, and firmness. None of the fruit were of commercial size, but one family, FVC 11, had individuals with fruit weights of almost 20 g, a fruit size deemed acceptable only 20 years ago outside of California. The reconstruction effort described here resulted in much larger fruited progeny than the one previously published (Luby et al., 2008). This greater success was likely the result of superior wild genotypes being used as parents. It is also possible that intercrossing geographically diverse selections within the species resulted in increased heterozygosity and greater heterosis in the reconstructed populations.

The question remains as to whether further intercrossing within reconstructed populations will yield new cultivars. It is possible that many of the heterotic interactions gained in the first interspecific cross may be lost in subsequent generations. We plan to take our elite FVC selections and intercross them and back-cross them to selected cultivars of *F.* ×*ananassa* to determine which strategy will be most effective in incorporating the diversity collected in the FVC selections in breeding improvement.

We also intend to generate a new family of wild *F. virginiana* × *F. virginiana* crosses to better capture the available diversity. We feel that we have represented *F. chiloensis* well with the inclusion of the South American material and Scotts Creek from California, but new *F. virginiana* clones have emerged that warrant testing as reconstruction parents (Hancock et al., 2001c, 2003). These include *F. virginiana* ssp. *grayana* (Vilm.ex L. Gay) CFRA 1170 and 1180 from Kentucky, *F. virginiana* ssp. *virginiana* Mill. CFRA 1385 from Quebec, and *F. virginiana* ssp. *platypetala* (Rydb.) Staudt CFRA 0110 from Oregon. All of these have fruit larger than any of the clones previously used. These will be intercrossed and then the most elite performing hybrids will be hybridized with our best FVC hybrids.

Literature Cited

Ahmadi, H. and R.S. Bringhurst. 1991. Genetics of sex expression in *Fragaria* species. Amer. J. Bot. 78:504–514.

Barritt, B.H. and C.H. Shanks, Jr. 1980. Breeding strawberries for resistance to the aphids

Chaetosiphon fragaefolii and *C. thomasi*. HortScience 15:287–288.
Bringhurst, R.S. and V. Voth. 1978. Origin and evolutionary potentiality of the day-neutral trait in octoploid *Fragaria*. Genetics 90:510.
Bringhurst, R.S. and V. Voth. 1984. Breeding octoploid strawberries. Iowa Sta. J. Res. 58:371–381.
Cameron, J.S. and C.A. Hartley. 1990. Gas exchange characteristics of *Fragaria chiloensis* genotypes. HortScience 25:327–329.
Cameron, J.S., T.M. Sjulin, C.H. Shanks, and C.E. Muñoz. 1991. Collection of *Fragaria chiloensis* in central and southern Chile, p. 108–118. In: Dale, A. and J. Luby (eds.). The strawberry into the 21st century. Timber Press, Inc, Portland, OR.
Carrasco, B., J.F. Hancock, R.M. Beaudry, and J.B. Retamales. 2005. Chemical composition and inheritance patterns of aroma in *Fragaria ×ananassa* and *F. virginiana* progenies. HortScience 40:1649–1650.
Crock, J.E., C.H. Shanks, and B.H. Barritt. 1982. Resistance in *Fragaria chiloensis* and *F. ×ananassa* to the aphids *Chaetosiphon fragaefolii* and *C. thomasi*. HortScience 17:959–960.
Dale, A., H.A. Daubeny, M. Luffman, and J.A. Sullivan. 1993. Development of *Fragaria* germplasm in Canada. Acta Hort. 348:75–80.
Darrow, G.M. 1966. The strawberry history, breeding and physiology. Holt, Rinehart and Winston, New York, NY.
Daubeny, H.A. 1990. Strawberry breeding in Canada. HortScience 25:893–894.
Doss, R.P. and C.H. Shanks. 1987. The influence of leaf pubescence on the resistance of selected clones of beach strawberry [*Fragaria chiloensis* (L.) Duchesne] to adult black vine weevils (*Otiorhynchus sulcatus* F.). Sci. Hort. 34:47–54.
Galletta, G.J., A.D. Draper, and J.L. Maas. 1989. Combining disease resistance, plant adaptation and fruit quality in breeding short day and day-neutral strawberries. Acta Hort. 265:43–51.
Gambardella, M., A. Cadavid, V. Díaz, and R. Pertuzé. 2005. Molecular and morphological characterization of wild and cultivated native *Fragaria* in southern Chile. HortScience 40:1640–1641.
Hancock, J.F. 1999. Strawberries. CABI Publishing, Wallingford, UK.
Hancock, J.F. and R.S. Bringhurst. 1979. Ecological differentiation in perennial, octoploid species of *Fragaria*. Amer. J. Bot. 66:367–375.
Hancock, J.F. and R.S. Bringhurst. 1989. Yield component interactions in wild populations of California *Fragaria*. HortScience 23:889–891.
Hancock, J.F., P.W. Callow, A. Dale, J.J. Luby, C.E. Finn, S.C. Hokanson, and K.E. Hummer. 2001a. From the Andes to the Rockies: Native strawberry collection and utilization. HortScience 36:221–225.
Hancock, J.F., P.W. Callow, S. Serçe, and A.M.C. Schilder. 2001b. Relative performance of strawberry cultivars and native hybrids on fumigated and nonfumigated soil in Michigan. HortScience 36:136–138.
Hancock, J.F., C.E. Finn, S.C. Hokanson, J.J. Luby, B.L. Goulart, K. Demchak, P.W. Callow, S. Serçe, A.M.C. Schilder, and K.E. Hummer. 2001c. A multistate comparison of native octoploid strawberries from North and South America. J. Amer. Soc. Hort. Sci. 126:579–586.
Hancock, J.F., P.W. Callow, S. Serçe, and P.Q. Son. 2003. Variation in the horticultural characteristics of native *Fragaria virginiana* and *F. chiloensis* from North and South America. J. Amer. Soc. Hort. Sci. 128:201–208.
Hancock, J.F., A. Dale, and J.J. Luby. 1993a. Should we reconstitute *Fragaria ×ananassa?* Acta Hort. 348:85–93.
Hancock, J.F., R.E. Harrison, J.J. Luby, and J.F. Hancock. 1993b. Morphological variation in *Fragaria virginiana* from the Rocky Mountains. Acta Hort. 348:94–101.
Hancock, J.F., C.A. Drake, P.W. Callow, and S. Serçe. 2005. Genetic improvement of the Beach strawberry. HortScience 40:1644–1645.
Hancock, J.F., J.L. Maas, C.H. Shanks, P.J. Breen, and J.J. Luby. 1990. Strawberries, p. 489–546. In: Moore, J.N. and J.R. Ballington (eds.). Genetic resources in temperate fruit and nut crop. Internat. Soc. Hort. Sci., Wageningen, The Netherlands.
Hancock, J.F., S. Serçe, C.M. Portman, P.W. Callow, and J.J. Luby. 2004. Taxonomic variation among North and South American subspecies of *Fragaria virginiana* Miller and *F. chiloensis* (L) Miller. Can. J. Bot. 82:1632–1644.
Hokanson, K.E., R.E. Harrison, J.J. Luby, and J.F. Hancock. 1993. Morphological variation in *Fragaria virginiana* from the Rocky Mountains. Acta Hort. 348:63–68.
Jensen, D. and J.F. Hancock. 1982. A multivariate analysis of California strawberries. Bull. Torrey Bot. Club 109:136–148.
Lavín, A. 1997. Caracterización botánica, fisiológica y agronómica de ecotipos chilenos de *Fragaria chiloensis* (L.) Duch., recolectados en las X and XI regiones de Chile. Informe final. Proyecto Fondecyt 1940083 (1996). Centro Experimental Cauquenes (INIA).
Lavín, A., C. Barrera, J.B. Retamales, and M. Maureira. 2005. Morphological and phenological characterization of 52 accessions of *Fragaria chiloensis* (L.) Duch. HortScience 40: 1637–1639.
Lewers, K.S., W.W. Turechek, S.C. Hokanson, J.L. Maas, J.F. Hancock, S. Serçe, and B.J. Smith. 2007. Evaluation of elite native strawberry germplasm for resistance to anthracnose crown rot disease caused by *Colletotrichum* species. J. Amer. Soc. Hort. Sci. 132:842–849.
Luby, J.J., A. Dale, J.F. Hancock, and S. Serçe. 2008. Reconstructing *Fragaria ×ananassa* utilizing wild *F. virginiana* and *F. chiloen*sis: Inheritance of winter injury, photoperiod sensitivity, fruit size, gender, female fertility and disease resistance in hybrid progenies. Euphytica 163:57–65.
Luby, J.J., J.F. Hancock, and J.R. Ballington. 1992. Collection of native strawberry (*Fragaria* ssp.) germplasm in the Pacific Northwest and Northern Rocky Mountains of the USA. HortScience 27:12–17.
Luby, J.J., J.F. Hancock, and S. Cameron. 1991. Expansion of the strawberry germplasm base in North America, p. 66–75. In: Dale, A. and J.J. Luby (eds.). The strawberry into the 21st century. Timber Press, Portland, OR.
Luby, J.J. and M.M. Stahler. 1993. Collection and evaluation of *Fragaria virginiana* in North America. Acta Hort. 345:49–54.
Luffman, M. and P.J. Macdonald. 1993. *Fragaria* germplasm at the Canadian clonal germbank. Acta Hort. 348:102–108.
Nishizawa, T., S. Nagasawa, Y. Mori, Y. Kondo, Y. Sasaki, J.B. Retamales, and A. Lavín. 2005. Characteristics of soluble sugar accumulation in commercially grown *Fragaria chiloensis*. HortScience 40:1647–1648.
Pinkerton, J. and C.E. Finn. 2005. Responses of strawberry species and cultivars to the root-lesion and northern root-knot nematodes. HortScience 40:33–38.
Sakin, M., J.F. Hancock, and J.J. Luby. 1997. Identifying new sources of genes that determine cyclic flowering in Rocky Mountain populations of *Fragaria virginiana* ssp. *glauca* Staudt. J. Amer. Soc. Hort. Sci. 122:205–210.
SAS Institute Inc. 2005. SAS users guide; SAS/STAT, version 6. SAS Institute Inc., Cary, NC.
Scott, D.H. 1959. Size, firmness and time of ripening of fruit of seedlings of *Fragaria virginiana* Duch. crossed with cultivated strawberry varieties. Proc. Amer. Soc. Hort. Sci. 74: 388–393.
Scott, D.H. and F.J. Lawrence. 1975. Strawberries, p. 71–97. In: Janick, J. and J.N. Moore (eds.). Advances in fruit breeding. Purdue University Press, West Lafayette, IN.
Serçe, S. and J.F. Hancock. 2005a. The temperature and photoperiod regulation of flowering in *Fragaria chiloensis, F virginiana*, and *F ×ananassa* genotypes. Sci. Hort. 103:167–177.
Serçe, S. and J.F. Hancock. 2005b. Inheritance of day-neutrality in octoploid species of *Fragaria*. J. Amer. Soc. Hort. Sci. 130:580–584.
Serçe, S., P.W. Callow, J.J. Ho, and J.F. Hancock. 2002. High temperature effects on CO_2 assimilation rate in genotypes of *Fragaria ×ananassa, F chiloensis* and *F virginiana*. J. Amer. Pomol. Soc. 56:57–62.
Shanks, C.H. and B.H. Barritt. 1974. *Fragaria chiloensis* clones resistant to the strawberry aphid. HortScience 9:202–203.
Shanks, C.H. and P.P. Moore. 1995. Resistance to two-spotted spider mite and strawberry aphid in *Fragaria chiloensis, F. virginiana*, and *F. ×ananassa* clones. HortScience 30:596–599.
Shanks, C.H., C.K. Chandler, E.D. Show, and P.P. Moore. 1995. *Fragaria* resistance to spider mites at three locations in the United States. HortScience 30:1068–1069.
Shanks C.H., Jr., D.L. Chase, and J.D. Chamberlain. 1984. Resistance of clones of wild strawberry, *Fragaria chiloensis*, to adult *Otiorhynchus sulcatus* and *O. ovatus* (Coleoptera: Curculionidae). Environ. Entomol. 13:1042–1045.
Sjulin, T.M. and A. Dale. 1987. Genetic diversity of North American strawberry cultivars. J. Amer. Soc. Hort. Sci. 112:375–385.
Spigler, R.B., K.S. Lewers, D.S. Main, and T.-L. Ashman. 2008. Genetic mapping of sex determination in a wild strawberry, *Fragaria virginiana* reveals earliest form of sex chromosome. Heredity 101:507–517.
Stahler, M.M., P.D. Ascher, J.J. Luby, and A.P. Roelfs. 1995. Sexual composition of populations of *Fragaria virginiana* (Rosaceae) collected in Minnesota and western Wisconsin. Can. J. Bot. 73:1457–1463.
Staudt, G. 1999. Systematics and geographic distribution of the American strawberry species: Taxonomic studies in the genus *Fragaria* (Rosaceae: Potentilleae). University of California Press, Berkeley, CA.