Performance of Californian and Eastern U.S. Strawberry Cultivars under Conditions Mimicking Eastern Production Systems

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Abstract. Twenty-one western and 13 eastern strawberry [*Fragaria* × *ananassa* (Duch.)] cultivars were grown in a polyethylene-covered greenhouse (polyhouse) in deep beds at either 10 × 10 or 25 × 25 cm spacing. Runners were removed weekly from the closest-spaced plants (hills), and the more open-spaced plants were allowed to set four runners on each side of the mother plant before the runners were removed (matted rows). Temperatures were allowed to fluctuate normally in the polyhouse, except that winter temperatures were maintained above 0°C. The average yield of eastern and western cultivars did not differ significantly in most comparisons, but the average fruit weight of the Californian cultivars was significantly higher than the eastern ones, and Californian cultivars allocated a higher proportion of their biomass to reproduction. Nonbearing plants of eastern and western cultivars produced similar numbers of runners per plant and daughters per runner. There was no significant relationship between CO₂ assimilation rate and yield. Interbreeding eastern cultivars with the most productive western genotypes might result in increased yields, but only if the higher reproductive efforts of the western types can be captured and transferred.

Strawberry yields in California are much higher than those found anywhere else in the United States. Commercial fields in California average > 55 t·ha⁻¹, while yields outside of California rarely exceed 20 t·ha⁻¹ (Bringhurst and Voth, 1990; Hancock and Scott, 1989). The traditional reason given for this difference in productivity is climatic variation (Galletta and Himelrick, 1990). The production regions in California have what is considered to be an ideal mediterranean climate, with cool nights, moderate day temperatures, and infrequent rain during harvest. Southern producers have problems with fluctuating winter temperatures and hot, moist summers that encourage fungal growth. Producers in the Pacific Northwest have a moderate climate, but average daily temperatures are considerably lower than for California, and rainfall is frequent during the fruit season. Midwestern and eastern producers must tolerate damage from frost and cold, and they also have a hot, humid summer. In short, growers outside of California must deal with many more environmental extremes than those within the state.

California breeders may also have concentrated more of their effort on yield and fruit size than other breeders, because their climatic and disease problems are more limited. Breeders in other areas have had to pay closer attention to abiotic stresses and disease resistances, and as a result breeders have had to be less concerned with maximum yield capacity. High yield and disease resistance are important in all areas, but environmental realities set priorities; particularly because it is very difficult to select for improvement in more than a few traits at one time (Bringhurst and Voth, 1984; Galletta et al., 1989).

Sjulin and Dale (1989) showed that the genetic backgrounds of the cultivars grown in different parts of the United States are generally distinct, and those from California produce a unique cluster. Californian types contain a much higher proportion of their genome from the founding clones 'Nich Ohmer' and 'Marshall', and may have higher proportions of genes from *Fragaria*

chiloensis (L.) Duch. (Bringhurst and Voth, 1984). *Fragaria chiloensis* has higher rates of CO₂ assimilation than other species (Cameron and Hartley, 1990; Hancock et al., 1989), and some of its populations have very high reproductive capacity (Hancock and Bringhurst, 1988).

Because of the high yields and large fruit size of Californian cultivars, North American strawberry breeders have become increasingly interested in incorporating more Californian germplasm into their breeding populations. Part of this interest has been stimulated by the success of the new day-neutral cultivars from California, but the short-day types also hold genetic promise. Unfortunately, Californian and eastern cultivars usually cannot be placed together in the field to directly measure their yield potentials because their temperature tolerances are so different. The experiments conducted here were intended to simulate eastern conditions, with the qualification that confounding consequences of very low temperatures were avoided.

Materials and Methods

To make a common garden comparison, we set up an artificial environment in which winter temperatures were maintained >0°C but otherwise mimicked eastern conditions. Six plywood frames were constructed on the floor of a greenhouse in East Lansing Mich. in Spring 1988 (Fig. 1). Their external dimensions were 1 × 1 × 50 m, and they were filled with a commercially purchased sand loam soil. A Gramm drip irrigation system (MacKenzie Nursery Supply, Perry, Ohio) with 12.5-cm rings was installed around each plant.

Dormant runner plants of 21 Californian and 13 eastern cultivars were provided as gifts from R.S. Bringhurst and G.J. Galletta, respectively. They were planted in the greenhouse on 15 Apr. 1988, and all flowers were removed as they appeared. The plants were set in double, offset rows in a split-plot design at either 10 × 10 or 25 × 25 cm spacing with four replications. Runners were removed weekly from the closer-spaced plants (hills), and the open-spaced plants were allowed to set four runner plants at each side of the mother plant before runners were removed (matted rows). The temperatures in the green-

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Abbreviations: A, CO₂ assimilation rates; b, regression coefficients.

Fig. 1. Picture of polyhouse showing beds where strawberries were grown.

house were allowed to fluctuate normally, except that they always were $>0^{\circ}\text{C}$. Summer temperatures ranged from 15 to 35°C and winter temperatures from 0 to 5°C .

In the first bearing year, a hive of honey bees was placed in the greenhouse during bloom. Ripe fruit (75% red) were picked every 5 days, counted, and weighed. After the harvest season, four of the five highest-yielding Californian and eastern cultivars were selected for further study and the other plants were removed from the planting. Although 'Midway' and 'Tahoe' had some of the highest yields, they were removed because a block of each had died of unknown causes. Runners were removed in this experiment biweekly.

Flowers were hand-pollinated in the next bearing year to assure maximum fruit set. This was done by rubbing all open flowers every 3 days with a camel-hair brush. Ripe fruit were again picked every 5 days, counted, and weighed. Twenty-five fruit from each plant were also dried at 50°C for 1 week, then weighed.

At the conclusion of fruiting, individual leaf areas were determined for 10 randomly selected leaves from each plant, and the total number of leaves per plant was counted. Total leaf surface area per plant was estimated by multiplying the average individual leaf area by total leaf count. The number of branch crowns was also counted on each plant, and the aboveground biomass was determined by drying at 50°C for 1 week. Reproductive success was estimated by dividing total dry fruit weight by the total aboveground biomass.

To measure the asexual reproductive potential of the selected cultivars, dormant runners were set in the beds in Spring 1990. Five plants of each cultivar were planted in a completely randomized design in the spaces left from the previous plant eliminations. All flowers were removed from the plants, but they were allowed to runner freely. In October, all branch crowns

and runners on each plant were counted, and the number of daughter plants per stolon was determined. The mother plant and its runners were then separated from each other and dried for 7 days at 50°C before being weighed. For ease of discussion, we will refer to these individuals as "nonbearing plants," while the fruited ones will be called "bearing plants."

Carbon dioxide assimilation rates (A) were determined on the 1- and 3-year-old plants on 12 Mar., 8 May, and 15 July 1990, using an Analytical Development Company portable photosynthesis system (Hoddesdon, England). These dates represented the midbloom, midharvest and runnering stages of development in the older plants. The newly set plants were not allowed to flower, but they were actively runnering by the final date. We determined A on two to three fully expanded leaves at the top of the canopy under conditions that would assure maximum A (photosynthetically active radiation $> 1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, at $22\text{--}28^{\circ}\text{C}$, Vapor pressure deficit (VPD) $< 2.5 \text{ KPa}$). The gas exchange characteristics were calculated according to Moon and Flore (1986).

Patterns of yield and dry matter accumulation were analyzed using analysis of variation techniques and least significant difference analysis (Sokal and Rolf, 1978). Regression coefficients (b) were used to estimate photosynthetic stability across seasons (Hancock, 1985; Hancock et al., 1989). Mean values for A were calculated for individual cultivars (cultivar mean) and for all cultivars on each sample date (environmental mean). The cultivar means were then regressed on the environmental means to obtain a b value.

Results

Bearing plants. The average yield of the eastern and western cultivars did not differ significantly in the first bearing year (Table 1). Californian and eastern cultivars averaged, respectively, 234 and 235 g/plant in matted rows and 583 and 614 g/plant in hills. 'Tioga', 'Chandler', 'Lassen', 'Tahoe', 'Midland', and 'Guardian' were the highest producers in matted rows (Fig. 2), while 'Lassen' and 'Oso Grande' were the highest yielders in hills (Fig. 3).

In the second bearing year, the Californian types had significantly higher average yields in matted rows, (331 vs. 287 g/plant) but not in hills (Tables 2 and 3). 'Lassen', 'Tioga', 'Chandler', and 'Guardian' were the highest producers in matted rows, while 'Lassen' had the highest yield in hills.

The average fruit weight of the Californian cultivars was significantly higher than that of the eastern ones in both years (Table 1), and the largest-fruited types were from California (Fig. 2; Tables 2 and 3). In the first bearing year, Californian and eastern cultivars averaged 12.2 vs. 8.9 g/fruit in matted rows and 12.6 vs. 9.3 g/fruit in hills. 'Pajaro' and 'Oso Grande' had the largest fruit in hills, while 'Pajaro' and 'Toro' had the largest fruit in matted rows. In the 2nd year, Californian and

Table 1. Significance levels for main effects and interactions of yield and vegetative characteristics.

Source of variation	Yield/plant		Individual fruit wt		Total dry wt	Fruit (%)	Crowns/plant	Leaves/crown	Area/leaf	Total leaf area
	1989	1990	1989	1990	1990	1990	1990	1990	1990	1990
Origin (O)	NS	0.05	0.001	0.001	0.01	0.01	0.05	0.05	0.01	0.05
Training system (T)	0.001	0.05	NS	0.05	0.01	0.05	0.01	0.05	NS	0.01
T $\times$ O	NS	NS	NS	NS	NS	NS	0.05	NS	NS	0.05
Cultivar (C/O)	0.05	0.01	0.001	0.001	0.001	0.01	0.001	0.05	0.001	0.001
T $\times$ C	NS	NS	NS	0.01	0.001	0.05	0.05	NS	NS	0.05

^{NS} Nonsignificant difference.

Fig. 2. Relationship between fruit weight and yield among strawberry cultivars in matted rows. Data are from the first bearing year. (Left) Californian cultivars in matted rows, $Y = 17.26 - 2.17x$, $r^2 = 0.28$; (right) eastern cultivars, $Y = 8.25 + 2.30x$, $r^2 = 0.08$. Californian cultivars: 1, 'Parker'; 2, 'Cruz'; 3, 'Solana'; 4, 'Pajaro'; 5, 'Wiltguard'; 6, 'Vista'; 7, 'Oso Grande'; 8, 'Douglas'; 9, 'Sequoia'; 10, 'Torrey'; 11, 'Aliso'; 12, 'Shasta'; 13, 'Fresno'; 14, 'Aiko'; 15, 'Soquel'; 16, 'Tustin'; 17, 'Tufts'; 18, 'Tahoe'; 19, 'Lassen'; 20, 'Chandler'; and 21, 'Tioga.' Eastern cultivars: 1, 'Redchief'; 2, 'Sunrise'; 3, 'Lateglow'; 4, 'Surecrop'; 5, 'Lester'; 6, 'Earliglow'; 7, 'Raritan'; 8, 'Blakemore'; 9, 'Pocahantas'; 10, 'Scott'; 11, 'Midway'; 12, 'Guardian'; and 13, 'Midland.'

Fig. 3. Relationship between fruit weight and yield among strawberry cultivars grown in hills. Data are from the first bearing year. (Left) Californian cultivars, $Y = 17.50 - 7.77x$, $r^2 = 0.17$; (right) eastern cultivars, $Y = 12.03 - 4.60x$, $r^2 = 0.20$. See legend for Fig. 2 for numerical designation of cultivars.

eastern cultivars averaged 10.6 vs. 8.5 g/fruit in matted rows and 11.4 vs. 8.5 g/fruit in hills. 'Chandler' and 'Tufts' had the largest fruit in both hills and matted rows.

Significant negative correlations were detected between fruit weight and yield among the Californian cultivars in the first bearing year (Table 4). However, there were outlier types with large fruit and high yields such as 'Chandler' in matted rows (Fig. 2) and 'Oso Grande' in hills (Fig. 3). The eastern cultivars were much less variable for fruit size than the Californian ones and showed no significant correlations between fruit weight and yield.

Plant size varied significantly between eastern and western cultivars (Tables 2 and 3). In both cultural systems, most western cultivars had significantly smaller total leaf areas and lower dry weights than the eastern ones. The notable exception was the old Californian cultivar Lassen, which had dry weights and leaf surface areas that were higher than or similar to most of the eastern types.

The larger leaf area of the eastern cultivars was due primarily to higher leaf production (Tables 2 and 3). In the hills, there were significantly more crowns per plant and more leaves per

crown on eastern than Californian cultivars. On matted rows, the eastern types had significantly more leaves per crown. The higher leaf counts of the eastern cultivars were offset in part by smaller individual leaf surfaces, but these differences were not great enough to overcome the influence of higher leaf counts on total leaf area.

The western cultivars allocated a higher proportion of their biomass to reproduction than the eastern ones (Tables 2 and 3). In both cultural systems, the western types partitioned >7% more of their total fixed C to fruit than the eastern types. 'Chandler' and 'Tufts' allocated >40% of their dry matter to fruit on matted rows, while 'Tioga' allocated >40% to sexual reproduction on hills. 'Guardian' had the highest reproductive success of any eastern cultivar (37% on matted rows).

A in bearing plants varied widely across cultivar and season. The eastern cultivars had the highest rate of photosynthesis during spring (bloom) and summer (fruiting), while the Californian cultivars had the highest rate during fall (runnering) (Table 5). There was no significant correlation between mean A and yield in any season or cultural system. There was also no apparent association between photosynthetic stability and yield (data not shown). The cultivars had b values ranging from 0.42 to 1.83 (Table 6).

Nonbearing plants. There were significant differences ($P > 0.05$) in crowns per plant, runners per plant, and daughters per runner between cultivars but not between sources (Table 7). 'Lassen' had the most crowns and runners per plant, while 'Tufts' had the most daughters per runner (Table 7). On average, mother and daughter plants of western cultivars had lower dry weights than eastern cultivars, although the western type 'Lassen' was one of the largest plants. In contrast to their smaller vegetative size, the western cultivars had significantly higher A than the eastern ones during the spring and summer (Table 6). Most of the cultivars displayed a large drop in A during the summer (data not shown), but there was no apparent association between the source of a cultivar and its photosynthetic stability.

Discussion

Tremendous strides have been made in the development of disease-resistant strawberry cultivars for the eastern and mid-western regions of the United States (Galletta et al., 1989; Hancock et al., 1990; Maas and Galletta, 1989). This success has allowed strawberries to be successfully grown in regions where it was not previously possible. For example, red stele prevented successful cultivation in vast portions of the United States and led to the abandonment of many cultivars. Resistant cultivars have also reduced fungicide and pesticide usage, an achievement of increasing importance. Now that these elite genotypes have been developed, interest has grown in using Californian cultivars as a source of genes to boost yields.

We have shown here that Californian types are not innately higher yielding than eastern types when they are compared under conditions that approximate eastern cultural practices but avoid severe winter cold injury. The highest-yielding Californian cultivars did occasionally outproduce eastern types in our test environment, but, in general, the eastern and western types had similar yields.

Still, infusion of California germplasm into eastern breeding populations might result in increased eastern yields, if the higher reproductive capacity of the Californian cultivars can be genetically transferred. The average A between sources was about equal in the bearing year, but the western types had a more thrifty canopy and allocated an average of >7% of their fixed

Table 2. Yield, dry weight distribution, and leaf area of eastern and Californian cultivars grown in hills. Plants were in their second bearing season.

Source and cultivar	Yield/plant (g)	Individual fruit wt (g)	Total dry wt/plant (g)	Fruit (%)	Crowns/plant	Leaves/crown	Area/leaf (cm ²)	Total leaf area (m ²)
Eastern								
Midland	1036	6.5	348	26.8	13.7	2.9	88	3.48
Guardian	927	10.8	325	25.7	10.0	3.1	108	3.35
Scott	1040	9.0	226	27.8	6.5	2.7	116	2.03
Pocahantas	669	7.7	205	31.6	7.7	3.2	79	1.94
Mean	918	8.5	276	28.0	9.5	3.0	97	2.70
California								
Tioga	995	10.0	192	43.2	8.0	2.1	91	1.53
Chandler	932	14.2	206	34.4	7.5	2.2	106	1.74
Lassen	1325	9.2	400	27.6	9.0	3.2	130	3.75
Tufts	821	12.5	191	37.8	5.7	2.3	117	1.53
Mean	1018	11.4	247	35.7	7.5	2.4	111	2.10
LSD(0.05)	112	1.9	88	7.3	2.3	0.7	22	0.80

Table 3. Yield, dry weight distribution, and leaf area of eastern and Californian cultivars grown in matted rows. Plants were in their second bearing season.

Source and cultivar	Yield/plant (g)	Individual fruit wt (g)	Total dry wt/plant (g)	Fruit (%)	Crowns/plant	Leaves/crown	Area/leaf (cm ²)	Total leaf area (m ²)
Eastern								
Midland	305	6.2	86	31.9	3.3	2.8	85	0.78
Guardian	329	9.3	80	37.3	2.1	2.6	105	0.57
Scott	276	8.8	74	29.9	2.7	2.1	110	0.62
Pocahantas	239	7.1	76	30.6	2.8	3.3	80	0.74
Mean	287	7.8	79	32.4	2.7	2.7	95	0.68
California								
Tioga	341	9.3	72	36.4	3.2	2.1	85	0.57
Chandler	334	12.5	58	42.0	2.1	1.6	101	0.34
Lassen	352	9.2	78	37.7	2.6	1.8	123	0.58
Tufts	295	11.5	55	42.6	1.8	1.9	116	0.39
Mean	331	10.6	66	39.6	2.4	1.8	106	0.47
LSD(0.05)	37	1.5	14	2.3	0.5	0.6	18	0.11

Table 4. Correlation between fruit weight and yield among Californian and eastern cultivars grown in matted rows and hills.

Bearing year	Source	Training system	R	df	P
First	Californian	Hills	-0.301	17	0.05
		Matted rows	-0.532	20	0.05
	Eastern	Hills	-0.199	6	NS
		Matted rows	-0.079	12	NS
Second	Californian	Hills	-0.747	2	NS
		Matted rows	-0.566	2	NS
	Eastern	Hills	0.005	2	NS
		Matted rows	0.337	2	NS

^{NS} Nonsignificant difference.

C to fruit. Nonbearing western plants also produced as many runner plants as eastern ones and had a higher A, indicating they are capable of forming strong matted rows under eastern conditions.

In many other studies, allocation patterns have been shown to play a much more important role in determining yield than A does (Gifford and Evans, 1981; Strik and Proctor, 1986). Hancock et al. (1989) suggested that the highest-yielding cultivars might be those whose gas exchange properties are most responsive to environmental and developmental change ($b > 1$), but the patterns observed here do not support this idea. The b of high-yielding cultivars varied anywhere from 0.42 to 1.83.

Table 5. Mean A (micromoles CO₂ per meter per second) for eastern and Californian cultivars measured in different seasons. Bearing and nonbearing plants are compared.

Status	Source	Spring	Summer	Fall
Bearing	Eastern	12.1	11.1	9.4
	Californian	11.4*	10.2*	10.1*
Nonbearing	Eastern	13.1	7.9	11.1
	Californian	14.8*	8.6*	10.9 ^{NS}

^{NS}, *Nonsignificant or significantly different at $P < 0.05$, according to a t test.

A reasonable strategy for increasing eastern yields might be to cross large-fruited Californian types with highly fruitful eastern types and then select for those with both larger-than-average fruit size and higher-than-average fruit counts. One might look for outliers with reduced leaf mass and increased reproductive capacity. This approach depends on breaking the overall negative association between fruit size and yield among Californian cultivars, but a concomitant shift in partitioning patterns might circumvent this bottleneck. Outlier types were identified in this and other studies (Hancock et al., 1990). Even if yield is not increased by this approach, new cultivars might be produced with much larger fruit and less leaf mass. A more thrifty vegetative habit would reduce disease and pest problems by increasing air flow and spray penetration.

Table 6. A and stability (slope, b) of bearing and nonbearing strawberry cultivars. Means for determinations in March, May, and July.

Source and cultivar	Bearing plants		Nonbearing plants	
	A	b	A	b
Eastern				
Midland	16.9	1.76	10.0	1.07
Guardian	10.7	1.83	10.6	0.95
Scott	11.9	0.69	10.7	1.08
Pocahantas	9.9	0.51	11.5	0.44
Mean	10.9		10.7	
Californian				
Tioga	11.6	0.42	12.1	0.63
Chandler	9.2	1.52	11.2	1.23
Lassen	10.7	0.66	11.4	0.95
Tufts	10.6	0.97	11.2	1.64
Mean	10.8		11.5	
LSD(0.05)	1.2		0.7	

Table 7. Vegetative performance of nonbearing plants of eastern and Californian cultivars.

Source and cultivar	Crowns/ plant	Runners/ plant	Daughters/ runner	Dry wt (g)		
				Mother plant	Runner plants	Total
Eastern						
Midland	3.0	13.2	2.8	41.7	77.3	119
Guardian	4.3	8.7	2.8	50.1	66.7	117
Scott	4.3	13.0	3.2	45.5	83.6	129
Pocahantas	4.0	16.0	3.4	36.6	110	147
Eastern	3.9	12.7	3.0	43.4	84.4	128
Californian						
Tioga	3.5	8.5	4.0	33.2	60.0	93.2
Chandler	3.0	7.3	3.1	35.0	52.7	87.7
Lassen	4.7	17.0	2.1	56.1	105	161
Tufts	3.3	12.0	4.3	31.5	107	139
Mean	3.6	11.2	3.4	38.9	81.4	120
LSD(0.05)	0.7	4.8	1.1	8.3	21.4	27.3

Successful infusion of Californian germplasm requires that the desirable traits of western types be combined with the positive characteristics of the eastern types, such as disease resistance, freeze tolerance, and fruit quality. Caution is needed because a substantial reduction in disease resistance could easily overcome a slight increase in fruit size and yield. However, several eastern cultivars, such as 'Kent', 'Annapolis', 'Vantage', 'Micmac', and 'Scott', have 'Tioga' in their immediate background, indicating that some western cultivars can indeed be successfully introgressed into eastern breeding programs without a substantial loss in adaptability (Luby et al., 1991).

In conclusion, the Californian types are not innately higher yielding than the eastern types under eastern conditions, but their allocation patterns may prove useful in developing larger-fruited types with reduced vegetative vigor. Undesirable linkages can probably be broken, since certain Californian cultivars have been successfully employed in the past in eastern breeding programs.

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