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Gas Exchange Characteristics of *Fragaria chiloensis* Genotypes

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Abstract. **Twenty-five female clones of *Fragaria chiloensis* (L.) Duchesene collected from the California and Oregon coasts were surveyed for gas exchange rates under field conditions. Carbon assimilation (A) rates of native clones were 25% to 69% higher than for 'Totem' *(Fragaria × ananassa* Duchesne) on a leaf-area basis (μmol of CO_2 per sec/m^2) and 7% to 77% higher when expressed on a leaf dry-weight basis (μmol of CO_2 per kg dry wt/sec). Higher rates of stomatal conductance (g_s) were observed in 16 of 25 *F. chiloensis* clones than in 'Totem', with nine of 25 clones also having higher rates of transpiration (E). All clones had higher rates of residual conductance (g_r) and greater water use efficiency (WUE) than the cultivated standard. The gas exchange characteristics of four strawberry cultivars *(F. × ananassa)* and four *F. chiloensis* genotypes were compared under standard greenhouse conditions. *F. chiloensis* genotypes had higher rates of A than cultivars when expressed on per leaf-area and dry-weight bases. Native clones also had higher rates of g_s, g_r, E, and WUE and greater quantum yield. Differences in chlorophyll content were observed among genotypes, but not between species.**

The native beach strawberry *(Fragaria chiloensis)* is one of the progenitor species of the cultivated strawberry *(Fragaria × ananassa)* and is an important resource for its genetic improvement. Strawberry breeders have considered *F. chiloensis* to be a source of traits such as insect and spider mite resistance (2, 14-17), disease resistance (1, 3, 12), and drought, salinity, and cold tolerance (1, 3), as well as various fruit characteristics (3). While ecological differentiation (7) and sexual dimorphism (8) have been studied in California populations of *F. chiloensis,* relatively little is known about the physiology of this species and what characteristics of its growth and development might be of value for genetic improvement of the strawberry. In preliminary field studies, we have observed that clones of *F. chiloensis* have higher rates of CO, assimilation than cultivated genotypes (unpublished data).

In this study, we screened a collection of *F. chiloensis* clones for variability in gas exchange rates in the field; secondarily, we obtained preliminary data characterizing the differences in gas exchange characteristics between genotypes of *F. chiloensis* and *F. × ananassa.*

Field study. A replicated planting with five blocks each of 459 clones of *F. chiloensis* from 25 sites along the coasts of northern California and Oregon (Table 1) was established at Vancouver, Wash. in 1984 (T.M. Sjulin and C.H. Shanks, Jr., personal communication). 'Totem' was included in each block as a standard cultivated genotype *(F. × ananassa).* Matted row plots were established within each block by allowing a single plant of each clone to runner freely within a 40 × 90-cm area. In 1987, one representative female genotype from each of the 25 collection sites was chosen for gas exchange measurements in the field. Fruit were harvested 10 days before this study. Measurements were made on single leaves from two plants within each matted plot, replicated over five blocks. The determinations were made on consecutive clear days (13-15 July 1987) between 0900-1300 HR (PDST) at a saturating photosynthetic photon flux (PPF) (2200 $\mu mol \cdot s^{-1} \cdot m^{-2}$) with air averaging 26 ± 3C and an ambient CO_2 concentration of 338 ± 4 ppm. Complete blocks were measured in turn to minimize the effects of environmental variability over time. No significant block effect was observed in the analysis.

Gas exchange measurements were made using a CO_2 analyzer (Model LCA-2, Analytical Development Co., Hoddesdon, Herts, U.K.) equipped with a Parkinson broadleaf chamber and operated as an open system. Measurements were made on the middle leaflet of the third or fourth fully expanded leaf. Carbon dioxide depletion by a 6.25-cm^2 leaf area in the chamber was monitored for 30 to 60 sec at a flow rate of 0.5 $liter \cdot min^{-1}$. All gas exchange characteristics were calculated using standard equations described by Moon and Flore (9). Dry weight per leaf unit area in the chamber was calculated based on the mean dry weight of three 0.31-cm^2 leaf punches per leaf.

Greenhouse study. Gas exchange characteristics of four strawberry cultivars were compared to those of four *F. chiloensis* clones. The four cultivated genotypes, 'Benton', 'Hood', 'Olympus', and 'Totem', are commercially important in the Pacific Northwest. The four *F. chiloensis* genotypes, CL-5, 'Del Norte', LCM-20, and ZB-19, have been identified as being resistant to one or more insect and/or arthropod pests (2, 15-17) and have been used in the Washington State Univ. strawberry breeding program.

Two-year-old plants of each genotype were grown in the greenhouse in 25-cm pots (10.9 liters) containing a 2 peat : 1.5 perlite : 1 sand mixture (by volume). Plants were fertilized weekly with a complete (20N-20P-20K) water-soluble fertilizer plus micronu-

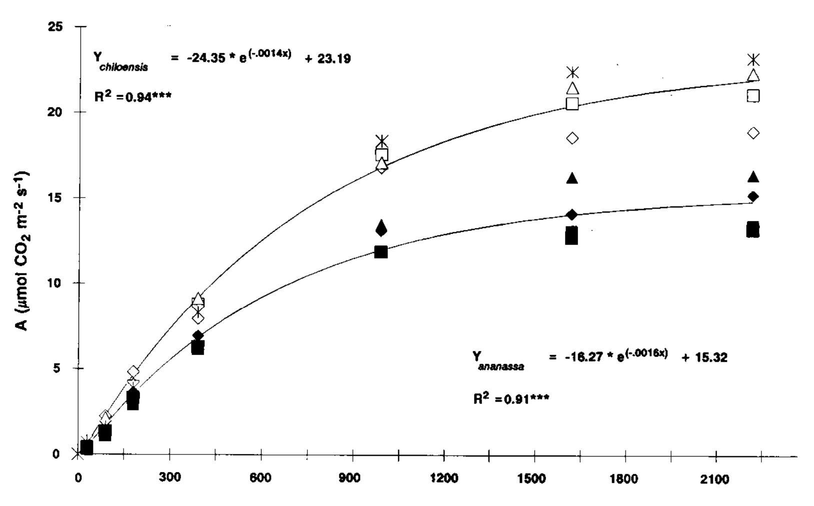

Fig. 1. Photosynthetic response of *F. chiloensis* (open symbols) and *F.* × ananassa (closed symbols) genotypes (listed in Table 3) to increasing photosynthetic photon flux (PPF). Measurements were made at an ambient CO_2 concentration of 376 ± 1 ppm with the chamber at 25.6 ± 2.5C. Different symbols within a species represent different genotypes.

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Table 1. Locations of 25 *F. chiloensis* collection sites in northern California and southern/central Oregon.

Clone[z]	Location	County
	California	
A17	Centerville Beach County Park	Humboldt
B12	Clam Park near Table Bluff Lighthouse	Humboldt
C19	Trinadad Beach State Park	Humboldt
D2	Big Lagoon County Park	Humboldt
E3	Stone Lagoon Campground	Humboldt
F4	Along U.S. 101 between Redwood Creek Beach Co. Park and Freshwater Lagoon	Humboldt
G5	False Klamath Cove	Del Norte
H9	Point St. George	Del Norte
I14	Kellog Beach	Del Norte
	Oregon	
J19	Undeveloped Oregon State Park along Oceanview Drive	Curry
K18	Harris Beach State Park	Curry
L11	Whalehead Beach, Boardman State Park	Curry
M7	Pistol River State Park	Curry
N6	Beach access area north of Rogue River outlet	Curry
O16	Battle Rock Wayside Park	Curry
P19	Cape Blanco State Park	Curry
Q16	Bullards Beach State Park	Coos
R5	Horsfall, Oregon Dunes Recreation Area, Siuslaw National Forest	Coos
S3	Siltcoos, Oregon Dunes Recreation Area, Siuslaw National Forest	Lane
T2	Siuslaw Harbor Vista County Park	Lane
U5	Ponsler Memorial Wayside	Lane
W15	Seal Rock Wayside State Park	Lincoln
X16	Moolack Beach Wayside State Park	Lincoln
Y58	Yachats State Park	Lincoln
Z3	Glenedon Beach State Park	Lincoln

[z]Clones collected by C.H. Shanks, Jr., and T.M. Sjulin in 1983.

trients. Leaves used for measurements in this study matured under a maximum ambient PPF of 1100 $\mu mol \cdot s^{-1} \cdot m^{-2}$ at plant level with days ranging from 17 to 34C and nights from 17 to 25C. Gas exchange measurements were made in the greenhouse under a high pressure sodium lamp with the ambient chamber at a mean temperature of 25.6 ± 2.5C and an ambient CO_2 concentration of 376 ± 2 ppm. Single leaflet measurements were made on four leaves from each of two plants of each genotype as described above, with a chamber flow rate of 0.5 $liter \cdot min^{-1}$. Chlorophyll was extracted from three 0.31-cm^2 leaf punches in 5 ml of N,N-dimethyl formamide and determined using the spectrophotometric assay described by Moran (11). The experiment was analyzed as a randomized block design with replication and nesting of treatments. Light response curves were generated by obtaining photosynthetic measurements at a saturating level of PPF (2200 $\mu mol \cdot s^{-1} \cdot m^{-2}$) and then reducing PPF in stepwise increments with screen filters. Data were fitted by computer to an asymptotic curve of the form $y = a \times e^{bx}$ (10, 13) using the Marquardt method of successive approximations (4).

In the field, CO_2 assimilation (A) rates as expressed on a leaf-area basis (µmol of CO_2 per sec/m2) were significantly higher (25% to 69%) for all the native clones than for 'Totem' (Table 2). When expressed on a dry-weight basis (µmol of CO_2 per kg dry wt/sec), A was significantly greater than 'Totem' in 19 of 25 *F. chiloensis* genotypes, with increases ranging from 7% to 77%. Stomatal conductance (g_s) was higher in 16 of 25 clones and residual conductance (g_r) was higher in all clones of *F. chi1oensis* than for the cultivated standard. Transpiration (E) rates were significantly higher in nine of the 25 native clones than in 'Totem', but all *F. chiloensis* genotypes had greater water use efficiency (WUE) than the cultivated standard.

In the greenhouse, significant differences

Table 2. Gas exchange characteristics[z] of 25 *F. chiloensis* clones and the cultivar Totem in the field.

Clone	A ($\mu mol \cdot s^{-1} \cdot m^{-2}$)	A (µmol/kg dry wt per sec)	g_s ($mmol \cdot s^{-1} \cdot m^{-2}$)	g_r ($mmol \cdot s^{-1} \cdot m^{-2}$)	E ($mmol \cdot s^{-1} \cdot m^{-2}$)	WUE (mol CO_2/mol H_2O) × 10^{-3}
A17	21.4	201	176	105	6.5	3.7
B12	17.7	161	146	88	5.4	3.7
C19	18.9	190	177	100	6.5	3.7
D2	17.4	186	141	87	4.8	3.6
E3	19.1	159	153	94	5.7	4.0
F4	22.9	193	194	111	7.1	3.8
G5	20.1	182	158	103	6.0	3.9
H9	20.5	176	182	95	6.2	4.0
I14	19.6	158	149	103	5.7	4.1
J19	19.8	176	177	98	5.9	4.0
K18	20.6	177	167	96	6.2	3.7
L11	21.3	261	205	96	5.4	3.4
M7	20.1	184	170	97	6.2	3.8
N6	21.7	201	188	103	6.6	3.7
O16	22.2	219	207	101	6.7	3.8
P19	23.0	214	191	112	5.1	3.9
Q16	19.5	211	150	102	6.1	3.8
R5	20.8	224	168	103	5.2	4.1
S3	17.0	189	127	93	5.2	3.8
T2	18.9	212	149	94	5.9	3.7
U5	19.1	236	157	94	5.5	4.0
W15	19.6	205	148	103	5.4	4.0
X16	21.5	218	198	98	6.7	3.8
Y58	17.5	203	153	82	5.8	3.5
Z3	19.5	254	168	93	5.3	3.7
'Totem'	13.6	148	121	65.4	4.6	3.0
Dunnett's q statistic ($P < 0.05$)	2.8	34.5	32.8	11.7	1.6	0.3

[z]Carbon dioxide assimilation (A), stomata1 conductance to CO_2 (g_s), residual conductance to CO_2 (g_r), transpiration (E), and water use efficiency (WUE) were measured at a saturating PPF of 2200 $\mu mol \cdot s^{-1} \cdot m^{-2}$, ambient CO_2 concentration of 338 ± 4 ppm, and a temperature of 26 ± 3C.

Table 3. Gas exchange and chlorophyll characteristics[z] of *F. chiloensis* clones and strawberry cultivars in the greenhouse.[y]

Species or genotype	A (μmol·s^{-1}·m^{-2})	A (μmol/kg dry wt per sec)	Quantum yield (A/PPF)	(mmol·s^{-1}·m^{-2})	(mmol·s^{-1}·m^{-2})	E (mmol·s^{-1}·m^{-2})	WUE (mol CO_2/mol H_2O) × 10^{-3}	Total chlorophyll (mg·dm^{-2})	Total chlorophyll (μg/mg dry wt)
All cultivars (*F.* × *ananassa*)	14.6 a	163 a	0.030 a	140 a	56.9 a	4.4	3.4	5.0	7.1
All native clones (*F. chiloensis*)	21.4 b	225 b	0.038 b	197 b	85.6 b	5.6	3.9	5.7	7.3
Cultivars									
Benton	15.2 ab	160 a	0.035 abcd	149 ab	58.3 a	4.7 ab	3.4	5.8 b	7.0 abc
Hood	13.4 a	143 a	0.026 ab	104 ab	51.4 a	3.8 a	3.6	5.5 ab	8.3 bc
Olympus	16.4 ab	156 a	0.029 ab	176 bc	60.8 a	5.3 ab	3.4	5.6 b	8.3 bc
Totem	13.2 a	193 b	0.031 a	104 a	57.1 a	3.9 a	3.5	3.0 a	4.9 a
Native clones									
CL-5	18.9 bc	194 bc	0.042 d	218 c	68.0 ab	5.8 ab	3.3	4.8 ab	5.6 ab
Del Norte	22.3 cd	227 c	0.036 bcd	164 abc	99.6 c	5.2 ab	4.4	7.3 b	9.9 c
LCM-20	23.2 d	270 d	0.034 abcd	223 c	90.2 c	6.5 b	3.6	5.5 ab	8.2 bc
ZB-19	21.5 cd	208 bc	0.039 cd	182 bc	84.5 bc	4.9 ab	4.4	5.2 ab	5.7 ab
P values									
Between species	0.001	0.019	<0.001	0.034	0.006	0.066	0.054	0.443	0.867
Among genotypes	<0.001	<0.001	<0.001	0.001	<0.001	0.012	0.084	0.007	0.003

[z]Carbon dioxide assimilation (A), stomatal conductance to CO_2 (g_s), residual conductance to CO_2 (g_r), transpiration (E), and water use efficiency (WUE) were measured at a saturating PPF of 2200 µmol·s^{-1}·m^{-2}, ambient CO_2 concentration of 376 ± 1 ppm, and a temperature of 25.6 ± 2.5C.
[y]Mean separation within columns by HSD, 5%.

in CO_2 assimilation rates were observed between species and among genotypes within species (Table 3). Rates of A, g_s, and g_r for *F. chiloensis* were significantly higher than those of cultivated genotypes; similar trends were observed for E *(P* = 0.066) and WUE *(P* = 0.054). Chlorophyll content differed among genotypes but not between species.

The response of both species to increasing levels of PPF is presented in Fig. 1. Apparent quantum yield (as represented by the slope of the linear portion of the light response curve) was significantly greater *(P* < 0.001) for native vs. cultivated *Fragaria* (Table 3).

We do not know the basis for the higher rates of gas exchange of *F. chiloensis* clones than of cultivated genotypes. Leaves of *F. chiloensis* have a thick cuticle and recessed stomata; factors important' in drought tolerance (3). It is not clear whether anatomical factors played a significant role in the differences in WUE and A observed in this study. Greater rates of CO_2 assimilation on a leaf dry-weight basis and greater rates of residual conductance may indicate that some *F. chiloensis* genotypes have a greater photosynthetic capacity than cultivated genotypes, but further studies are required to determine the nature of these differences.

Breeding for improved crop yields by direct genetic enhancement of photosynthetic processes has not been a successful strategy (5). The primary component of crop yield, which is open to modification by plant breeders, is partitioning of photoassimilates to economically important sinks (6). Thus, although *F. chiloensis* genotypes may have higher rates of net photosynthesis, ongoing evaluations of carbon partitioning patterns and resulting yield component interactions will be of primary importance in determining the breeding value of this germplasm.

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