Generating a Unique Germplasm Base for the Breeding of Day-neutral Strawberry Cultivars

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Royce S. Bringhurst and Victor Voth at the University of California-Davis (UC-Davis) revolutionized the strawberry industry in 1979 with the release of their first “day-neutrals” ‘Aptos’, ‘Brighton’, and ‘Hecker’ (Bringhurst and Voth, 1980). These day-neutrals could be programmed to produce fruit 3 months after planting and continued to fruit for up to 5 months regardless of day-length, greatly expanding the production season in California.

These unique cultivars were generated by backcrossing for three generations to conventional short-day types from a hybrid Bringhurst made between ‘Shasta’ and a *Fragaria virginiana* subsp. *glauca* clone from the Wasatch Mountains in Utah. Bringhurst continued backcrossing his elite day-neutral selections annually, releasing the very successful ‘Selva’ from the fourth generation and ‘Seascape’ from the fifth. This same strategy has been continued by Bringhurst’s replacements resulting in a string of day-neutral cultivar releases from the UC-Davis program.

As word spread about Bringhurst’s accomplishments, it did not take worldwide strawberry breeders long to begin using his day-neutral germplasm to generate new repeat flowering types. The standard approach was to hybridize a UC-Davis day-neutral selection or cultivar with their local short-day selections and then backcross like Bringhurst had done into their local breeding population. The USDA’s ‘Tristar’ and ‘Tribute’ were the first day-neutrals to be released outside of California in 1981. They were generated by Donald Scott in a 1974 cross using the parent of ‘Brighton’ and ‘Hecker’—Cal. 65.65-601 (Draper et al., 1981).

Over the last few decades, several day-neutral cultivars have been developed outside of California using Bringhurst’s source of day-neutrality, but none of these has achieved the commercial success of the UC-Davis cultivars. In general, their fruit are softer and smaller, and their floral development is inhibited by the hot summer temperatures common in temperate climates (Hancock et al., 2008). Because temperature has such a strong impact on performance, we have suggested that the day-neutrals are more appropriately called remontant (Bradford et al., 2010).

To facilitate the development of remontant cultivars outside of California, it is likely that local germplasm bases must be expanded. Levels of future success may be tied to incorporating new genetics into local breeding programs that are unique to the UC-Davis germplasm base. It might also be beneficial to incorporate genes specifically from genotypes that are known to be heat tolerant. Herein, we describe our efforts to generate such a diverse population that we would like to share with the breeding community.

Origin and Development

Our germplasm development work progressed in three stages. In the Stage 1, we crossed a set of the most widely planted North American cultivars and native *F. virginiana* with UC-Davis ‘Hecker’, ‘Seascape’, ‘Selva’, and ‘Chandler’. A list of the native and cultivar parents can be found in Hancock et al. (2002). We also hybridized eastern cultivars with USDA-ARS selections developed by coauthor C.E. Finn containing blends of elite Pacific Northwestern selections, native germplasm, and California cultivars. The California cultivars were ‘Aromas’ and ‘Camarosa’ and the native selections were *F. virginiana* from Montana and Minnesota, and a land race of *Fragaria chiloensis* from Ecuador (Finn et al., 1998).

Most of the native selections that we used as parents are included in what was named the “Supercore Collection” (Hancock et al., 2000) and deposited in the National Clonal Germplasm Repository (NCGR) in Corvallis, OR. This collection is composed of 38 wild strawberry accessions that are horticulturally superior and represent a considerable range of the natural diversity found in the octoploids ($2n = 8x = 56$) *F. chiloensis* and *F. virginiana* (Hancock et al., 2000, 2001a, 2001b). It was based on evaluations of more than 2500 native *F. virginiana* from across the United States and Canada and more than 6000 *F. chiloensis* from California, Chile, and the Pacific Northwest.

In Stage 2 of our germplasm development, we hybridized the most elite selections from Stage 1 with four remontant *Fragaria* × *ananassa* genotypes known to be heat tolerant (able to readily initiate flowers at 26 °C or higher). We took two approaches to identify and incorporate greater heat tolerance into our breeding population. In the first, we screened 13 cultivars and wild selections for their ability to flower and runner across a range of temperatures from 18 to 30 °C (Serge and Hancock, 2005). We found the old Wyoming cultivar Fort Laramie to be much more heat tolerant than any other of the screened genotypes. We also compared the heat tolerance of the popular Midwestern cultivar Honeoye to the remontant ‘Tribute’ and found it to be more heat tolerant at 26 °C (Bradford et al., 2010). We then generated a segregating population of ‘Tribute’ × ‘Honeoye’ (T × H) and selected the most heat-tolerant individuals to use as parents (Mookerjee et al., 2013).

In our Stage 3 of germplasm development, we hybridized our most promising remontant selections from the first two stages of crosses with elite F₂ selections from the *F. ×ananassa* “reconstruction” project (Hancock et al., 1993, 2010; Stegmeir et al., 2010). We also intercrossed most of the elite F₂ hybrids identified in that project. In the reconstruction work, 10 elite wild and cultivated *F. chiloensis* and 16 native *F. virginiana* were first intercrossed within species, and then the most promising hybrids were crossed between species. An effort was made to incorporate as much geoeological diversity of each species as possible. Most of the original parents were represented in the Supercore Collection.

The hybrid families generated in 2013 and 2015 were planted in groups of 20–25 together in rows at 1.2 m × 1.2 m spacing at the Southwestern Michigan Research and Extension Center (Benton Harbor, MI) in late May in 2014 and 2016. In an adjacent field were planted ‘Seascape’ and ‘Albion’. The first round of flowers was removed from each plant and any runners that emerged were trained by cross row cultivation into 1 × 1 m² squares. Starting in mid-July, the plantings were evaluated weekly to identify superior genotypes until all flowering was significantly diminished in September. Subjective notes (1–10) were taken on the most elite

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Table 1. Most interesting remontant selections in the MSU strawberry breeding program.

MSU ID	PI number	CFRA	Other ID	Cross	Composition						
					EST SD	EST RM	CA SD	CA RM	PNW SD	Fc	Fv
Redstart			MSU 67	'Honeoye' × 'Chandler'	50	0	50	0	0	0	0
Wasatch			MSU 68	'Seascape' × MSU 38	25	25	0	50	0	0	0
MSU 75	686943	2302	MI 13-1-42	MSU 25 × MI 10-24-52	25	50	0	25	0	0	0
MSU 76	686944	2303	MI 13-5-14	MSU 61 × TH 9-16-5	25	50	12.5	0	6.25	6.25 ^z	0
MSU 77	686945	2304	MI 13-6-18	MSU 21 × MI 10-24-52	0	50	25	25	0	0	0
MSU 79	686946	2305	MI 13-12-69	MI 8-66-47 × TH 9-16-26	37.5	37.5	0	25	0	0	0
MSU 82	686947	2306	MI 13-12-70	MI 8-66-47 × MI 10-11-32	25	12.5	0	50	0	0	12.5 ^y
MSU 83	686948	2307	MI 13-16-52	MI 8-27-73 × TH 9-16-26	25	37.5	0	31.25	0	0	6.25 ^x
MSU 84	686949	2308	MI 13-17-43	'Seascape' × MI 10-11-32	12.5	0	0	75	0	0	12.5 ^y
MSU 85	686950	2309	MI 15-16-31	FVC 11-58 × 'Redstart'	25	0	25	0	0	25 ^w	25 ^v
MSU 86	686951	2310	MI 15-22-26	MSU 70 × MSU 73	25	12.5	0	56.25	0	0	6.25 ^x
MSU 87	686952	2311	MI 15-35 (2)	'Redstart' × TH 9-16-26	50	25	25	0	0	0	0
MSU 88	686953	2312	MI 15-7-41	FVC 16-1 × FVC 11-58	0	0	0	0	0	50 ^u	50 ^t
MSU 89	686954	2313	MI 15-19-11	FVC 10-2 × FVC 8-1	0	0	0	0	0	50 ^s	50 ^t
MSU 90	686955	2314	MI 15-21-2	FVC 28-1 × FVC 8-1	0	0	0	0	0	50 ^s	50 ^t

^zEcuador.^yMinnesota.^xMontana.^wCalifornia and Chile.^vMontana and Ontario.^uBritish Columbia, California, and Chile.^tMinnesota, Montana, and Ontario.^sCalifornia, Chile, and Ecuador.^rMinnesota and Montana.EST SD = eastern short-day cultivars; EST RM = eastern remontant cultivars; CA SD = California short-day cultivars; CA RM = California remontant cultivars; PNW SD = Pacific Northwest short-day cultivars; Fc = native *Fragaria chiloensis*; Fv = native *Fragaria virginiana*.

selections for season, productivity, vigor, fruit size, appearance, firmness, internal and external color, and flavor.

Horticultural Characteristics

Well-adapted, elite hybrids were recovered from all our various crossing endeavors (Tables 1 and 2). Eleven hybrids were selected from crosses of our elite breeding material and UC-Davis cultivars and two of these have been released as cultivars (Redstart and Wasatch). Details on the two cultivar releases can be found at <http://msut.technologypublisher.com/technology/22785> and <http://msut.technologypublisher.com/technology/22786>. Wasatch is a strong remontant and likely inherited this trait from its parent 'Seascape', containing the Wasatch source of remontancy. Redstart is a weak remontant and was derived from a cross of two short-day cultivars, Chandler and Honeoye. In the MSU breeding program, both these two short-day types have been found to produce a small percentage of remontant progeny.

From the Stage 2 crosses, we selected three hybrids with heat-tolerant T × H in their background (MSU 79, 83, and 87), two with 'Fort Laramie' (MSU 75 and 77), four with *F. virginiana* (MSU 82, 83, 84, and 86), and one with *F. chiloensis* (MSU 76). MSU 83 combines genes from *F. virginiana* and heat-tolerant T × H. The origins of the *F. virginiana* contributors were Minnesota (RH 30) and Montana (LH 50-1), whereas the *F. chiloensis* donor was from Ecuador. The Ecuador contributor entered through one of C.E. Finn's complex hybrids with California and Pacific Northwestern germplasm in its background.

Table 2. Pedigrees of the parents of elite remontant MSU strawberry selections.

ID	Parents
Del Norte	wild <i>Fragaria chiloensis</i> subsp. <i>lucida</i> from California (CFRA 38; PI 551449)
Frederick 9	wild <i>Fragaria virginiana</i> subsp. <i>virginiana</i> from Ontario (CFRA 1695; PI 612493)
FVC 8-1	(Scotts Creek × NAH 3) × (RH 30 × LH 50-4)
FVC 10-2	(NAH 3 × MAR 1A) × (RH 30 × LH 50-4)
FVC 11-58	(Frederick 9 × LH 50-4) × (Scotts Creek × MAR 1A)
FVC 16-1	[(Sable Beach 1 × Del Norte) × (Lighthouse 3 × Del Norte)] × (Montreal 10 × RH 23)
FVC 28-1	(HM 1 × NAH) × (RH 30 × MR 10)
NAH 3	wild <i>F. chiloensis</i> f. <i>chiloensis</i> from Huachi, Ecuador (CFRA 1480; PI 612318)
Lion's Head 3	wild <i>F. chiloensis</i> subsp. <i>pacific</i> from British Columbia
LH 50-4	wild <i>F. virginiana</i> subsp. <i>glauca</i> from Montana (CFRA 1697; PI 612495)
MAR 1A	wild <i>F. chiloensis</i> f. <i>patagonica</i> from Chile (CFRA 1075; PI 602567)
MI 07-34	'Tribute' × ORUS 2461
MI 8-27-73	'Seascape' × MSU 07-34
MI 8-66-47	'Seascape' × MSU 38
MI 10-11-32	'Selva' × MSU 5
MI 10-24-52	'Seascape' × 'Fort Laramie'
Montreal River 10	wild <i>F. virginiana</i> subsp. <i>virginiana</i> from Ontario (CFRA 1699; PI 612497)
MSU 5	RH 30 × 'Honeoye'
MSU 21	'Tribute' × 'Chandler'
MSU 25	'Tribute' × 'Allstar'
MSU 38	'Tribute' × 'Honeoye'
MSU 61	'Tribute' × ORUS 2264
MSU 70	'Seascape' × MI 07-34
MSU 73	'Earliglow' × 'Seascape'
ORUS 2063-1	'Redcrest' × NAH 3
ORUS 2264-1	'Camarosa' × ORUS 2063
ORUS 2461-1	'Aromas' × LH 50-4
RH 23	wild <i>F. virginiana</i> subsp. <i>virginiana</i> from Minnesota (CFRA 1700; PI 612498)
RH 30	wild <i>F. virginiana</i> subsp. <i>virginiana</i> from Minnesota (CFRA 1701; PI 612499)
Sable Beach 1	wild <i>F. chiloensis</i> subsp. <i>pacific</i> from British Columbia
Scotts Creek	wild <i>F. chiloensis</i> subsp. <i>pacific</i> from California (CFRA 1692; PI 61690)
TH 9-16-26	'Honeoye' × 'Tribute'

From the Stage 3 crosses, three selections were made that were composed of only wild derived genes (MSU 88, 89, and 90) and another one that had half of its genes from wild sources (MSU 85). These selections combine genes in multiple combinations of *F. chiloensis* from British Columbia, California,

Chile, and Ecuador and *F. virginiana* from the locations Ontario, Minnesota (2), and Montana.

In general, the selections performed favorably compared with 'Albion' and 'Seascape' (Table 3). All except 'Redstart' appeared to be strong remontants, flowering

Table 3. Performance of MSU elite remontant selections at the Southwest Michigan Research and Extension Center, Benton Harbor, MI. Ratings: 1 (poor) to 10 (excellent).

ID	Vigor	Yield	Size	Appearance	Internal color	External color	Firmness	Flavor
Albion	6.7	7	9	8	6.5	7.7	9.7	8
Seascape	7.2	7.5	6	8	8	8.5	8.2	6.5
Redstart	8	8	6.5	8	7	7.7	7.7	7.7
Wasatch	8.2	8.7	7	7.5	7.5	8.2	8.2	8
MSU 75	9.5	8	8.0	8	8	8	7.5	7
MSU 76	9	8	7.7	7.5	8	7.5	7.2	6
MSU 77	9.5	9.5	6	8	7.5	6	6	6
MSU 79	7	8	8	8	7.5	6	7	6
MSU 82	8	9	6.5	6	8	7.5	8	8
MSU 84	8	8	6	7.5	7.5	8	7	7
MSU 85	9.5	8	7	7.5	7.5	7.5	7.5	7.5
MSU 86	8	8	8	7.5	7.5	7.5	7	7
MSU 87	9.5	9.5	7	8	8	8	5	7
MSU 88	8	7.5	7.5	7.5	6	6	6	9
MSU 89	8	7.5	7	7.5	7.5	8	6	7
MSU 90	8	8	7	7.5	7.5	8	6	7

well into September. ‘Albion’ fruit were larger and firmer than the fruit of any of the selections, but all of the hybrids had higher yields, vigor, and more internal color than Albion. ‘Seascape’ was firmer and had better external color than all the selections except ‘Wasatch’, but most of the hybrids were superior to ‘Seascape’ for vigor, yield, size, and flavor.

Summary and Availability

Through these efforts, we believe we have constructed a unique breeding population for developing new remontant strawberry cultivars. We have successfully mixed cultivars from California, the eastern United States, and the Pacific Northwest with genes from native *F. virginiana* and *F. chiloensis*.

These four native *F. virginiana* selections could carry genes for day-neutrality that are unique from those of Bringham’s Wasatch selection. LH 50-4 is in the same Rocky Mountain subspecies (subsp. *glauca*) as the Wasatch selection, but the other three, RH 23, RH 30, and Montreal River 10, are all in a different, eastern subspecies (subsp. *virginiana*). We brought an old heat-tolerant cultivar (Fort Laramie) into the mix along with a genotype from a hybrid family of *F. xananassa* specifically screened for heat

tolerance. ‘Fort Laramie’ was likely developed using *F. virginiana* subsp. *glauca* that is also unique to the Wasatch selection (Hildreth and Powers, 1940; Powers, 1954).

Time will tell if this breeding population will meet expectations, but if genetic diversity is the key to breeding success, this population should be useful to many strawberry breeders. Clones of these MSU selections have been deposited into the U.S. NCGR at Corvallis, OR, for research use. Seasonally available plant materials such as runners, leaves, pollen, or other forms can be requested through GRIN-Global at <https://npgsweb.ars-grin.gov/gringlobal/search.aspx?> or by communicating with the Curator, Dr. Kim Hummer.

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