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High Temperature Effects on CO_2 Assimilation Rate in Genotypes of *Fragaria xananassa*, *F. chiloensis* and *F. virginiana*

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Abstract

CO_2 assimilation rates (A) in two *Fragaria xananassa* cultivars, ten native *F. chiloensis* genotypes, and nine native *F. virginiana* genotypes were compared in growth chambers held at two day/night temperature regimes: 20/15°C and 30/25°C. Light intensity (PAR) was maintained at 500 μ mol m^{-2} s^{-1} and day lengths were held at 14 hours. At 20/15°C, *F. virginiana* had significantly lower A (10.4 μ mol CO_2 m^{-2} s^{-1}) than either *F. xananassa* (11.6 μ mol CO_2 m^{-2} s^{-1}) or *F. chiloensis* (11.7 μ mol CO_2 m^{-2} s^{-1}). All species showed a significant reduction in A at 30/25°C; however, *F. virginiana* dropped the least at 24%, while *F. xananassa* fell 42% and *F. chiloensis* dropped 54%. 'Seascape' and 'Tribute' had intermediate levels of A under cool temperatures (12.8 μ mol CO_2 m^{-2} s^{-1} and 10.4 μ mol CO_2 m^{-2} s^{-1}) and their CO_2 assimilation rates were reduced by 39-44% by high temperatures. Several *F. chiloensis* genotypes had higher A than the *F. xananassa* genotypes under cool temperatures, but they were more negatively effected by high temperatures. In *F. virginiana*, LH 50-4 and RH 18 had A values comparable to 'Seascape' and 'Tribute', and they showed more modest reduction in A at high temperatures (< 5%). These two genotypes may be good parents to improve heat tolerance in cultivated day-neutral germplasm.

Introduction

While the cultivated strawberry, *F. x ananassa* Duchesne in Lamarck, is grown across an enormous environmental range; its progenitor species, *F. chiloensis* (L.) Miller and F. *virginiana* Miller have an even broader range (15). The utilization of the wild germplasm could be useful in strawberry improvement, particularly in the development of day-neutral cultivars, since one of the major factors limiting productivity in strawberry cultivars is midsummer heat (16). High temperatures reduce day-neutral yield, cause smaller, softer fruits in the middle months of summer (7, 10) and inhibit flower bud initiation (8, 10, 29).

While the three octoploid species have never been compared together in the same study, reported values for the CO_2 assimilation rate (A) in *F. xananassa* range from 15 - 25 μ mol CO_2 m^{-2} s^{-1} (11), which is intermediate to published values of 7 - 15 μ mol CO_2 m^{-2} s^{-1} for *F. virginiana* (19) and 20 - 30 μ mol CO_2 m^{-2} s^{-1} *F. chiloensis* (4). Several factors can affect A of strawberries including: light level (3, 9, 21), nutrient availability (21, 23), CO_2 concentration (3), developmental stage (19, 20), cultural systems (1), mode of propagation (5), and removal of flowers, runners (24) and fruits (6, 22, 26, 27, 28).

The objectives of this study were: 1) compare A in *F. xananassa* and its progenitor species in a common environment, 2) determine the effect of high temperature on A in these octoploid species, and 3) discover if there is genetic variation in the photosynthetic heat tolerance of *F. chiloensis*, *F. virginiana*, and *F. xananassa*.

Material and Methods

The genotypes studied were: 1) day-neutral *F. xananassa*: 'Seascape' and 'Tribute', 2) short-day *F. chiloensis*: BRA 1A (PI 612316), CAR 2A (PI 602570), FRA 0596, FRA 0688 (PI612487), FRA 0883, FRA 1267 (PI 612488), NAH 5 (PI 612318), PAL 2C (PI 602568), Scotts Creek (PI 612490), and TAB 4B (PI 612317), 3) day-neutral *F. virginiana*: LH 30-4 (PI 612501), LH 50-4 (PI 612495), RH 23 (PI 612498), RH 30 (PI 612499), RH 43 (PI 612496), and 4) short-day *F. vir-*

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giniana: Eagle 14 (PI 612492), N8420, Montreal River-10 (PI 612497), and RH 18. Further information on the horticultural characteristics of these genotypes can be found in Hancock et al. (17, 18) and www.berrygenetics.org.

Runners from greenhouse grown plants were rooted under mist and then planted into a commercial peat and perlite potting mixture in 15 x 5 x 5cm pots. Two weeks after potting, they were placed in two growth chambers in a randomized complete block design. Two replicates of each genotype were placed in individual growth chambers held at either 20/15°C (day/night) or 30/25°C, under 500 μ mol m^{-2} s^{-1} photosynthetic active radiation (PAR) and 14-hour-days. The plants were allowed to acclimate to the growth chambers conditions for one month, and then the CO_2 assimilation rate (A) (μ mol CO_2 m^{-2} s^{-1}) of each plant was recorded three times weekly for three weeks. The gas exchange measurements were made within the growth chambers using an Analytical Development Company portable photosynthesis system equipped with a Parkinson broad leaf chamber (Hoddesdon, England). Depletion of CO_2 by a 6.25-cm^2 area of a single leaf in the chamber was monitored at a flow rate of 0.4 l min^{-1} using ambient air from outside the growth chamber (340 - 360 (μl $liter^{-1}$ CO_2). On each recording date, the A of three individual leaves of each plant were measured, and the mean values for each plant were used in further analysis. Analysis of variance and significant mean separations were evaluated using the GLM procedure of the SAS (25). Subspecies were nested in species, and genotypes were nested in subspecies and species.

Results

There was not significant variability detected across replication in either of the temperature regimes (Table 1), indicating that the two samples of each genotype performed similarly within treatment. Significant variation in A was observed among species and genotypes at 20/15°C and 30/25°C, and among subspecies at 20/15°C. Significant variation was also observes among species, subspecies and genotypes for % ΔA (the percentage change in A at 30/25° C compared to 20/15°C).

Overall, *F. virginiana* had significantly lower A under cool conditions (10.4 μ mol CO_2 m^{-2} s^{-1}) than *F. xananassa* (11.6 μ mol CO_2 m^{-2} s^{-1}) and *F. chiloensis* (11.7 μ mol CO_2 m^{-2} s^{-1}), but A in *F. virginiana* was only reduced by 24% at high temperatures compared to 42% in *F. xananassa* and 54% in *F. chiloensis* (Table 1; Fig. 1). The cultivated races of *F. chiloensis* ssp. *chiloensis* f. *chiloensis* had significantly higher A (14.8 μ mol CO_2 m^{-2} s^{-1}) than any of the other taxa (98.3 to 10.3 8 μ mol CO_2 m^{-2} s^{-1}), although this value was based on only two genotypes. A in all the taxa of *F. chiloensis* was dramatically reduced at high temperatures (50-56%), while *F. virginiana* ssp. *glauca* and *F. virginiana* ssp. *virginiana* fell by only 19 and 29%.

'Seascape' and 'Tribute' had about average A under cool conditions (10.4 vs. 12.8 μ mol CO_2 m^{-2} s^{-1}), but A was reduced in both cultivars by 39-44% under high temperatures (Table 1 and Fig. 1). Under cool conditions, A in *F. chiloensis* genotypes ranged from 7.8 μ mol CO_2 m^{-2} s^{-1} (TAP 4B) to 15.3 μ mol CO_2 m^{-2} s^{-1} (Scotts Creek), while genotypes of *F. virginiana* ranged from 6.0 μ mol CO_2 m^{-2} s^{-1} (LH 30-4) to 13.8 μ mol CO_2 m^{-2} s^{-1} (N8420). FRA 0883 (80%) and Scotts Creek (70%) showed the highest reduction in A at high temperature among the *F. chiloensis* genotypes and FRA 0688 (24%) had the lowest reduction. In *F. virginiana*, RH 43 showed a slight increase in A at high temperature (+ 6%) and LH 50-4 (-5%) and RH 18 (-14%) were only slightly reduced. RH 18 and LH 50-4 also had among the highest A of all *F. virginiana* genotypes (11.1 and 12.8 μ mol CO_2 m-2 s-1). The least heat tolerant genotypes of *F. virginiana* were Eagle 14 (-49%) and Montreal River-10 (-44%).

Discussion

As in previous studies, we found mean A in *F. chiloensis* to be significantly high-

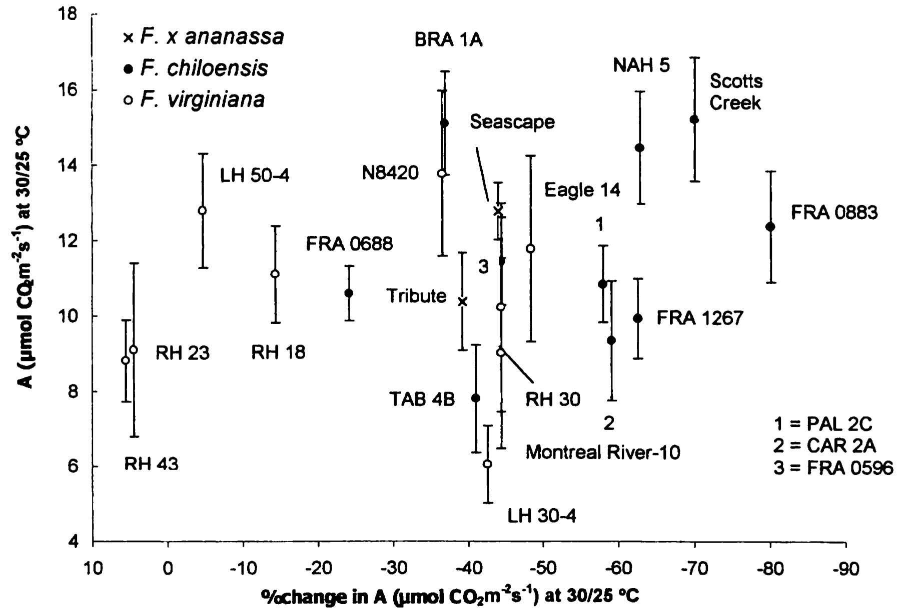

Figure 1. Mean CO_2 assimilation rates (A) of *F. xananassa* cultivars and elite *F. chiloensis* and *F. virginiana* genotypes grown under cold (20/15°C) and hot (30/25°C) temperature regimes.

er than *F. xananassa* at moderate temperatures (4, 12), although a considerable amount of variation was observed among genotypes of *F. chiloensis*. Our work is also in agreement with other studies that found mean A in *F. virginiana* to be generally lower than *F. xananassa* at moderate temperatures (19, 20).

Overall, *F. chiloensis* did poorer than *F. virginiana* and *F. xananassa* under high temperature. These results are consistent with Caldwell et al. (2) who found that *F. virginiana* was superior to *F. chiloensis* at acclimating to high temperature. This is not surprising, as *F. chiloensis* is found in a narrow band along the Pacific Ocean from California to Alaska and in Chile where temperatures are moderate and relatively stable, while *F. virginiana* is located in continental climates that are more subject to high temperatures and daily fluctuations. Still, considerable variability was found among the *F. chiloensis* subspecies and genotypes, with the cultivated forms of *F. chiloensis* ssp. *chiloensis* f. *chiloensis* having much higher A than the wild forms, and BRA 1A from Chile and FRA 0688 from British Columbia displaying much higher photosynthetic heat tolerance than the other *F. chiloensis* genotypes. Genotypes of *F. virginiana* also showed substantial variability, with *F. virginiana* ssp. *glauca* genotypes being generally more stable across low and high temperature than *F. virginiana* ssp. *virginiana*. This may also relate to habitat, as *F. virginiana* ssp. *glauca* is found in mountainous areas with higher daily temperature fluctuations than *F. virginiana* ssp. *virginiana* which exists in hot, but less variable continental climates (14).

Most of the *F. virginiana* genotypes showed higher photosynthetic heat stability than the two day-neutral *F. xananassa* cultivars we examined, indicating that the native genotypes could be a valuable source of genes for breeding for heat tolerant strawberry cultivars. In particular, LH

Table 1. Analysis of variance for CO_2 assimilation rates of *F.* x*ananassa* cultivars and elite *F. chiloensis* and *F. virginiana* genotypes under cool (20/15°C) and hot (30/25°C) temperature regimes.

	Geographical origin	Growth conditions		
		20/15°C	30/25°C	%ΔA[1]
Species				
F. x*ananassa*		11.6	7.0	-42
F. chiloensis		11.7	5.5	-54
F. virginiana		10.4	7.8	-24
SubSpecies				
F. chiloensis ssp. *chiloensis* f. *chiloensis*		14.8	7.7	-50
F. chiloensis ssp. *chiloensis* f. *patagonica*		9.3	4.5	-53
F. chiloensis ssp. *pacifica*		11.9	5.3	-56
F. virginiana ssp. *glauca*		10.6	8.9	-19
F. virginiana ssp. *virginiana*		10.3	7.0	-29
Genotypes				
BRA 1A	Chile (Region X)	15.1	9.9	-37
CAR 2A	Chile (Region XI)	9.4	4.0	-59
Eagle 14	Ontario	11.8	6.8	-49
FRA 0596	British Columbia	11.5	6.4	-45
FRA 0688	British Columbia	10.6	8.4	-24
FRA 0883	British Columbia	12.4	2.9	-80
FRA 1267	British Columbia	10.0	3.9	-63
LH 30-4	Montana	6.0	3.6	-43
LH 50-4	Montana	12.8	12.4	-5
Montreal River-10	Ontario	9.0	4.6	-44
NAH 5	Ecuador	14.5	5.6	-63
N8420	Minnesota	13.8	9.1	-37
PAL 2C	Chile (Region XI)	10.9	4.6	-58
RH 18	New York	11.1	10.6	-14
RH 23	Minnesota	9.1	8.0	+4
RH 30	Minnesota	10.2	4.8	-44
RH 43	Alaska	8.8	9.5	+6
Scotts Creek	California	15.3	4.9	-70
Seascape	Cultivar	12.8	7.3	-44
TAB 4B	Chile (Region XI)	7.8	4.8	-41
Tribute	Cultivar	10.4	6.7	-39
ANOVA	**df**	**Mean Square**		
Replication	1	8.0	95.1	9.0
Species (S)	2	31.1*[2]	10544.5***	55.5**
Subspecies (SS)/S	3	73.0***	550.9	40.4*
Genotype(G)/S, 22	15	23.4*	2440.2***	31.9*
Sub-plot error	20	11.3	475.4	15.5
Week (W)	2	13.4	1373.5*	11.0
W*S	4	23.1*	450.2	9.3
W*SS(S)	6	8.3	714.2	6.7
W*G(S*SS)	30	8.5	503.3	13.0
Whole-plot error	40	9.3	532.2	532.2

[1] % change in A at 30/25°C compared to 20/15°C.

[2] *, **, *** Significant at 0.10, 0.05, and 0.01 respectively.

50-4 and RH 18 had values for A at cool temperatures comparable to 'Seascape' and 'Tribute', with a much more modest reduction in A at high temperatures. In previous studies, we have found that the highest yielding cultivars often have the least variability in A across environments (12), although this is not always the case (13).

Of particular utility in strawberry breeding would be to find new sources of day-neutrality that were also heat tolerant, as most of the existing day-neutral cultivars do poorly under warm summer conditions (7, 10). Among the most tolerant genotypes uncovered in this study, RH 18 is a short-day type, but LH 50-4 is a day-neutral that has previously been identified as superior for other horticultural traits (17, 18).

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Strawberry - Anthocyanin

The transcript level of PAL and CHS genes did not change markedly throughout strawberry fruit development. The transcript level of chaconne isomerase (CHI) and dihydroflavonol 4 - reductase (DFR) gene was high in young fruit, decreased to an almost undetectable level at the white - mature stage, and then increased again until fully ripe stage paralleling the accumulation of anthocyanin. From Li et al J.Japan.Soc.Hort. Sci 70(1):28-32.

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ABA - Apple Nursery Trees

Sprays of ABA enhanced apple shoot growth cessation and bud dormancy which were closely related. Maximum growth cessation and bud dormancy were attained in mid-December with similar results for both treated and untreated. Stem cold hardiness in early November was enhanced by ABA. ABA enhanced N mobilization from leaves into perrennial woody tissue. From Guak and Fuchigami 2001. J. Hort. Sci. Biotech. 76(4):459-464.