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Changes in Morphological, Biochemical and Physiological Traits in Strawberry in the Northeastern United States During One Hundred Years of Breeding

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Abstract

Two of the more popular northeastern strawberry cultivars from each decade spanning 1891 – 2003 were obtained from various sources and grown in a common environment. Morphological, physiological and biochemical traits were measured in each cultivar to determine if directional changes have occurred through selective breeding over time. Fruit firmness, size, and fruit set increased over time, whereas soluble solids and leaf area ratio (LAR) decreased. Photosynthesis tended to become less efficient over time, while plant pigments showed no consistent change. Yields peaked in the 1980s and have remained somewhat constant for the past 30 years. For most traits, cultivars exhibited values midway between those of the progenitor species, suggesting that traits are partially heritable. *F. chiloensis* appears to have a more efficient photosynthetic apparatus than *F. virginiana*, so might be a good candidate for recurrent breeding. We suggest several approaches for productivity improvement including increasing fruit number per plant, modifying plant architecture and carbon allocation, improving carbon assimilation and increasing photosynthetic efficiency. Incorporating day neutrality into adapted cultivars also could have a significant impact on yield.

Evidence of strawberry cultivation can be found in literature dating back to the sixth century. The first systematic breeding of strawberries began in England in 1817 by Thomas A. Knight. Early American strawberry cultivars were selections of the small fruited species *F. virginiana*, known as the Scarlet strawberry, and at least 30 cultivars were available by 1820 (Jones, 1976). However, when the much larger fruited *F.* x *ananassa* cultivars from Europe were introduced into the United States, they quickly became the dominant strawberry grown and formed the basis of new American breeding programs (Hancock, 1999). Cultivars continued to be released in the early part of the 20th century such as 'Dunlap', 'Klondike', 'Howard 17' and 'Aberdeen,' all of which played an important role in the growing American strawberry industry (Darrow, 1966). During the early stages of cultivar development improvement in fruit size was a priority, but increasingly, characteristics such as disease resistance and fruit quality (i.e. flavor, firmness, color) were also considered. By the early 1900s, breeders were focused on developing cultivars for a particular region; this regional focus on cultivar development continues today.

We were interested in the changes that occurred in strawberry cultivars over the past 100 years of breeding in the northeastern United States (US). One might assume that yield, fruit size and quality have improved as older cultivars have been replaced with newer, but little is known about the basis for this improvement, especially changes in the plant's biochemistry and physiology that might be related to improved performance. The objective of this study was to evaluate

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the more popular cultivars that have been released in the northeastern U.S. over the past century, identify morphological, physiological and/or biochemical changes over time, and determine if any traits might be related to changes in performance. By identifying possible factors associated with growth and yield, new strategies might be identified to improve cultivar performance.

Materials and Methods

Greenhouse trial. Twenty strawberry (*F.* x *ananassa*) cultivars (Table 1) and one representative genotype of each of the progenitor species, *F. chiloensis* (PI551455) and *F. virginiana* (PI612495), were obtained from various commercial nurseries or from the National Germplasm Repository (Corvallis, OR) during spring 2005. Plants were set into a greenhouse mist bed where they were deflowered and derunnered. Over the next several months stolons were transplanted into 4-L pots filled with 1:2:1 (perlite:peat:vermiculite). Transplants were placed in a greenhouse under supplemental high pressure sodium lights to facilitate establishment. Average light levels were 500 μmol $m^{-2}s^{-1}$ with day/night temperature of 23/18°C. Once a sufficient number of plants was obtained, cultivars were arranged on benches in a randomized complete block design with four blocks and six plants in each experimental unit. Plants from the greenhouse were used to assess leaf pigments and certain photosynthetic variables.

Field trial. Plants from the greenhouse trial were cold acclimated at the end of 2005 and placed in a cooler for 6 weeks to meet chilling requirements. In May 2006 these potted plants were transplanted into the field in Ithaca, NY (Lat. 42.4N, Long. 76.5W). The trial was set up in a randomized com-

Table 1. Cultivar name, date of release, parentage and breeding program of 20 strawberry cultivars. Cultivar names followed by * indicate selections used in carotenoid analysis.

Cultivar	Release date	Parentage	Origin
Royal Sovereign*	1891	Noble x King of the Earliest	United Kingdom
Marshall	1893	American selection of unknown pedigree	Massachusetts
Dunlap*	1900	Likely Cresent x Cumberland	Illinois
Klondike*	1901	Pickerproof x Hoffman	Louisiana
Aberdeen*	1924	Likely Late Stevens x Chesapeake	NewJersey
Blakemore	1929	Missionary x Howard 17	Maryland
Fairfax*	1933	Royal Sovereign x Howard 17	Maryland
Sparkle*	1942	Fairfax x Aberdeen	New Jersey
Jerseybelle*	1955	NJ953 x NJ925	New Jersey
Surecrop	1956	Fairland x USMD1972	Maryland
Raritan*	1968	Redglow x Jerseybelle	New Jersey
Guardian*	1969	NC1768 x Surecrop	Maryland
Earliglow	1975	MDUS2359 (Fairland x Midland)	Maryland
Honeoye*	1979	Vibrant x Holiday	New York
Allstar	1981	US4419 x (NCUS1768 x Surecrop)	Maryland
Jewel*	1985	NY1221 x Holiday	New York
Northeaster*	1993	MDUS4380 x Holiday	Maryland
Cabot	1999	K87-5 x K86-19	Nova Scotia
L'Amour*	2003	(MDUS5252 x Etna) x Cavendish	New York
Ovation	2003	Lateglow x Etna	Maryland

plete block design with four replications and six plants in each experimental unit.

Photosynthesis. Simultaneous gas exchange and light adapted chlorophyll fluorescence data were collected using the LICOR 6400 gas analyzer with a fluorescence head attachment (LICOR, Lincoln, NE). Data were collected on a recently expanded leaf between the hours of 10:00 and 14:00. Light levels in the chamber were set to match ambient conditions for each trial; for the greenhouse trial light was set at 500 mmol PAR m^{-2} s^{-1} and the field trial at 1500 mmol PAR $m^{-2} \cdot s^{-1}$.

Chlorophyll Fluorescence. Chlorophyll fluorescence was measured using a LI-COR 6400 infrared gas analyzer with a chlorophyll fluorescence head attached to allow simultaneous gas exchange and fluorescence measurements. Measurements were made under full sunlight at noon to attain the steady state fluorescence of leaves adapted to ambient light conditions and again when exposed to a supersaturating pulse of light. The proportion of light absorbed by photosystem II (PSII) that is used in photochemistry is expressed as Φ_{PSII}, a measure of the rate of linear electron transport that reflects overall photosynthesis. Ambient fluorescence minus dark-adapted fluorescence divided by saturated fluorescence (Fv'/Fm') is a measure of the maximum quantum yield of PSII when all reaction sites are open.

Carotenoid/chlorophyll content. A subset from the greenhouse trial of 12 cultivars and one genotype of *F. chiloensis* and *F. virginiana* were used for pigment analysis. Leaf discs were collected between 11:00-13:00 from the center leaflet of the last fully expanded leaf, weighed and placed in liquid N_2. Pigments were extracted under low light from 50-100 mg of leaf tissue. Tetrahydrofuran and methanol (MeOH) were used as solvents with butylated hydroxytoluene as an antioxidant. Pigments were then transferred to ether via phase partitioning, the ether removed *in vacuo*, and the extract resuspended in MeOH/methyl t-butyl ether (1:1). HPLC was performed with an ASI-100 automated sample injector linked to a P680 HPLC pump and a PDA-100 photodiode array detector (Dionex Corp., Sunnyvale, CA). Pigments were eluted from a C30 reverse-phase column (Waters Inc., Milford, MA) via a linear solvent gradient (20 min) consisting of ammonium-acetate in MeOH (1 $g \cdot L^{-1}$) and methyl t-butyl ether.

Growth analysis. Flower counts were recorded on three plants in every field plot during the spring of 2007. After harvest, three plants per plot were excavated from the field and used for destructive growth analysis. Plants were washed and separated into individual growth components (leaves, crown, roots) then dried at 75°C for 3 days to a constant weight before recording. Leaf area was measured on all plants with a leaf area meter (Model 3000, LICOR Inc., Lincoln, NE) before drying leaves. Leaf area ratio (LAR) was calculated by dividing leaf area by the dry weight of the plant at harvest.

Fruit quality. Subsamples of 10 primary fruits from each plot were collected during the fruiting period and used to measure berry firmness using a Wagner Force Rive FDV-30 force gauge (Wagner Instruments, Greenwich, CT) with a 15 mm tip. Twenty g subsamples of fruit were collected during the fruiting period to measure soluble solids with a digital refractometer (ATAGO USA Inc., Bellevue, WA).

Anthocyanins and phenolics. Whole fruits were extracted in 80% methanol and 0.2% folic acid buffer solution. Total anthocyanins were measured using the pH differential method and total phenolics were measured using the Folin-Ciocalteu procedure (Singleton et al., 1999). All samples were analyzed in triplicate.

Fruit yield. All fruit was harvested from each plot twice per week during the harvest season and weighed. Marketable and unmarketable fruit were weighed separately. A random subsample of 1-L per plot was counted and this number was

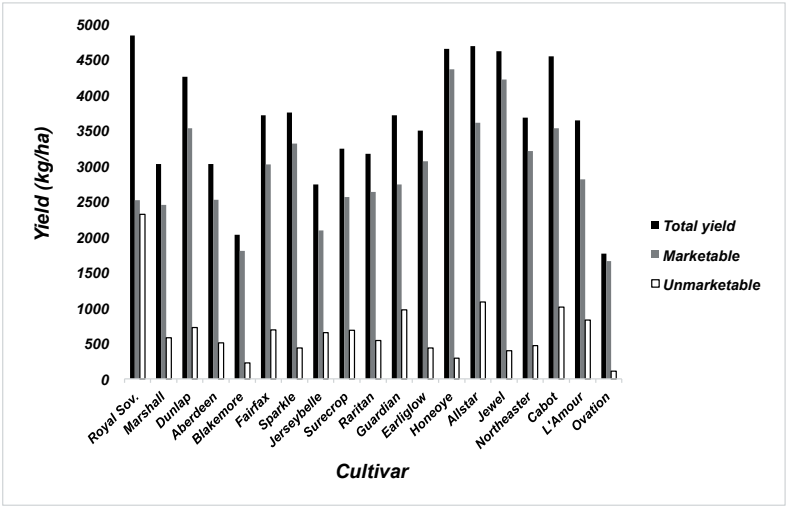

Fig. 1. Total, marketable and unmarketable (5 g or less or misshapen fruit) of 20 cultivars released over the last century. Cultivars listed in order of release date. Standard errors: total = 390; marketable = 380; unmarketable = 129.

divided into total fresh weight to determine average individual fresh fruit weight.

Results

Total, marketable and unmarketable yield were highly variable across cultivars; however, there was no significant correlation between yield and decade of release. Cultivars released in the 1970s and 1980s had the highest marketable yields (Fig. 1). Although there were no significant trends in yield, average weight of both primary fruit and lower order fruit (2º, 3º and 4º) increased over time (Fig. 2) whereas average fruit number per plant decreased (Fig. 3).

Fruit firmness increased significantly with year of release with current cultivars being almost 50% firmer than those released in the

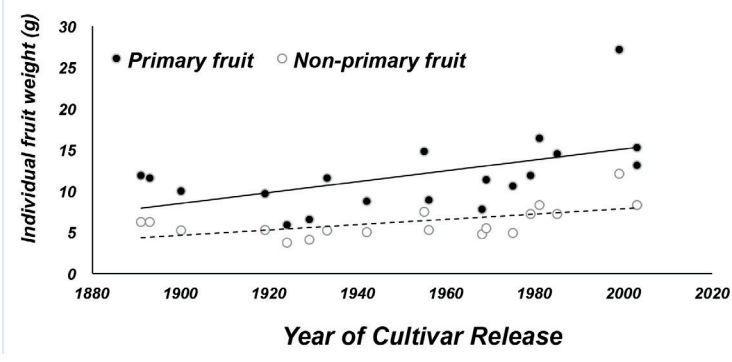

Fig. 2. Average individual fruit weight of primary (king, 1º) vs. 2º, 3º, and 4º berries.
Regression equations: Primary berry, y=106.3+0.0606*Year (r=0.41, p<0.0001); 2º, 3º, 4º y=-57.3 + 0.033*Year (r=0.54, p<0.0001)

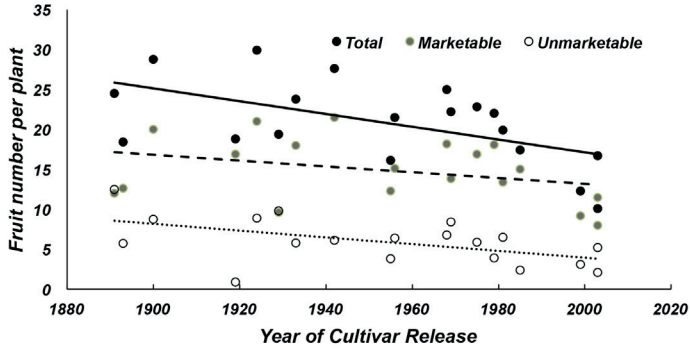

Fig. 3. Average total, marketable and unmarketable (<5g or misshapen) fruit number per plant for 20 cultivars grown in a matted row field trial in Ithaca, NY regressed against year of cultivar release. Regression equations: Total, y= 150 - 0.067*Year (r=-0.37, p=0.004), solid line; Marketable = 82.2 - 0.035*Year (r=-0.22, p=0.04), dashed line; Unmarketable, y= 64.2 - 0.03*Year (r=-0.37, p=0.004), dotted line.

early 1900s (Fig. 4A). Average percent soluble solids decreased slightly over time from approximately 8.7% to 7.6% (Fig. 4B).

Anthocyanin content ($mg \cdot g^{-1}$ fruit fresh weight) varied almost three fold from the lowest in 'Klondike' (25 mg/100 g) to the highest in 'Northeaster' (72 mg/100 g). Phenolic content also varied between cultivars with the lowest value of 224 mg/100 g observed in 'Cabot' to a high of 409 mg/100 g in 'Aberdeen' (Table 2). There were no significant trends over release year in either anthocyanin content or phenolic content, except for leutin.

Cultivars increased in total dry matter accumulation over time, primarily due to increased crown dry weight and a slight increase in root dry weight (Fig. 5). There was no significant change in leaf dry weight or leaf area observed in our study, no significant correlations between growth characteristics and yield, but Leaf Area Ratio (LAR) significantly decreased over time (Fig. 6).

In both the greenhouse and field trial, there was no difference in the rate of photosynthesis on a leaf area basis among the cultivars

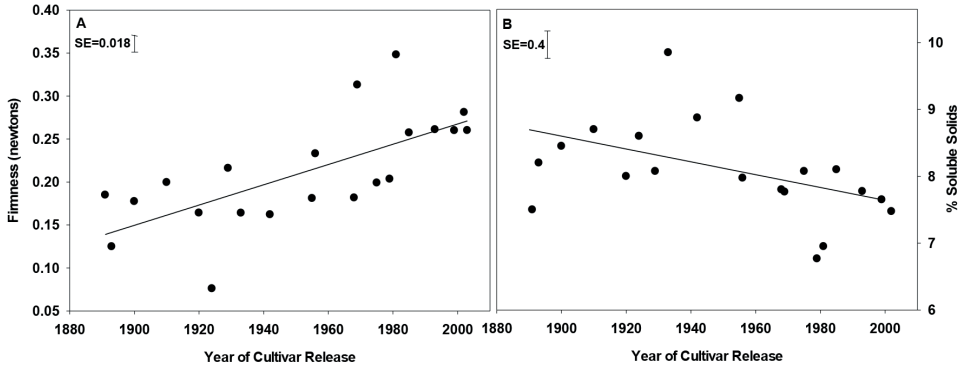

Fig. 4. Fruit firmness (newtons) and °Brix value of strawberry cultivars released over the last century. Points indicate mean of 20 berries. Regression equations: Firmness=-2.09 + 0.0012*Year (r=0.69; p=0.0006); Brix =26.84 - 0.0096*Year (r=-0.33, p=0.003).

Table 2. Anthocyanin and phenolic content (expressed in mg 3-phenyl-glucoside equivalents) of field-grown fruit from 20 cultivars and two progenitor species representing a range of release dates (FW=fresh weight).

Cultivar	Release Date	Anthocyanins (mg/100g FW)	Phenolics (mg 3-P-glu/100g FW)
Royal Sovereign	1891	27	225
Marshall	1893	60	278
Dunlap	1900	53	318
Klondike	1901	25	343
Aberedeen	1924	39	409
Blakemore	1929	29	265
Fairfax	1933	45	253
Sparkle	1942	69	275
Jerseybelle	1955	66	271
Surecrop	1956	57	345
Raritan	1968	46	308
Guardian	1969	42	350
Earliglow	1975	59	380
Honeoye	1979	59	326
Allstar	1981	32	305
Jewel	1985	62	301
Northeaster	1993	72	317
Cabot	1999	52	224
L'Amour	2003	36	266
Ovation	2003	37	341
SE		3	24
p-value		<0.0001	<0.0001
r-value		-0.32 (NS)	0.25 (NS)

(Fig. 7). Due to the higher light levels in the field during peak fruiting, A_{CO2} and g_s were higher compared to the greenhouse (Fig. 8). The mean of the cultivars in the greenhouse (14.1 µmol CO_2 $m^{-2} \cdot s^{-1}$) was intermediate to the photosynthetic rates of the progenitor species; *F. virginiana* (11.6 µmol CO_2 $m^{-2} \cdot s^{-1}$) and *F. chiloensis* (17.8 µmol CO_2 $m^{-2} \cdot s^{-1}$). In the field trial, photosynthetic data were collected at three phenological stages; flowering (11 May), peak fruiting (15 June) and late fruiting (31 June). The highest rates of A_{CO2}, g_s and ΦPSII (effective quantum yield of PSII) occurred during the peak fruiting stage. There was a trend of decreasing A_{CO2}, g_s, and ΦPSII with cultivars released over time (Fig. 7), but trends were not significant.

Regression analysis of the light-adapted fluorescence data indicates that there has been a decrease of 5% in the Fv'/Fm' over the last century of breeding as measured in the greenhouse (Fig. 8C). Initial mean Fv'/Fm' for the early cultivars (0.68) was intermediate to the two progenitor species; *F. chiloensis* (0.72) and *F. virginiana* (0.62) (Fig. 9C). Φ_{PSII} also decreased by 10% during the last century (Fig. 8D). Again, initial rates were intermediate to the progenitor species; *F. chiloensis* (0.61) and *F. virginiana* (0.50) and have become more similar to *F. virginiana*. α-carotene, β-carotene, zeaxanthin and violaxanthin levels of the cultivars have

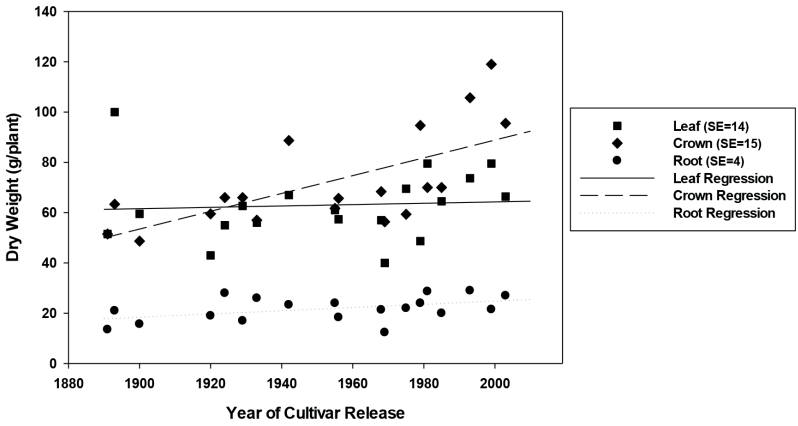

Fig. 5. Leaf, crown and root dry weights per plant of 20 strawberry cultivars grown in matted row field trial and regressed against year of cultivar release. Regression equations: Leaf (NS); Crown = -619 + 0.35*Year (r=0.45, p=0.0005); Root= -103 + 0.064*Year (r=0.28, p=0.03).

not changed directionally over time and are intermediate to the progenitor species that were evaluated (Table 3). The total amount of chlorophyll (a+b) on a leaf area basis is also intermediate to the progenitor species.

Discussion

Many cultivars have been released over the years in the northeastern United States with the goal of producing a higher yielding cultivar with superior fruit quality. However, data from this study suggest that there has been limited progress for several traits, particularly over the last three decades.

Fruit traits. Total, marketable and unmarketable yield were highly variable among cultivars grown under identical conditions and there were no significant trends over the last century (Fig. 1). This is consistent with New York census data (USDA, National Ag.

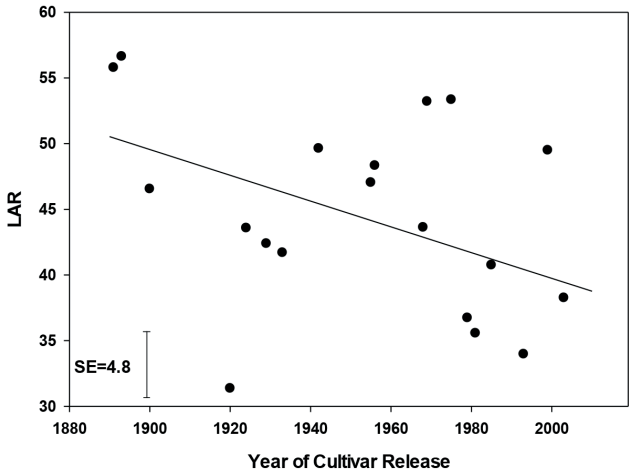

Fig. 6. Leaf area ratio (LAR= leaf area/plant dry weight) of 20 cultivars regressed against year of cultivar release. Regression equations: LAR= 236 - 0.098*Year (r=-0.36, p<0.01)

Table 3. Leaf chlorophyll and carotenoid content of greenhouse-grown fruit from 12 cultivars and two progenitor species representing a range of release dates.

Cultivar	Release Date	Chl A (g/cm^2)	Chl B (g/cm^2)	Chl A:B	α-carotene (mg/m^2)	β-carotene (mg/m^2)	Zeaxanthin (mg/m^2)	Violaxanthin (mg/m^2)	Leutin (mg/m^2)
Royal Sovereign	1890	44.8	12.4	3.6	87.8	1250	88.8	56.3	1136
Marshall	1893	39.9	10.7	3.6	79.5	1082	65.1	33.3	1090
Dunlap	1900	42.9	12.1	3.6	75.1	1154	63.7	45.8	1101
Aberdeen	1924	35.1	9.4	3.4	79.0	1059	81.8	44.0	1090
Fairfax	1933	48.6	14.1	3.5	91.5	1287	40.2	26.5	1366
Sparkle	1942	42.8	12.2	3.6	87.3	1215	52.9	36.4	1224
Jerseybelle	1955	46.3	13.6	3.6	102.2	1297	52.9	37.5	1400
Raritan	1968	44.9	12.2	3.6	81.7	1224	79.1	47.3	1252
Honeoye	1979	49.5	13.6	3.7	98.5	1356	64.7	54.0	1467
Jewel	1985	39.7	11.6	3.3	77.4	1126	78.7	47.0	1267
Northeaster	1993	50.3	15.1	3.0	96.2	1373	54.4	35.2	1548
L'Amour	2003	45.3	13.0	3.5	87.9	1226	72.8	42.5	1336
F. chiloensis		72.7	19.9	3.7	146.3	2113	68.6	44.0	1750
F. virginiana		31.3	9.3	2.8	57.3	853	111.8	66.7	884
SE		2.8	1.1	0.25	6.7	79.2	11.6	8	78.8
p-value		0.0083*	0.0189*	NS	<0.0001	<0.0001	0.0092	NS	<0.0001
r-value		0.41	0.48	-0.43	0.40	0.47	-0.10	0.07	0.77

[1] Significant linear regression over time ($p<0.001$).

Stat. Svc., New York) showing relatively stable yield per unit area over the past three decades. In fact, yield per ha in 2015 was almost identical to yield per ha in 1998. The highest marketable yields in our study were for 'Honeoye' (released in 1979), 'Allstar' (released in 1981) and 'Jewel' (released in 1985), three cultivars which continue to be widely planted in the northeastern U.S. This lack of yield improvement is in contrast to national strawberry yield averages which have increased steadily over the same period of time. The national average is heavily influenced by California and Florida which have benefited from the conversion to an annual production system and the introduction of day neutral cultivars in the mid-1980s (Pollack and Perez, 2005).

Although the overall yield of northeastern cultivars appears to have reached a threshold for short-day plants, significant changes in fruit size occurred during the last century of breeding. The average fruit size of both the primary and lower order berries steadily increased (Fig. 2); however, this has been accompanied by a reduction in fruit number per plant (Fig. 3). Fruit set also significantly increased over time as flower number decreased more (-50%) than the reduction in fruit number (-18%) per plant. Increases in fruit size can contribute to increased yield but will require a stable or increase in fruit number as well (Lacey, 1973). Yield increases based on fruit size have occurred in tomato (Grandillo et al., 1999) and several grain crops (Feil, 1992). Western strawberry cultivars are a potential source of greater individual fruit weight (Hancock et al., 1992).

The most pronounced change over time was fruit firmness. Increasing firmness was driven by market demand and does not seem to be related to any other physiological variable. Percent soluble solids decreased slightly over time (Fig. 4), but this variable is highly influenced by the environment so trends may not represent genetic changes. A study of Italian cultivars showed a negative relationship between soluble solids and productivity (Faedi et al., 2002). Heritability studies on California strawberry cultivars showed that the selection response for soluble solids is highly affected by the environment the selection occurs in, but it is possible to select for higher content (Shaw, 1990). The reduction in soluble solids observed over time may be due to a dilution effect of an increase in fruit size with the newer cultivars, although it is clearly possible to simultaneously achieve large fruit size and high soluble solids (e.g. 'Albion', 'Chandler'). Weather plays a role in soluble solids content, so this modest trend may not reflect a true genetic change in strawberry soluble solids content.

The health components of fruit are becoming increasingly important to consumers, but most of these components have not been intentionally selected. A large variation in biochemical constituents was observed between cultivars, with an almost three-fold difference in anthocyanin content and almost two-fold difference in the phenolic content of the fruit. Previous studies indicate that cultivar can have a large influence on the content of phenolics and anthocyanins (Heinonen et al., 1998; Maas et al., 1991). However, these differences were not related to year of cultivar release. Previous work suggests that the composition of the specific compounds in cultivars is significantly different from the progenitor species (Aharoni et al., 2004) suggesting that some of this difference could be genetic. Additional analysis of metabolite profiles in the cultivars may elucidate changes in composition that have occurred over time.

Physiological Traits. Several crops which have undergone selective breeding have shown significant increases in yield; soybean (*Glycine max)* with 0.5-0.9% per year (Luedders, 1977), sorghum (*Sorghum bicolor* L.) with 1-2% per year (1950-1980) (Miller and Kebede, 1984), maize 1.4% per year (1930-1980) (Duvick, 1984), white clover (*Trifolium repens*) 0.6% per year (1930-1990) (Woodfield and Carandus, 1994) and tomatoes with 1.5% per year (Grandillo et al.,

1999). Similar trends have not occurred for northeastern strawberries despite many new cultivars being released. An expectation that direct-marketed northeastern cultivars will have high flavor may constrain significant yield improvement.

One possible avenue to increase yield is to improve canopy architecture and carbon partitioning. Optimal canopy architecture for light interception and carbon partitioning has been correlated with significant yield improvements in several other crops (Duncan et al., 1978; Duvick and Cassman, 1999; Feil, 1992; Irvine, 1975) although a dense plant canopy can result in greater disease pressure as well as greater interleaf shading within the canopy. Research on strawberry canopy characteristics showed large variability in dry matter partitioning between cultivars grown in a matted row (Strik and Proctor, 1988b). Studies investigating correlations between carbon allocation and yield also showed variable results. For example, a negative correlation was observed between yield and leaf number (Lacey, 1973), a positive correlation between leaf dry weight and leaf area in the fall with yield (Strik and Proctor, 1988c) and a positive correlation between crown dry weight and yield (Strik and Proctor, 1988a; Strik and Proctor, 1988b). Based on previous studies and the results of the current study, there has been no consistent change in canopy architecture or carbon partitioning suggesting that there has not been a focused effort to breed strawberry plants for a particular canopy architecture. This is in contrast to many crops that have shown significant increases in yield through changing plant architecture and carbon allocation patterns (Feil, 1992).

Yield and plant size also might be influenced by more efficient photosynthetic processes. The efficiency of PSII decreased over time, but only the results in the greenhouse were significant. The cultivated strawberry has photosynthetic rates that are intermediate to the progenitor species, *F. chiloensis* and *F. virginiana*, suggesting that these rates are heritable. Breeding studies also showed that the high photosynthetic characteristics of *F. chiloensis* may be quantitatively inherited (Hancock et al., 1989). Intentionally breeding for enhanced photosynthetic capacity or efficiency may be another route to improve yield of the cultivated strawberry, perhaps by incorporating more *F. chiloensis* genes into progeny.

Results from the greenhouse study showed that cultivars have maintained A_{CO2} rates that are intermediate to the two progenitor species (*F. chiloensis* and *F. virginiana*), similar to results of previous studies (Hancock, 1999; Hancock et al., 1989; Hancock et al,. 2002; Sedat et al., 1989). However, Hancock et al. (1992) found no relationship between CO_2 assimilation and yield in 34 strawberry cultivars. Other studies showed no correlation between yield and A_{CO2} (Evans, 1993). Similar observations in other crop species have led to the hypothesis that most crops are sink limited and that increasing A_{CO2} will not lead to increased yield. However, the relationship between carbon assimilation and dry matter production cannot be ignored. Dry weight accumulation of crops is related to the absolute amount of light intercepted by green foliage (Monteith and Moss, 1977); however, the effect that this has on yield is complicated by factors such as partitioning, interleaf shading, pest and disease pressure and respiration. Long et al. (2006) suggests that as photosynthesis is influenced by morphological characteristics, the potential influence that A_{CO2} has on yield may be masked by differing plant characteristics, particularly leaf area and canopy density.

Evidence that the strawberry plant also may be sink-limited is the observation that photosynthetic rates did not change significantly or slightly decreased over a century of breeding (Fig. 8 and 9) despite an increase in crown and root dry weight and a decrease in LAR (Fig. 7). If strawberry plants are source-limited, then photosynthetic rates per unit of leaf area would be expected to increase with a relative reduction in leaf area (LAR).

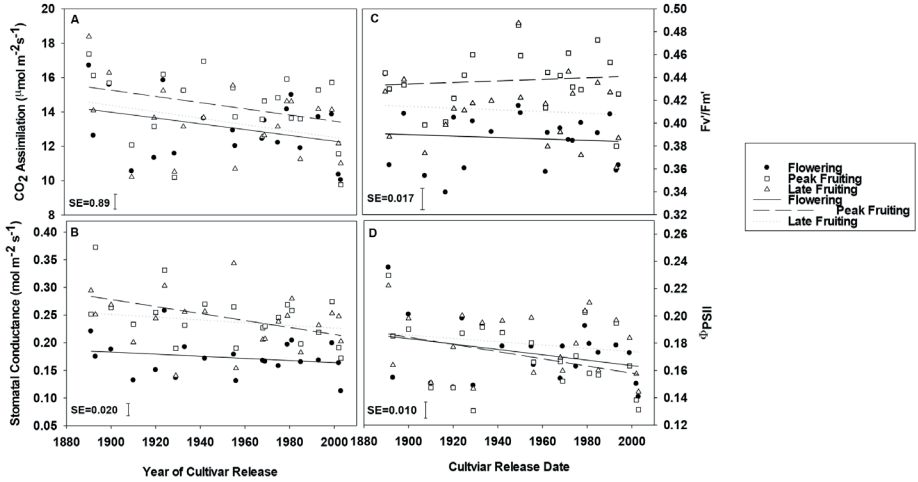

Fig. 7. Maximum CO_2 assimilation rates (A), stomatal conductance (B), Fv'/Fm' (C) and PSII efficiency (D) measured in the field on three dates for 20 cultivars and regressed against year of release. 1) Flowering (15 May 2008), 2) Peak Fruiting (11 June 2008) and 3) Late Fruiting (30 June 2008). Light level in chamber was 1500 µmol PFD $m^{-2}s^{-1}$. Regressions were not significant.

In the greenhouse trial, the progenitor species *F. chiloensis* had significantly higher rates of photosynthesis, higher photosynthetic efficiency Fv'/Fm' (Fig.), higher amounts of chlorophyll and lower xanthophyll content. *F. virginiana* had rates that were lower than cultivars with decreasing Fv'/Fm' and ΦPSII in cultivars over time. The results of

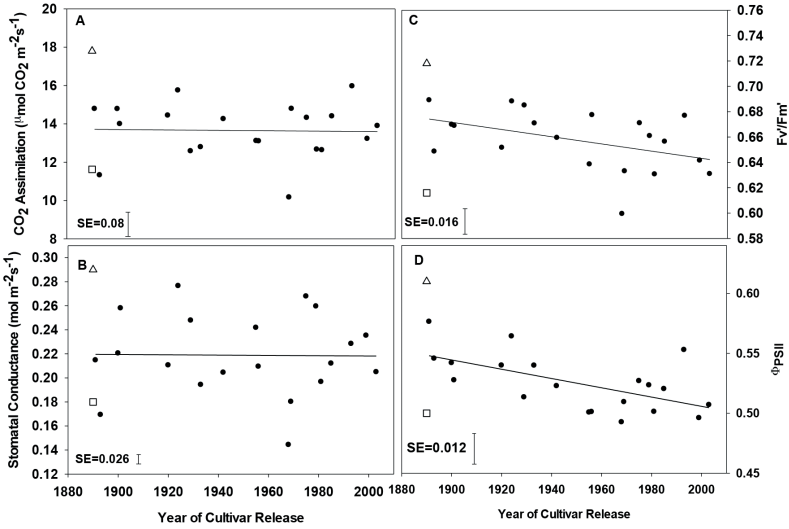

Fig. 8. Photosynthetic characteristics of greenhouse grown cultivars (mean of 6 points for each cultivar) and the progenitor species; *F. chiloensis* (open triangle) and *F. virginana* (open square) regressed against release date. CO_2 assimilation (A); stomatal conductance (B); Fv'/Fm' (C); PSII efficiency (D). Regression equations: Fv'/Fm' = 1.21 - 0.00028*Year (r=-0.39, P<0.002); **Φ**PSII = 0.23 - 0.00036*Year (r=-0.39, p<0.003).

this study suggest that *F. chiloensis* appears to have higher photosynthetic capacity and may provide a source for increasing carbon accumulation and yield of the cultivated strawberry. Serce et al (2002) also found that *F. chiloensis* genotypes have a higher assimilation rate than those of *F. virginiana*, but the former were affected more negatively when temperature increased. Such a response will make breeding for increased season long photosynthetic capacity difficult in a changing environment with warmer temperatures.

One of the major differences between strawberry production in California and Florida compared to the Northeast is the widespread use of day neutral cultivars and annual production systems. The development of improved day neutral cultivars that are well suited to the Northeast will contribute to increasing yield potential there.

Incorporation of new germplasm into the breeding stock will be an important component to improve both yield potential and fruit quality for northeastern strawberry cultivars by introducing traits such as high carbon assimilation and optimized partitioning, day neutrality, fruit number and improved fruit quality. Several studies (Dale and Sjulin, 1990; Hancock et al., 2002; Sjulin and Dale, 1987) have demonstrated that the genetic variability in the cultivated strawberry is narrow. Although there are a few breeding programs that have used wild species, the majority of programs rely on germplasm from *F.* x *ananassa* (Faedi and Coman, 2002). Introduction of new germplasm also will be important as growers are facing increasing challenges in dealing with increasingly variable environmental conditions.

Our study suggests several avenues might be available for productivity improvement including increasing fruit number per plant while maintaining fruit size, increasing fruit size while maintaining fruit numbers, modifying plant architecture and carbon allocation, improving carbon assimilation, and increasing photosynthetic efficiency. Incorporating day neutrality into adapted cultivars also could have a significant impact on yield. Increasing yield while maintaining the high flavor expectations for northeastern cultivars will be a significant challenge for breeders, particularly as temperatures warm.

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Correction

In volume 70(2), in the article by Hyun-Kil Jo[1], Jin-Young Kim[2*] and Hye-Mi Park[2] "Effects of pear orchards on carbon reduction", the following two additional footnotes were mistakenly omitted at the bottom of page 63:

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Also, the footnote for Table 2 on page 67 should have been (the same with Table 3 and Fig. 3) (rather than Table 6 and Fig. 2 as shown)