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Phenotypic variability in a panel of strawberry cultivars from North America and the European Union

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Abstract

The phenotypic diversity in 96 antique and modern strawberry cultivars from the European Union and North America was evaluated in Michigan and Oregon, in 2011 and 2012. A total of thirty-five fruit and developmental characteristics were measured. Significant differences ($p < 0.05$) were observed among cultivars and environment for most of the characteristics, although only a few significant genotype × environment interactions were found. Several cultivars were superior for multiple traits including 'Aromas' from California (size, glossiness, crop load and weeks of flowering), 'Allstar' from the Mid-Atlantic States (glossiness, firmness, drip loss and soluble solids concentration), 'Florida Radiance' (external color, skin strength, size, drip loss and acidity), 'Gorella' from the European Union (skin strength, internal color and soluble solids concentration) and 'Melody' from the European Union (external color, skin strength and drip loss). No antique cultivars carried superior traits that were not found in modern cultivars. The data in these trials will be combined with DNA diagnostic tests to identify genes of importance for strawberry breeding.

Breeding programs revolve around identifying the optimal traits for a cultivar. Most strawberry (*Fragaria ×ananassa* Duch. ex Rozier) breeding programs utilize traditional approaches to identify desirable types, such as walking along rows of crosses in the field and scoring selections or doing simple laboratory assays on fruit quality and disease resistance. However, in many other crops, "marker assisted breeding" (MAB) is used to facilitate and speed up the release of new cultivars (Bliss, 2010; Iezzoni et al., 2010).

MAB is based on DNA diagnostic tests that can identify potential parents and progeny carrying desirable traits. This process allows selection to be moved all the way back to conception in the breeders' minds, allowing them to only make crosses that create desirable trait combinations in offspring increasing the efficiency of the entire process. It also allows selection to be moved from the field to the greenhouse, so that only seedlings predicted to be superior are planted in the field for further evaluation. In addition, MAB allows for the assessment of traits that are difficult to predict in the field such as post-harvest quality, disease resistance, flavor and remontancy.

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MAB has only been used to a limited extent in strawberry; however, many molecular resources are now available in strawberry and include: 1) the *F. vesca* L. 815 × *F. bucharica* Losinsk 601 (FV × FB) reference map for diploid strawberry (Sargent et al., 2008), 2) a reference genome sequence of *F. vesca* (woodland strawberry) (Shulaev et al., 2011), and 3) linkage maps for five *F.* ×*ananassa* populations, 'Capitola' × CF1116 (Lercerteau-Köhler et al., 2003; Rousseau-Gueutin et al., 2008), 'Tribute' × 'Honeoye' (Weebadde et al., 2008; Castro et al., 2014), 'Redgauntlet' × 'Hapil' (Sargent et al., 2009), 'Holiday' × 'Korona' (Van Dijk et al., 2014) and '232' × '1392' (Zorrilla-Fontanesi et al., 2011).

A few breeding programs have identified potentially useful markers. Quantitative trait loci (QTL) were found for remontancy and runnering (Gaston et al., 2013; Castro et al., 2014; Weebadde et al., 2008), as well as important fruit quality characters such as soluble solids concentration, ascorbic acid concentration, titratable acidity, color, flavor and firmness (Lerceteau-Köhler et al., 2012; Zorrilla-Fontanesi et al., 2011; 2012). Molecular markers have been discovered for red stele resistance (*Phytophthora fragariae* Hickman) (Eric van de Weg, personal communication) and resistance to *Colletotrichum acutatum* J.H. Simmonds (Whitaker, 2011).

Over the last five years, considerable inroads have been made towards making MAB a routine practice in strawberry through research conducted in the RosBREED project (Iezzoni et. al., 2010). RosBREED is a multi-state, multi-national project dedicated to the genetic improvement of US rosaceous crops. Coordinated by Amy Iezzoni at Michigan State University, it aims to bridge the chasm between the science of "genomics" and traditional rosaceous crop breeding programs (apple, peach, sweet cherry, tart cherry, and strawberry). This project is supported by the Specialty Crop Research Initiative of USDA's National Institute of Food and Agriculture. The major goal of the RosBREED project is to find "jewels in the genome" – locations of the hereditary units (genes) controlling critical production and fruit quality traits. Identification of these genes can then be used to develop markers for future integration into marker assisted breeding. RosBREED also has a socio-economic aspect to determine and prioritize market-driven needs.

Phenotypic and genotypic data are needed to pursue MAB breeding in strawberry. RosBREED's strawberry group identified 947 *Fragaria* genotypes that represent the diversity found in octoploid strawberries. These genotypes include wild strawberry selections, an array of old and new cultivars from across the world, and five mapping populations that are segregating for traits of interest to local breeding programs. Characterizing this diverse germplasm will help strawberry breeders gain a better understanding of the diversity available for breeding, and the phenotypic database can be combined with genome-wide genotypic data to identify important marker-locus trait associations.

Herein, our objectives are to describe a panel of strawberry cultivars representative of breeding programs from North America and the EU, grown in Michigan and Oregon, in 2011 and 2012. The traits evaluated were related to fruit quality (shape, appearance, capping, calyx position, percent of filled achenes, achene color, gloss, skin toughness, external and internal color, depth of internal color, flavor, average weight), fruit chemistry (soluble solids concentration, titratable acidity, pH, drip loss) and plant development (vigor, flowering dates, harvest dates, flower number, runner number, truss size, diseases, remontancy). The data from these trials will be combined with DNA diagnostic tests to label genes of importance for strawberry breeding in a separate publication.

Materials and Methods

A complete description of how the characters were measured can be found in

Mathey et al. (2013) and at http://www.rosbreed.org/resources/fruit-evaluation.

Cultivar selection

An attempt was made to analyze representative cultivars released from the European Union and the major climatic zones of North America. The climatic zones were: California (CA), Eastern (ES - Massachusetts, New York, Nova Scotia, and Quebec), Florida (FL), Mid-Continent (MC - Illinois, Michigan, Minnesota, Ontario, Wisconsin, and Wyoming), Mid-Atlantic (AT – Maryland, and New Jersey), Pacific Northwest (PNW - British Columbia, Oregon, and Washington), Southern (SN - Arkansas, Louisiana, and North Carolina) and European Union (EU - France, Italy, The Netherlands, and United Kingdom). We also evaluated antique to modern cultivars with release dates spanning the decades from the 1890s to the present.

Field design

Two plants of each cultivar were set at the Oregon State University Vegetable Farm in Corvallis, OR (44°34'21" N, 123°14'44" W) and Southwest Michigan Research & Extension Center in Benton Harbor, MI (42°05'17" N, 86°21'28" W). Plants were spaced 0.91 m apart in row and 0.91 m between rows. Standard commercial practices were used for fertilization, irrigation, and weed control.

Plant development

Several plant characteristics were evaluated in the field and scored on a scale from 1-9, including crop load, plant vigor and number of runners. The presence of open flowers was recorded weekly until the end of July or the first week of August in 2011 and 2012. Remontancy was evaluated in two ways: 1) whether the cultivars flowered in the short days of spring or in the spring and during the long days of summer (1 vs 2 flowering cycles), and 2) how many weeks the cultivars flowered after July 17 (approx. one month after the longest day of the year).

Growing degree days for the first bloom and for harvest date were calculated as the mean of the maximum and minimum daily temperature minus the base 50°F (10°C). Days from 1 January for bloom and harvest dates were also calculated by summing the number of days from 1 January to the calendar date on which the first bloom was observed and 30-50% of the fruit were ripe.

Flowering and fruit characteristics

The average number of flowers in three trusses was used as an estimate of truss size. The location of the truss in relation to the canopy (above or below) and the relative peduncle length was measured. All ripe fruit were harvested from each plant when 30-50% of the fruit were ripe. The fruit from each plant were placed in plastic bags and stored in a -20°C freezer for further evaluation. Several fruit traits were scored on a 1 - 9 scale including appearance, achene color, achene position, percent of filled achenes, gloss, cap size, position of the calyx and ease of cap removal. The percentage of filled achenes was estimated in 10% increments. Cap size was scored as greater than, less than or equal to the width of the fruit. The position of the calyx was scored visually as raised, even or sunken relative to the shoulder of the fruit. Fruit shape was scored as long conic, globose, globose conic, cordiform, or oblate (1 to 5).

Other fruit characteristics measured included fruit firmness, skin toughness, external and internal color, depth of internal color, and flavor. Fruit firmness was scored by compressing fully ripe fruit between thumb and forefinger. Skin strength was based on how easily fruit was abraded when the evaluator's thumb was firmly dragged over surface of the fruit. The berries were sliced down the meridian and internal color was scored ranging from white to deep red. The estimation of depth of internal color was based on the percent of the flesh that was colored. Flavor scores were largely based on the perception of sweetness but also the presence/absence of off-flavors was considered.

Fruit quality and chemistry

The harvested fruit were counted and weighed. The frozen fruit samples were allowed to fully thaw at room temperature and drip loss, pH, soluble solids concentration (SS) and titratable acidity (TA) were measured. SS were determined using a handheld refractometer (Westover Model RHB-32; Southwest United Industries, Tulsa, OK, USA). Results are reported in percent SS (w/w) on a fresh weight (fw) basis. 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 (w/w) on a fw basis. Total drip loss was calculated by the formula W_1-W_2/W_1 where W_1 was the average weight of frozen berries and W_2 was the average weight of thawed berries after drip loss.

Data analysis

Analyses of variance (ANOVA) were performed for all cultivars, environments and the cultivar × environment interactions. Because the cultivars were not replicated within sites, environmental variation was calculated using sites and years as replicates. Cultivar and environment differences were detected using a model where genotypes were fixed effects and environments were random effects. The significance of interaction of genotypes × environments were measured as fixed effects in a linear model.

Results

Overall variation patterns

Significant differences ($p < 0.05$) were observed among cultivars for the plant characteristics (Table 1) - crop load and vigor, the phenology and flowering traits - total weeks of flowering, weeks flowering after July 26, repeat flowering, number of flowering cycles, days from Jan. 1 to full bloom, GDD to first bloom, days from Jan. 1 to harvest and GDD to harvest; the external fruit characteristics achene color, percentage filled achenes, external color, gloss, and skin strength; the internal fruit characteristics - firmness, internal color and depth of internal color; and the fruit quality and chemistry characteristics - fruit weight, drip loss, pH, percentage soluble solids and titratable acidity.

Significant environmental differences ($p < 0.05$) were noted for the measured characteristics except the phenology and fruiting traits - weeks of flowering after July 17, repeat flowering and flowering cycles, and the internal fruit characteristic flavor (Table 1). GDD to first bloom was longer in both years in MI than OR, along with ratings of fruit glossiness and skin strength, and percentage soluble solids. Average fruit weights were larger in OR than MI both years. Days from Jan.1 to full bloom and percentage soluble solids were higher in 2011 at both sites compared to 2012. Days from Jan. 1 to harvest, fruit appearance, and depth of internal color were lower at both sites in 2011 than 2012.

Significant ($p < 0.05$) G × E interactions were found for only the phenology and fruiting characteristic - weeks of flowering after July 17, flowering cycles, GDD to harvest and the external fruit characteristic - cap size (Table 1).

Cultivar differences in plant development

CA ‘Aromas’ and ‘Salinas’, MC ‘Governor Simcoe’, and PNW ‘Valley Red’ and ‘Northwest’ had the highest crop loads (6.1 to 7.0), while MC ‘Ogallala’, CA ‘Capitola’, ES ‘Catskill’, FL ‘Dover’ and ‘Florida Radiance’, EU ‘Gorella’, ‘Melody’ and ‘Oberschlesien’, ES ‘L’Amour’ and MC ‘Ourown’ had the smallest crop loads (1.5 to 2.0) (Table 2). ‘Florence’ from the EU had by far the highest vigor (9) while CA ‘Hecker’, ‘Dover’, and EU ‘Jurica’ had the lowest vigor (1.5 to 2.7).

The CA remontants ‘Albion’, ‘Aromas’, ‘Diamante’, ‘Fern’, ‘Seascape’, and ‘Hecker’ and the MC remontant ‘Ogallala’ flowered for the most weeks (13 to 11.5), although the short day CA ‘Aiko’, and ‘Ettersburg 121’ also flowered for extended periods of time (11 to 9 weeks) (Table 3). Remontant

Table 1. Analysis of variance for cultivar (C), environment (E), and C x E for 97 cultivars grown in Michigan (MI) and Oregon (OR) in 2011 and 2012.

	Significance (P value)			Means - locations and years			
Trait	C	E	C x E	MI-2011	MI-2012	OR-2011	OR-2012
Plant characteristics							
Crop Load	**0.025**	**0.001**	0.924	4.8	4.6	4.4	3.4
Vigor	**0.025**	**0.001**	0.569	4.5	4.3	4.7	3.9
Number of runners	0.062	**0.001**	0.941	1.5	4.7	3.3	1.2
Phenology and flowering traits							
Peduncle length	0.544	**0.001**	0.855	4.5	2.9	3.4	3.2
Total weeks flowering	**0.001**	**0.001**	0.749	2.6	6.9	6.2	6.6
Weeks flowering after July 26	**0.001**	0.427	**0.001**	0.3	0.6	0.4	0.3
Repeat flowering (DN)	**0.001**	0.026	0.352	0.1	0.2	0.3	0.2
Flowering cycles	**0.001**	0.097	**0.021**	1.1	1.2	1.1	1.1
Days from Jan 1 to full bloom	**0.001**	**0.001**	0.999	138.5	102.4	119.4	115.0
GDD to first bloom	**0.001**	**0.001**	0.894	251.8	286.5	172.3	182.3
Flower location	0.239	**0.001**	0.936	1.2	1.5	1.4	1.7
Truss size	0.176	**0.001**	0.712	5.8	3.9	NA	5.5
Days from Jan 1 to harvest	**0.001**	**0.001**	0.906	164.6	156.3	172.1	162.9
GDD to harvest	**0.001**	**0.001**	**0.012**	571.7	775.1	576.9	588.9
External fruit characteristics							
Shape	0.380	**0.013**	0.583	5.8	6.0	5.5	6.1
Appearance	0.134	**0.001**	0.948	4.8	5.2	4.9	5.9
Achene color	**0.028**	**0.001**	0.640	1.6	4.3	6.2	4.1
Achene position	**0.058**	**0.001**	0.489	2.8	2.5	1.9	2.0
Percentage filled achenes	**0.040**	**0.008**	0.962	78.6	90.9	89.6	87.2
External color	**0.002**	**0.001**	0.988	7.6	6.4	7.1	6.7
Gloss	**0.043**	**0.001**	0.313	7.3	6.6	6.1	5.1
Skin strength	**0.005**	**0.001**	0.398	6.9	5.9	4.0	5.6
Cap size	**0.056**	**0.001**	**0.001**	1.0	1.7	1.2	1.0
Calyx position (Neck line)	0.304	**0.017**	0.816	2.9	3.7	3.4	3.1
Internal fruit characteristics							
Firmness	**0.001**	**0.001**	0.943	7.6	5.5	4.8	6.2
Ease of capping	0.391	**0.001**	0.933	6.6	3.5	5.4	5.5
Internal color	**0.001**	**0.001**	0.943	7.8	4.7	4.7	5.3
Depth of internal color (%)	**0.004**	**0.001**	0.321	42.8	80.5	81.5	95.2
Flavor	0.757	0.118	0.485	NA	3.9	4.6	4.8
Fruit quality and chemistry							
Fruit weight (g)	**0.004**	**0.001**	0.998	6.0	6.9	16.3	8.5
Drip loss (%)	**0.001**	**0.001**	0.994	NA	13.4	33.9	26.2
pH	**0.001**	**0.001**	0.551	3.6	3.5	3.5	3.3
Percentage soluble solids (SS)	**0.001**	**0.001**	0.978	10.85	9.78	8.31	7.50
Titratable acidity (TA)	**0.002**	**0.001**	0.972	0.8	1.1	0.8	0.7
SS/TA	0.511	**0.001**	0.988	14.6	9.3	11.0	11.3

Table 2. Year of release, origin, crop load and vigor of strawberry cultivars grown in Oregon and Michigan in 2011 and 2012.

Cultivar	Region[z]	Date[x]	Crop load[y]	Vigor[y]
Remontant				
Albion	CA	2006	5.5	4.0
Aromas	CA	1998	7.0	4.5
Capitola	CA	1990	2.0	4.0
Diamante	CA	1994	4.0	4.0
Fern	CA	1983	5.5	3.5
Fort Laramie	MC	1973	3.5	3.5
Hecker	CA	1979	3.3	2.7
Mara des Bois	EU	1993	5.0	5.5
Ogallala	MC	1958	1.5	4.5
Selva	CA	1974	3.5	4.0
Seascape	CA	1991	4.0	3.0
Tribute	AT	2010	4.0	3.7
Short-day				
Aberdeen	AT	1910	4.5	4.5
Aiko	CA	1976	6.0	4.5
Allstar	AT	1981	5.0	5.5
ArKing	SN	1981	3.7	3.7
Atlas	SN	1970	4.7	3.0
Benton	PNW	1975	5.0	6.0
Blakemore	AT	1929	3.3	4.8
Brunswick	ES	2006	5.0	3.7
Cabot	ES	1998	4.8	4.5
Camarosa	CA	1992	4.0	4.5
Cardinal	SN	1974	4.3	4.0
Catskill	ES	1934	2.0	3.5
Cavendish	ES	1991	6.0	4.7
Charm	PNW	2013	4.3	4.7
Clancy	ES	2003	4.3	5.0
Daroyal	EU	2006	5.0	5.7
Dover	FL	1980	2.0	2.3
Earliglow	AT	1975	2.5	4.0
Elsanta	EU	1981	3.0	3.5
Ettersburg 121	CA	1907	3.5	3.5
Fairfax	AT	1969	2.5	4.5
Firecracker	PNW	1999	5.0	5.3
Florence	EU	1998	4.0	9.0
Florida Belle	FL	1975	3.0	4.0
Florida Elyana	FL	2008	3.5	4.0
Florida Radiance	FL	2005	2.0	3.0
Glooscap	ES	1983	5.0	5.5
Gorella	EU	1960	2.0	4.0
Governor Simcoe	MC	1985	6.0	4.5
Guardian	AT	1899	3.0	5.0
Holiday	ES	1972	4.0	5.5
Hood	PNW	1965	4.3	3.7
Howard 17	ES	1907	5.7	5.0
Hummi Grandee	EU	1973	5.5	3.5
Idea	EU	1991	5.3	4.0
Joe	AT	1987	4.5	6.0

Jurica	EU	1974	4.3	2.7
Kaiser Samling	EU	1910	4.5	4.5
Kent	ES	1981	5.0	3.0
Klondike	SN	1901	2.5	5.0
Korona	EU	1978	4.5	5.5
L'Amour	ES	2006	2.0	4.5
Lassen	CA	1945	5.3	4.5
Lateglow	AT	1969	4.7	5.7
Marlate	AT	1944	3.7	5.0
Melody	EU	1992	2.0	4.0
Mesabi	MC	1999	4.0	3.7
Midland	AT	1990	3.5	5.0
Northwest	PNW	1949	6.7	4.7
Oberschlesien	EU	1919	6.0	3.5
Ourown	MC	1975	2.0	3.5
Puget Beauty	PNW	1956	4.5	4.0
Puget Reliance	PNW	1995	5.0	4.5
Puget Summer	PNW	1995	4.5	3.5
Rainier	PNW	1972	4.0	3.5
Redcoat	MC	1957	3.5	3.5
Redcrest	PNW	1990	3.0	3.5
Redgem	PNW	1993	3.0	4.0
Repita	EU	1960	4.5	4.0
Robinson	MC	1940	4.0	4.0
Rosa Linda	FL	1997	4.0	3.0
Salinas	CA	1966	7.7	3.7
Scott	AT	1964	2.7	4.3
Shuksan	PNW	1970	4.3	5.0
Sierra	CA	1945	3.7	3.7
Strawberry Festival	FL	1997	4.0	5.5
Sumas	PNW	1986	4.0	5.5
Sumner	SN	1980	3.7	4.3
Sunrise	AT	1943	3.0	3.7
Sweet Bliss	PNW	2011	5.0	4.0
Sweet Sunrise	PNW	2012	3.8	4.5
Tangi	SN	1973	2.7	4.7
Temple	AT	1981	3.0	4.5
Tillamook	PNW	2004	5.0	3.3
Tioga	CA	1964	5.5	4.5
Toro	CA	1976	4.7	4.7
Totem	PNW	1971	5.5	5.0
Treasure	FL	2002	3.0	5.0
Valley Red	PNW	2009	7.0	6.0
Valley Sunset	ES	2013	6.0	5.5
Veestar	MC	1967	3.3	4.7
Ventana	CA	2003	5.5	4.5
Wendy	ES	2007	3.0	4.7
Winona	MC	1996	3.3	4.0
Winter Dawn	FL	2010	4.0	4.0

[z] AT (Atlantic - Maryland, New Jersey), CA (California), ES (Eastern - Massachusetts, New York, Nova Scotia) EU (European Union - France, Germany, Netherlands, United Kingdom), FL (Florida), MC (Mid-continent - Illinois, Iowa, Michigan, Minnesota, Ontario, Wisconsin), PNW (Pacific Northwest - British Columbia, Oregon, Washington), SN (Southern - Arkansas, Louisiana, North Carolina).

[y] Rated on a scale of 1 (poor) to 9 (superior).

[x] Year of release.

'Mara des Bois' from the EU only flowered for a total of 8.5 weeks, but it along with CA 'Aromas', 'Diamante', 'Fern' and 'Seascape' and MC 'Ourown' flowered the most weeks after July 24 (3.5 weeks). Remontant, AT 'Tribute' only flowered for an average of 6.3 weeks and for only 1 week after July 26. It was also the only remontant cultivar that averaged less than 1.5 flowering cycles except 'Selva'. The short day CA 'Sierra' and FL 'Florida Radiance' had 1.5 or more flowering cycles (Table 3).

SN 'Klondike', AT 'Temple', CA 'Ventana', 'Aiko' and 'Ogallala' were among the earliest to bloom (days to bloom) - (96.5 to 99.0 d after Jan. 1), while PNW 'Firecracker', MC 'Governor Simcoe', MC 'Winona' and PNW 'Redcrest' were the latest to bloom (130.5 to 138.3). The GDD to first boom was shortest (<160 GDD) for AT 'Fairfax', FL 'Florida Belle' and 'Treasure', AT 'Joe', and EU 'Hummi Grandee', and longest (> 300 GDD) for ES 'Valley Sunset', EU 'Florence' and 'Oberschlesien', MC 'Redcoat', and PNW 'Firecracker' (Table 3). CA 'Aromas' and 'Ventana', AT 'Scott' and 'Temple', EU 'Gorella' and SN 'Tangi' and 'Klondike' had the earliest harvest dates (154.0 to 150.5 days after Jan.1), while 'Ogallala' and 'Hecker' had the latest harvest dates (193.0 to 178.5 days after Jan.1). CA 'Hecker' and MC 'Ogallala' had GDD to harvest that were 50% to 100% greater than most other cultivars.

Cultivar differences in flowering and fruit characteristics

MC 'Ogallala' had the lightest colored achenes (1.0), while ES 'Glooscap', CA 'Aiko' and FL 'Treasure' had the darkest ones (7.5 to 7.0) (Table 4). Most cultivars had achenes recessed or level to the fruit surface except CA 'Hecker' and 'Salinas', ES 'Glooscap', AT 'Aberdeen', 'Allstar', 'Guardian' and 'Tribute', EU 'Korona' and 'Melody', and PNW 'Rainier' whose achenes were set above the surface of the fruit. Most cultivars had regularly shaped fruit with over 75% of the achenes filled except for CA 'Hecker', AT 'Aberdeen', EU 'Hummi Grandee', MC 'Mesabi', PNW 'Valley Red' and MC 'Mesabi' and 'Winona'.

CA 'Camarosa' and 'Fern', MC 'Ogallala', AT 'Fairfax' and 'Scott', FL 'Florida Radiance', EU 'Melody' and PNW 'Puget Summer' and 'Valley Red' had the darkest fruit color (8.5 to 8.0) (Table 4). The weakest colored were SN 'Tangi' and AT 'Temple' (4.0). The glossiest fruit were CA 'Aromas' and 'Camarosa', 'Diamante' and 'Ventana', ES 'Holiday' and 'Allstar', and SN 'Dover' (8.5 to 8.0). The least glossy were EU 'Melody' and 'Repita', MC 'Fort Laramie', PNW 'Puget Summer' and 'Redgem' and EU 'Repita' (4.0). CA 'Seascape', ES 'Clancy', FL 'Dover', 'Strawberry Festival', 'Florida Radiance', 'Treasure' and 'Winter Dawn', EU 'Melody', and AT 'Scott' had the toughest skin (8.5 to 8.0). AT 'Fairfax', MC 'Ogallala', ES 'Glooscap', EU 'Hummi Grande' and 'Repita' and PNW 'Puget Summer' and 'Valley Red' had the weakest skin.

ES 'L'Amour' and 'Clancy', CA 'Albion', FL 'Florida Belle', 'Strawberry Festival' and 'Winter Dawn', and AT 'Allstar', 'Marlate' and 'Scott' had the firmest fruit (9.0 to 8.0) (Table 4). AT 'Fairfax', MC 'Ogallala', EU 'Hummi Grandee' and 'Repita', and PNW 'Valley Red' had the softest fruit (1.0 to 3.0). SN 'Cardinal', EU 'Gorella', PNW 'Charm', 'Redcrest', 'Valley Red' and 'Sweet Bliss' had the darkest internal color (8.0 to 7.5) and most were colored throughout. The least internal color was found in EU 'Kaiser Samling' and 'Melody' and CA 'Sierra' (1.0 to 1.5). Twenty cultivars from all regions had color throughout 100% of the flesh while CA 'Diamante', EU 'Mara des Bois', and SN 'Atlas' had color that penetrated less than one third of the way from the surface into the flesh.

Cultivar differences in fruit quality and chemistry

EU 'Florence', FL 'Florida Radiance', PNW 'Charm' 'Puget Beauty' and 'Valley Red', CA 'Selva', 'Aromas', 'Capitola' and

Table 3. Means of traits associated with phenology and flowering of strawberry cultivars grown in 0regon and Michigan in 2011 and 2012.

	Phenology and flowering traits							
	Total weeks flowering	Weeks flowering after July 26	Repeat flowering	Flowering cycles	Days to full bloom	GDD first bloom	Days to harvest	GDD harvest1
Remontant								
Albion	12.0	3.0	1.0	1.5	106.0	214.6	162.0	643.8
Aromas	13.0	4.0	1.0	1.5	103.0	198.4	152.0	712.6
Capitola	6.0	1.0	1.0	1.0	123.0	226.6	158.0	539.8
Diamante	10.5	4.0	1.0	2.0	108.5	204.2	160.0	666.1
Fern	13.0	4.0	1.0	2.0	103.0	198.4	157.0	590.7
Fort Laramie	8.0	0.5	0.5	1.5	105.0	231.6	160.5	692.6
Hecker	11.3	3.3	1.0	2.0	102.3	184.1	193.0	1639.1
Mara des Bois	8.5	4.0	1.0	2.0	127.0	221.7	165.5	605.2
Ogallala	11.5	2.5	1.0	2.0	99.0	185.3	178.5	1057.3
Selva	6.0	0.0	0.5	1.0	124.0	209.8	169.0	596.7
Seascape	11.5	3.5	1.0	2.0	101.5	217.4	158.5	661.0
Tribute	6.3	1.0	0.3	1.3	114.0	198.9	159.0	549.6
Short-day								
Aberdeen	5.5	0.0	0.0	1.0	112.5	240.8	162.0	677.0
Aiko	11.0	2.0	1.0	1.5	99.0	185.3	165.0	675.8
Allstar	5.0	0.0	0.0	1.0	115.0	245.3	157.5	638.8
ArKing	4.7	0.0	0.0	1.0	123.3	259.7	163.7	641.0
Atlas	5.0	0.0	0.0	1.0	118.3	224.1	153.7	567.6
Benton	4.7	0.0	0.0	1.0	121.0	251.7	160.5	692.6
Blakemore	5.5	0.0	0.0	1.0	108.5	160.6	155.3	581.2
Brunswick	5.0	0.0	0.0	1.0	113.7	208.2	162.3	617.5
Cabot	8.0	0.8	0.3	1.0	108.8	174.8	165.8	642.3
Camarosa	3.5	0.0	0.0	1.0	128.0	327.3	158.5	642.2
Cardinal	5.0	0.0	0.0	1.0	118.0	225.7	158.0	607.2
Catskill	5.5	0.5	0.5	1.5	115.5	264.7	157.0	645.2
Cavendish	5.0	0.0	0.0	1.0	118.3	227.7	163.0	612.9
Charm	5.0	0.0	0.0	1.0	121.0	250.2	160.7	602.2
Clancy	5.5	0.3	0.3	1.3	120.8	246.7	162.8	609.3
Daroyal	7.0	0.0	0.0	1.0	106.7	177.4	157.0	564.0
Dover	4.7	0.0	0.0	1.0	113.7	227.9	161.7	647.2
Earliglow	5.5	0.0	0.0	1.0	113.0	141.8	159.5	491.1
Elsanta	5.0	0.0	0.0	1.0	114.5	183.2	164.3	632.5
Ettersburg 121	9.0	0.5	1.0	1.0	117.0	180.3	174.5	667.1
Fairfax	6.0	0.0	0.0	1.0	110.0	158.0	163.0	528.0
Firecracker	3.0	0.0	0.3	1.3	138.3	347.3	172.5	734.6
Florence	4.5	0.0	0.0	1.0	126.0	309.1	171.0	818.9
Florida Belle	6.0	0.0	0.0	1.0	110.0	127.0	165.0	557.4
Florida Elyana	5.0	0.0	0.5	1.0	124.0	209.8	165.0	557.4
Florida Radiance	7.5	2.0	1.0	2.0	113.5	166.1	157.5	470.8
Glooscap	7.0	0.0	0.5	1.0	113.5	166.1	164.0	533.9
Gorella	3.5	0.0	0.0	1.0	120.0	261.9	150.0	705.8
Governor Simcoe	3.5	0.0	0.0	1.0	130.5	235.9	162.0	561.7
Guardian	4.5	0.5	0.5	1.0	116.5	249.9	164.0	680.4
Holiday	7.0	0.0	0.0	1.0	100.5	182.7	157.0	645.2
Hood	5.3	0.0	0.0	1.0	121.0	251.7	168.3	694.9

Howard 17	5.0	0.0	0.0	1.0	118.7	242.2	164.0	651.0
Hummi Grandee	7.0	0.0	0.0	1.0	110.0	158.0	176.5	682.1
Idea	5.7	0.0	0.0	1.0	114.0	221.1	169.3	705.4
Joe	5.0	0.0	0.0	1.0	117.0	156.3	168.0	583.7
Jurica	6.3	0.3	0.0	1.0	118.0	225.7	164.0	667.2
Kaiser Samling	6.5	0.0	0.0	1.0	115.5	264.7	163.5	715.0
Kent	7.0	0.5	0.5	1.0	112.0	252.7	160.0	671.5
Klondike	5.5	0.0	0.0	1.0	96.5	168.2	150.5	585.9
Korona	7.0	0.0	0.0	1.0	101.5	217.4	163.5	715.0
L'Amour	4.5	0.0	0.0	1.0	120.5	195.4	159.5	491.1
Lassen	5.0	0.0	0.0	1.0	114.8	197.8	165.0	641.2
Lateglow	4.0	0.0	0.0	1.0	118.7	242.1	168.3	707.3
Marlate	5.0	0.0	0.0	1.0	121.0	250.1	163.5	715.0
Melody	5.0	0.0	0.0	1.0	120.5	195.4	164.0	592.3
Mesabi	6.0	0.0	0.0	1.0	114.0	209.2	159.7	623.3
Midland	5.5	0.0	0.0	1.0	115.5	266.9	160.0	671.5
Northwest	6.0	0.0	0.0	1.0	113.7	206.5	167.0	677.0
Oberschlesien	5.0	0.0	0.0	1.0	122.5	301.9	163.5	715.0
Ourown	8.5	3.5	1.0	2.0	104.0	221.9	164.0	592.3
Puget Beauty	6.5	0.0	0.0	1.0	120.5	170.6	169.0	596.7
Puget Reliance	8.0	0.0	0.0	1.0	112.0	252.7	163.5	715.0
Puget Summer	5.0	0.0	0.0	1.0	120.5	195.4	169.5	597.8
Rainier	3.0	0.0	0.0	1.0	127.0	283.5	165.0	675.8
Redcoat	5.0	0.0	0.0	1.0	115.0	331.1	167.0	702.8
Redcrest	4.0	0.0	0.0	1.0	131.0	249.7	164.0	592.3
Redgem	5.0	0.0	0.0	1.0	115.5	264.7	158.5	661.0
Repita	7.0	0.0	0.0	1.0	103.0	198.4	162.0	633.4
Robinson	6.3	0.0	0.0	1.0	106.3	192.6	165.7	703.8
Rosa Linda	7.5	0.5	0.5	1.0	103.0	198.4	167.0	702.8
Salinas	5.0	0.0	0.0	1.0	116.7	223.3	161.7	599.3
Scott	6.0	0.0	0.0	1.0	104.0	221.9	154.0	622.8
Shuksan	4.7	0.0	0.0	1.0	120.7	250.2	164.0	667.2
Sierra	9.3	2.0	1.0	1.7	111.0	240.8	171.0	722.9
Strawberry Festival	5.5	0.5	0.3	1.0	112.5	186.1	160.3	582.1
Sumas	5.5	0.0	0.0	1.0	119.0	271.9	160.0	671.5
Sumner	5.7	0.3	0.3	1.3	114.0	206.6	161.3	616.4
Sunrise	6.3	0.0	0.0	1.0	111.7	213.1	160.0	606.9
Sweet Bliss	4.5	0.0	0.0	1.0	127.0	221.7	164.5	582.1
Sweet Sunrise	5.3	0.0	0.0	1.0	123.8	250.4	162.0	652.3
Tangi	5.0	0.0	0.0	1.0	111.7	195.0	154.0	622.8
Temple	7.0	0.0	0.0	1.0	96.5	168.2	154.0	622.8
Tillamook	6.0	0.0	0.0	1.0	118.3	213.4	166.0	644.2
Tioga	5.0	0.0	0.0	1.0	121.8	235.8	166.8	656.1
Toro	5.3	0.0	0.0	1.0	122.7	200.4	164.3	562.2
Totem	5.0	0.0	0.0	1.0	126.0	267.3	163.5	617.2
Treasure	8.5	1.5	1.0	1.5	110.0	127.0	168.0	583.7
Valley Red	6.0	0.0	0.0	1.0	120.0	181.8	169.0	623.6
Valley Sunset	4.0	0.0	0.0	1.0	127.0	301.9	168.5	718.5
Veestar	5.7	0.0	0.0	1.0	114.0	221.1	162.7	619.7
Ventana	7.5	0.5	0.5	1.0	98.0	181.6	152.0	712.6
Wendy	5.7	0.0	0.0	1.0	109.7	207.8	160.7	602.2
Winona	4.0	0.0	0.0	1.0	132.0	255.6	170.0	622.3
Winter Dawn	8.3	1.0	0.7	1.0	102.3	162.5	158.0	574.5

Table 4. Means of traits associated with external and internal fruit characteristics of strawberry cultivars grown in Oregon and Michigan in 2011 and 2012.

	External fruit characteristics						Internal fruit characteristics		
Cultivar	Achene color	Achene position	% filled achenes	External color	Gloss	Skin strength	Firmness	Internal color	Depth of color
Remontant									
Albion	5.5	1.5	95.0	6.5	7.0	6.5	8.0	4.0	70.0
Aromas	4.5	1.5	100.0	7.0	8.0	7.5	6.5	5.0	50.0
Capitola	NA	1.0	NA	NA	NA	NA	NA	NA	NA
Diamante	2.5	2.0	90.0	7.0	8.0	6.5	6.5	5.5	25.0
Fern	5.0	2.0	90.0	8.0	7.0	4.5	6.0	7.0	90.0
Fort Laramie	6.0	2.0	85.0	7.0	3.0	4.0	6.0	7.0	90.0
Hecker	3.0	3.0	70.0	6.0	7.0	6.0	6.0	4.0	50.0
Mara des Bois	2.5	2.5	85.0	6.5	5.0	6.0	7.5	5.5	30.0
Ogallala	1.0	2.0	90.0	8.0	7.0	2.0	2.0	6.0	90.0
Selva	5.5	2.5	80.0	7.0	5.0	6.0	6.0	5.5	100.0
Seascape	4.0	2.0	95.0	7.0	5.5	8.0	7.0	5.0	100.0
Tribute	4.3	3.0	93.3	6.7	7.0	5.3	5.7	5.3	93.3
Short-day									
Aberdeen	3.0	3.0	70.0	5.5	6.5	5.5	5.5	3.5	55.0
Aiko	7.0	1.5	90.0	6.5	7.0	4.0	4.5	3.5	75.0
Allstar	5.0	3.0	80.0	6.0	8.0	7.5	8.5	5.5	20.0
ArKing	3.7	2.3	83.3	7.0	6.0	5.0	6.0	4.0	100.0
Atlas	4.3	2.3	80.0	6.5	5.7	7.5	7.5	5.0	30.0
Benton	5.0	1.7	83.3	6.0	6.7	5.5	5.0	2.5	40.0
Blakemore	5.0	2.3	80.0	6.0	5.3	7.0	7.5	6.0	40.0
Brunswick	6.0	1.5	95.0	7.0	5.5	7.0	6.5	6.0	75.0
Cabot	6.0	2.5	77.5	6.3	6.5	6.0	5.8	4.5	92.5
Camarosa	4.0	2.0	100.0	9.0	8.0	7.0	7.0	8.0	100.0
Cardinal	4.7	2.7	86.7	7.5	5.7	6.0	5.0	7.5	95.0
Catskill	4.0	2.5	100.0	6.0	4.5	7.0	6.0	5.0	80.0
Cavendish	5.0	2.0	76.7	7.0	7.0	5.0	5.3	6.0	66.7
Charm	2.7	1.7	100.0	7.7	5.0	4.7	5.7	7.7	100.0
Clancy	5.3	2.5	96.3	6.8	5.8	8.5	8.5	5.8	87.5
Daroyal	4.7	2.3	96.7	7.5	6.7	6.5	5.0	6.5	80.0
Dover	2.0	2.0	80.0	7.0	8.0	8.0	7.0	3.0	90.0
Earliglow	3.0	2.0	100.0	7.0	5.5	6.0	6.0	6.0	100.0
Elsanta	5.0	2.0	100.0	6.5	5.5	7.5	6.5	5.0	85.0
Ettersburg 121	5.5	1.5	95.0	7.0	4.5	4.0	4.5	3.5	60.0
Fairfax	6.0	1.5	100.0	8.0	6.0	1.0	2.0	6.0	90.0
Firecracker	5.5	2.5	90.0	6.5	7.5	7.0	7.0	4.5	95.0
Florence	3.0	2.5	90.0	7.0	5.5	5.0	5.0	7.0	100.0
Florida Belle	4.5	1.5	100.0	7.0	5.5	7.0	8.0	4.0	90.0
Florida Elyana	5.0	2.5	90.0	NA	6.0	NA	NA	NA	NA
Florida Radiance	6.0	1.0	90.0	8.0	6.0	8.0	6.0	6.0	80.0
Glooscap	7.5	3.0	90.0	7.0	5.0	2.0	4.0	4.0	40.0
Gorella	5.0	2.0	90.0	7.0	7.0	8.0	6.0	8.0	90.0
Governor Simcoe	5.0	2.5	95.0	7.5	6.0	7.0	7.5	6.5	55.0
Guardian	5.0	3.0	90.0	6.0	7.5	4.5	4.5	4.0	75.0
Holiday	2.5	1.5	100.0	6.5	8.5	6.0	7.5	5.5	95.0
Hood	4.7	2.0	93.3	7.0	6.0	3.7	4.3	6.3	100.0
Howard 17	5.0	2.3	96.7	7.3	5.7	4.3	5.3	6.0	90.0
Hummi Grandee	5.0	1.5	70.0	6.0	7.5	2.0	4.0	5.0	40.0

Idea	6.0	2.7	86.7	6.0	6.7	6.5	5.5	5.0	100.0
Joe	5.0	2.0	90.0	6.0	7.0	3.0	5.0	3.0	100.0
Jurica	3.7	2.7	93.3	7.5	7.3	4.5	5.5	6.5	65.0
Kaiser Samling	4.0	2.5	85.0	6.0	5.5	3.0	4.0	1.0	100.0
Kent	3.0	2.5	80.0	6.0	6.5	5.0	5.0	5.0	100.0
Klondike	3.5	2.0	90.0	7.0	4.5	4.0	4.0	4.0	50.0
Korona	4.0	3.0	100.0	6.0	4.5	4.0	4.0	3.0	50.0
L'Amour	5.0	2.0	90.0	7.0	6.0	7.0	9.0	5.0	90.0
Lassen	2.5	2.3	90.0	7.3	6.3	3.7	4.7	5.0	66.7
Lateglow	4.7	2.3	100.0	7.0	6.3	3.3	4.3	5.0	100.0
Marlate	5.0	2.5	100.0	7.0	4.5	7.5	8.0	4.0	70.0
Melody	NA	3.0	90.0	8.0	4.0	8.0	7.0	1.0	90.0
Mesabi	3.0	2.3	73.3	6.5	7.5	7.0	6.0	7.0	45.0
Midland	4.5	2.0	90.0	7.0	6.5	5.0	5.5	5.0	90.0
Northwest	4.7	2.0	90.0	6.7	6.0	3.3	4.0	6.0	96.7
Oberschlesien	4.0	2.5	85.0	6.0	6.5	3.5	3.5	4.0	70.0
Ourown	5.5	2.5	95.0	7.0	7.5	4.0	4.0	5.0	80.0
Puget Beauty	2.5	1.5	95.0	7.0	5.5	4.5	4.5	6.5	100.0
Puget Reliance	2.5	2.5	95.0	7.0	6.5	6.0	6.5	5.0	95.0
Puget Summer	5.5	1.5	95.0	8.0	4.0	1.0	3.0	7.0	100.0
Rainier	2.0	3.0	100.0	7.0	7.0	4.0	5.0	7.0	100.0
Redcoat	6.5	2.5	80.0	6.0	6.5	6.0	4.5	2.5	55.0
Redcrest	NA	2.0	100.0	7.0	6.0	7.0	6.0	8.0	100.0
Redgem	3.5	2.5	85.0	6.0	4.0	4.0	4.0	3.0	60.0
Repita	4.0	2.0	75.0	7.0	4.0	2.0	2.5	5.5	90.0
Robinson	3.3	1.7	86.7	6.7	5.3	3.7	4.3	4.0	80.0
Rosa Linda	5.5	2.0	95.0	6.5	5.5	6.5	6.0	4.5	50.0
Salinas	4.0	3.0	86.7	7.3	5.0	4.0	5.0	6.3	76.7
Scott	4.0	2.0	75.0	6.0	5.0	8.0	8.0	7.0	80.0
Shuksan	2.0	1.7	90.0	7.3	7.3	5.0	6.3	6.7	70.0
Sierra	4.0	2.0	90.0	5.5	6.0	3.5	4.5	1.5	95.0
Strawberry Festival	4.0	2.5	78.8	7.5	5.3	8.3	8.0	5.3	97.5
Sumas	4.5	2.5	90.0	6.5	7.5	2.5	4.0	5.5	95.0
Sumner	5.0	2.3	70.0	6.5	5.3	5.0	3.5	3.0	100.0
Sunrise	6.5	2.5	90.0	7.0	7.0	4.5	4.5	4.5	80.0
Sweet Bliss	2.0	2.5	80.0	7.5	5.5	5.5	5.5	7.5	100.0
Sweet Sunrise	4.5	2.3	87.5	7.3	5.8	6.3	6.8	6.5	65.0
Tangi	4.0	2.5	90.0	4.0	5.0	6.0	5.0	4.0	60.0
Temple	5.5	2.0	90.0	4.0	6.0	3.0	4.0	5.0	80.0
Tillamook	4.0	2.8	82.5	6.5	6.5	7.0	6.8	6.5	80.0
Tioga	2.3	2.3	91.3	7.0	6.0	5.3	6.8	4.8	75.0
Toro	4.7	2.7	80.0	7.0	4.7	5.5	4.5	5.5	50.0
Totem	3.3	2.5	87.5	7.3	7.0	4.8	6.8	6.3	87.5
Treasure	7.0	1.5	95.0	7.0	5.0	8.0	6.0	4.0	40.0
Valley Red	4.5	2.0	70.0	8.0	6.5	2.0	3.0	8.0	100.0
Valley Sunset	5.0	2.5	85.0	6.5	7.5	5.5	4.5	5.0	75.0
Veestar	3.7	2.0	83.3	6.0	5.3	5.0	5.3	2.0	100.0
Ventana	5.0	1.5	100.0	6.5	8.5	5.5	6.5	5.0	85.0
Wendy	4.0	2.5	95.0	7.5	7.0	5.5	6.0	5.0	70.0
Winona	5.0	2.3	60.0	6.3	6.0	6.3	6.0	5.0	70.0
Winter Dawn	5.0	2.0	95.0	7.0	6.5	8.0	8.0	4.0	90.0

'Ventana' produced the largest fruit (average of 17.8 to 15.4 g) (Table 5). Fruit of CA 'Hecker', AT 'Aberdeen' and 'Midland', EU 'Jurica', ES 'Catskill' and 'L'Amour', and MC 'Ogallala', 'Ourown' and 'Winona' were the smallest (2.0 to 4.4 g). The lowest amount of drip loss was found for AT 'Allstar' and 'Blakemore', FL 'Florida Radiance' and EU 'Melody' (2.8 to 7.1%). The greatest amount of drip loss came from EU 'Hummi Grandee', AT 'Joe', PNW 'Puget Beauty' and 'Valley Red', CA 'Toro' and FL 'Treasure' (51.4 to 43.3%). The highest percentage soluble solids was in fruit of CA 'Hecker', EU 'Gorella', AT 'Aberdeen', 'Allstar' and 'Tribute', ES 'Howard 17' and CA 'Salinas' (13.6 to 11.2%). The lowest percentage soluble solids was found in fruit of CA 'Selva' and FL 'Florida Belle', 'Florida Elyana' and 'Florida Radiance' (5.7 to 6.2%). CA 'Selva', AT 'Fairfax', and FL 'Florida Belle', 'Florida Elyana' and 'Florida Radiance' had the lowest acidity (0.46 to 0.52), while CA 'Hecker', AT 'Blakemore', ES 'Holiday' and SN 'Klondike' had the highest acidity (1.21 to 1.38) (Table 5). ES 'Holiday', AT 'Joe' and 'Temple', SN 'Klondike', EU 'Melody', and PNW 'Redcrest' had pH levels below 3.3 while ES 'Wendy', EU 'Jurica' and FL 'Rosa Linda' and 'Treasure' had a much higher pH (3.7) (Table 5).

Discussion

For most of the traits evaluated, there was no significant G x E interaction. This suggests that cultivar performance in one year in either OR or MI is a good indication of performance in other years and locations. A similar conclusion was made in a comparison of a panel of wild selections grown previously in OR, MI, MD and PA (Hancock et al., 2001). Basing breeding efforts on marker associations observed in a single environment still seems risky to us, but our results do suggest that only a few environments are needed to identify robust markers.

Superior traits identified in antique cultivars were also found in modern cultivars. This suggests that for the characteristics we evaluated, it may not be necessary to go back to less improved cultivars to capture genes for new cultivar improvement. A more efficient approach might be to utilize modern cultivars from breeding programs that are using a different germplasm base. We found several cultivars from California, Florida, Eastern States and the EU with superior characteristics that also had above average yield and vigor in our environments. These included 'Albion', 'Aromas', 'Aiko', 'Ventana', 'Florence', 'Strawberry Festival' and 'Valley Sunset'.

Scoring as opposed to measuring traits, while often the only practical way to evaluate a trait, gives results that can be less straightforward to interpret when evaluating such diverse germplasm. For instance, when estimating crop load as opposed to harvesting and weighing all fruit to determine yield, a very high score may mean that a plant is weak and unhealthy and is "fruiting itself to death". When the genotypes have roughly the same vigor, a subjective score can be very effective. However with such diverse germplasm, nuances like this can be lost and means that growing a potential parent in the target environment is still a good idea. For this reason, one should look at both the vigor and crop load scores in evaluating the adaptation of a cultivar.

A number of cultivars from several different regions proved superior for multiple traits. DN 'Aromas' from CA was elite for size, glossiness, crop load, and weeks of flowering. SD 'Allstar' from MD was outstanding for gloss, firmness, drip loss, and percentage soluble solids. SD 'Florida Radiance' was superior for external color, skin strength, size, drip loss, and acidity. SD 'Gorella' from the EU was elite for skin strength, internal color, and percentage soluble solids. SD 'Melody' from the EU was superior for external color, skin strength, and drip loss.

DNA diagnostic markers could prove useful in utilizing these elite cultivars in our

Table 5. Means of traits associated with fruit quality and chemistry of strawberry cultivars grown in Oregon and Michigan in 2011 and 2012.

	Fruit quality and chemistry				
Cultivar	Weight (g)	Drip loss (%)	Soluble solids[z]	Titrable acidity[x]	pH
Remontant					
Albion	14.6	16.3	8.3	0.86	3.5
Aromas	15.9	18.5	8.3	0.78	3.6
Capitola	15.4	38.2	NA	0.64	NA
Diamante	8.7	27.1	8.3	0.62	3.5
Fern	6.2	31.2	8.5	0.80	3.5
Fort Laramie	7.9	23.0	6.7	0.53	3.6
Hecker	2.8	15.7	13.6	1.32	3.4
Mara des Bois	5.4	30.5	8.6	0.60	3.5
Ogallala	4.1	24.0	8.9	0.94	3.3
Selva	16.6	14.7	5.7	0.48	3.5
Seascape	7.1	15.9	9.2	0.83	3.4
Tribute	13.7	17.1	12.3	1.10	3.4
Short-day					
Aberdeen	4.4	27.5	11.7	1.18	3.5
Aiko	6.7	28.0	7.0	1.05	3.5
Allstar	8.7	5.6	12.0	0.82	3.8
ArKing	11.1	22.3	6.3	0.90	3.2
Atlas	5.5	14.8	9.1	0.82	3.5
Benton	9.1	30.9	9.9	1.11	3.3
Blakemore	6.9	7.1	10.4	1.21	3.3
Brunswick	12.5	24.6	7.4	0.91	3.4
Cabot	11.9	27.1	9.2	0.81	3.3
Camarosa	11.0	9.4	9.3	0.88	3.6
Cardinal	7.7	12.7	10.8	0.84	3.4
Catskill	4.1	13.3	8.5	1.02	3.4
Cavendish	8.6	23.1	8.4	0.90	3.5
Charm	17.2	24.3	8.8	0.99	3.4
Clancy	12.4	25.9	9.9	0.74	3.4
Daroyal	11.4	32.9	8.0	0.72	3.5
Dover	6.1	9.1	8.2	0.76	3.4
Earliglow	7.6	27.7	9.3	0.87	3.3
Elsanta	10.7	18.4	9.2	0.88	3.5
Ettersburg 121	7.4	16.3	9.3	0.81	3.4
Fairfax	7.7	21.3	10.7	0.51	3.6
Firecracker	12.8	26.2	10.8	1.15	3.3
Florence	17.8	25.3	9.0	1.06	3.3
Florida Belle	10.0	16.8	6.2	0.51	3.4
Florida Elyana	13.7	36.7	5.7	0.52	3.5
Florida Radiance	17.6	2.8	6.0	0.46	3.4
Glooscap	15.0	38.0	9.0	0.71	3.4
Gorella	12.1	17.7	12.8	0.74	3.6
Governor Simcoe	12.2	20.2	10.2	0.75	3.4
Guardian	10.1	19.4	8.6	0.77	3.6
Holiday	7.1	14.9	7.3	1.21	3.2
Hood	10.2	26.8	10.2	0.98	3.6
Howard 17	9.0	35.5	11.2	0.71	3.5
Hummi Grandee	7.9	51.4	7.0	0.66	3.5
Idea	14.2	13.7	7.8	0.85	3.3

Joe	10.1	45.1	9.4	0.76	3.2
Jurica	4.3	8.0	9.1	0.67	3.7
Kaiser Samling	4.6	41.5	8.7	0.85	3.5
Kent	8.9	19.9	9.0	0.88	3.4
Klondike	6.5	34.4	8.7	1.38	3.2
Korona	7.6	18.6	10.0	0.74	3.4
L'Amour	3.6	16.8	10.2	0.72	3.3
Lassen	8.5	14.3	7.7	0.94	3.5
Lateglow	8.2	34.6	9.7	1.07	3.3
Marlate	10.2	14.7	8.9	0.87	3.6
Melody	7.2	6.9	7.9	0.95	3.2
Mesabi	6.1	26.7	7.7	0.80	3.5
Midland	4.2	20.5	9.0	1.04	3.4
Northwest	10.0	28.8	8.3	0.74	3.3
Oberschlesien	7.4	33.6	7.4	0.78	3.3
Ourown	4.4	31.7	9.2	0.94	3.4
Puget Beauty	17.2	43.4	8.1	0.69	3.3
Puget Reliance	9.8	15.2	9.4	1.09	3.4
Puget Summer	8.4	32.1	10.2	0.84	3.4
Rainier	12.1	16.9	8.9	0.98	3.3
Redcoat	6.9	28.0	8.6	1.14	3.5
Redcrest	11.9	17.8	8.5	0.96	3.1
Redgem	5.2	13.5	9.9	0.87	3.3
Repita	8.8	42.3	9.6	0.93	3.4
Robinson	7.6	38.4	9.0	0.70	3.5
Rosa Linda	12.9	13.7	10.7	0.96	3.7
Salinas	12.8	23.5	11.5	0.83	3.5
Scott	11.5	18.7	7.7	0.89	3.3
Shuksan	8.5	20.8	10.2	0.91	3.4
Sierra	9.7	38.0	9.3	0.99	3.3
Strawberry Festival	10.6	8.0	8.2	0.75	3.5
Sumas	7.1	18.0	9.1	0.79	3.4
Sumner	9.2	19.0	8.4	0.82	3.4
Sunrise	8.1	35.1	8.2	0.91	3.6
Sweet Bliss	9.2	27.6	8.6	0.85	3.4
Sweet Sunrise	10.1	18.0	8.8	0.87	3.3
Tangi	10.9	30.9	8.4	0.94	3.3
Temple	5.0	37.7	8.5	1.12	3.2
Tillamook	7.1	17.8	8.9	0.91	3.5
Tioga	10.1	24.8	8.5	0.79	3.4
Toro	10.0	48.7	7.1	0.73	3.5
Totem	9.1	21.4	10.3	0.89	3.5
Treasure	15.2	21.9	7.4	0.71	3.7
Valley Red	16.1	43.3	6.6	0.69	3.4
Valley Sunset	14.1	14.2	8.0	0.85	3.5
Veestar	14.8	26.7	9.5	0.87	3.4
Ventana	15.7	18.4	9.4	0.94	3.5
Wendy	9.2	23.4	6.9	0.69	3.7
Winona	3.7	10.3	6.8	0.86	3.4
Winter Dawn	10.0	12.9	7.7	0.85	3.3

[z] SS was determined using a hand-held refractometer (Westover Model RHB-32; Southwest United Industries, Tulsa, OK, USA). Results are reported in percent SS (w/w) on a fresh weight (fw) basis.

[x] 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 percent citric acid equivalent (w/w) on a fw basis.

northern breeding programs, not only as a tool to capture the positive traits, but also as a means to eliminate negative characteristics. The internal color of 'Aromas' was weak and its soluble solids concentration was low. The fruit size of 'Allstar' was small and its internal color was weak. 'Florida Radiance' had very low vigor, productivity and soluble solids concentration. 'Melody' and 'Gorella' also had low productivity and vigor, and the fruit color of 'Melody' was dull. Marker assisted breeding could prove highly beneficial in using these genotypes as well as others with only a few superior traits, by allowing us to efficiently tease apart the beneficial from the deleterious genes after backcrossing.

Efforts are now underway in the RosBREED project to identify QTL for most of the characteristics analyzed in this study. The cultivar panel described herein and a number of other segregating families are being utilized in this effort. To date, robust microsatellite and single sequence repeat (SNP) markers have been identified for soluble solids concentration, titratable acidity and remontancy in these populations, and other research groups have found markers for a wide array of loci regulating strawberry development, fruit quality, and disease resistance. We expect that diagnostic DNA markers will soon be deployed and used routinely in the breeding of strawberries.

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Literature Cited:

Bliss, F.A. 2010. Marker-assisted breeding in horticultural crops. Acta Hort. 859:339-350.

Castro, P., J.M. Bushakra, P. Stewart, C.K. Weebadde, D. Wang, J.F. Hancock, C.E. Finn, J.J. Luby, and K.S. Lewers. 2015. Genetic mapping of remontantity in cultivated strawberry. Mol. Breeding 35:1-16..

Gaston, A., J. Perrotte, E. Lerceteau-Köhler, A. Petit, M. Rousseau-Gueutin, M. Hernould, C. Rothan, and B. Denoyes. 2013. PFRU, a single dominant locus regulates the balance between sexual and asexual plant reproduction in cultivated strawberry. J. Exp. Bot. 64:1837-1848.

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. 2001. A multistate comparison of native octoploid strawberries from North and South America. J. Amer. Soc. Hort. Sci. 126:579-586.

Iezzoni, A., C. Weebadde, J. Luby, Y. Chengyan, E. Van De Weg, G. Fazio, D. Main, C.P. Peace, N.V. Bassil, and J. McFerson. 2010. RosBREED: Enabling marker assisted breeding in Rosaceae. Acta Hort. 859:389-394.

Lerceteau-Köhler, E., G. Guérin, F. Laigret, and B. Denoyes-Rothan. 2003. Characterization of mixed disomic and polysomic inheritance in the octoploid strawberry (*Fragaria ×ananassa*) using AFLP mapping. Theor. Appl. Genet. 107:619-28.

Lerceteau-Köhler, E., A. Moing, G. Guérin, C. Renaud, A. Petit, C. Rothan, and B. Denoyes. 2012. Genetic dissection of fruit quality traits in the octoploid cultivated strawberry highlights the role of homoeo-QTL in their control. Theor. Appl. Genet. 124:1059-1077.

Mathey, M.M., C.E. Finn, S. Mookerjee, K. Gündüz, J.F. Hancock, A.F. Iezzoni, L.L. Mahoney, T.M. Davis, N.V. Bassil, K.E. Hummer, P.J. Stewart, V.M. Whitaker, D.J. Sargent, B. Denoyes, I. Amaya, and W.E. van de Weg. 2013. Large-scale standardized phenotyping of strawberry in RosBREED. J. Amer. Pom. Soc. 67:205-216.

Rousseau-Gueutin, M., E. Lerceteau-Köhler, L. Barrot, D.J. Sargent, A. Monfort, D. Simpson, P. Arùs, G. Guérin, and B. Denoyes-Rothan. 2008. Comparative genetic mapping between octoploid and diploid *Fragaria* species reveals a high level of colinearity between their genomes and the essentially disomic behavior of the cultivated octoploid strawberry. Genetics 179:2045-2060.

Sargent, D.J., G. Cipriani, S. Vilanova, D. Gil-Ariza, P. Arús, D.W. Simpson, K.R. Tobutt, and A. Monfort. 2008. The development of a bin mapping population and the selective mapping of 103 markers in the diploid *Fragaria* reference map. Genome 51:120–127.

Sargent, D.J., F. Fernandéz-Fernandéz, J.J. Ruiz-Roja, B.G. Sutherland, A. Passey, A.B. Whitehouse, and D.W. Simpson. 2009. A genetic linkage map of the cultivated strawberry (*Fragaria ×ananassa*) and its comparison to the diploid *Fragaria* reference map. Mol. Breeding 24:293-303.

Shulaev, V., D.J. Sargent, R.N. Crowhurst, T.C. Mockler, O. Folkerts, A.L. Delcher, P. Jaiswal, K. Mockaitis, A. Liston, S.P Mane, P. Burns, T.M Davis, J.P. Slovin, N. Bassil, R.P. Hellens, C. Evans, T. Harkins, C. Kodira, B. Desany, O.R Crasta, R.V. Jensen, A.C. Allan, T.P. Michael, J.C., Setubal, J.M. Celton, D.J.G. Rees, K.P. Williams, S.H. Holt, J.J.R. Rojas, M. Chatterjee, B. Liu, H. Silva, L. Meisel, A. Adato, S.A. Filichkin, M. Troggio, R. Viola, T.L. Ashman, H. Wang, P. Dharmawardhana, J.E., R. Raja, H.D. Priest, D.W. Bryant Jr., S.E. Fox, S.A. Givan, L.J. Wilhelm, S. Naithani, A. Christoffels, D.Y. Salama, J. Carter, E.L. Girona, A. Zdepski, W. Wang, R.A. Kerstetter, W. Schwab, S.S. Korban, J. Davik, A. Monfort, B. Denoyes-Rothan, P. Arus, R. Mittler, B. Flinn, A. Aharoni, J.L. Bennetzen, S.L. Salzberg, A.W. Dickerman, R. Velasco, M. Borodovsky, R.E. Veilleux, and K.M. Folta. 2011. The genome of woodland strawberry (*Fragaria vesca*). Nat. Genet. 43:109-118.

Sugimoto, T., K. Tamaki, J. Matsumoto, Y. Yamamoto, K. Shiwaku, and K. Watanabe. 2005. Detection of RAPD markers linked to the everbearing gene in Japanese cultivated strawberry. Plant Breeding. 124:498-501.

Van Dijk, T., Y. Noordijk, T. Dubos, M.C.A.M. Bink, B.J. Meulenbroek, R.G.F. Visser, and W.E. van de Weg. 2012. Microsatellite allele dose and configuration establishment (MADCE): an integrated approach for genetic studies in allopolyploids. BMC Plant Bio. 12:25.

Van Dijk, T., G. Pagliarani, A. Pikunova, Y. Noordijk, H. Yilmaz-Temel, B. Meulenbroek, R. Visser, and E. van de Weg. 2014. Genomic rearrangements and signatures of breeding in the allo-octoploid strawberry as revealed through an allele dose based SSR linkage map. BMC Plant Biology. 14(1):55.

Verma, S., N. Salinas, M. Mathey, U. Rosyara, J. Hancock, C. Finn, N. Bassil, M. Bink, I. Amaya, D. Sargent, B. Denoyes, V. Whitaker, C. Peace, A. Iezzoni, and E. van de Weg. 2015. QTL discovery and validation for SSC, TA and remontantity within RosBREED strawberry germplasm. 7th International Rosaceae Genomics Conference, WA. June 24-26, Seattle, WA.

Weebadde, C.K., D. Wang, C.E. Finn, K.S. Lewers, J.J. Luby, J. Bushakra, T.M Sjulin, and J.F. Hancock. 2008. Using a linkage mapping approach to identify QTL for remontantity in the octoploid strawberry. Mol. Plt. Breed. 127:94–101.

Whitaker, V.M. 2011. Applications of molecular markers in strawberry. J. Berry Res. 2:115–127.

Zorrilla-Fontanesi, Y., A. Cabeza, P. Dominguez, J.J. Medina, V. Valpuesta, B. Denoyes-Rothan, J.F. Sanchez-Sevilla, and I. Amaya. 2011. Quantitative trait loci and underlying candidate genes controlling agronomical and fruit quality traits in octoploid strawberry (*Fragaria ×ananassa*). Theor. Appl. Genet. 123:755-778.

Zorrilla-Fontanesi, Y., J.L.L. Rambla, A. Cabeza, J.J. Medina, J.F. Sanchez-Sevilla, V. Valpuesta, M.A. Botella, A. Granell, and I. Amaya. 2012. Genetic analysis of strawberry fruit aroma and identification of O-methyltransferase FaOMT as the locus controlling natural variation in mesifurane content. Plant Physiol. 159:851- 870.