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Net Carbon Exchange Rate of *Fragaria* Species, Synthetic Octoploids, and Derived Germplasm

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Abstract. The net carbon exchange rate (NCER) of *Fragaria* species, synthetic octoploids [SO (interspecific hybrids)], F_1 (SO × cultivar), and first outcross [OC1 (F_1 × cultivar)] hybrids were evaluated in both field and greenhouse conditions. Plants were grown in a field trial at the Elora Research Station in Ontario, Canada, for one season and then plants were dug and moved into a greenhouse where the trial was repeated during the next season. Single leaf photosynthesis measurements and light response curves were generated at different stages of plant development. Photosynthetic capacity of the species was related to the ecological background of the species with sun-adapted species having higher rates compared with the shade-adapted species. The *Fragaria* species and introgressed hybrids (F_1 and OC1) had significantly higher NCERs compared with the cultivars with rates 28% and 23% higher, respectively. Species and hybrids also appear to have increased adaptability to both high and low light conditions. These increases in NCER may be a heterotic effect because NCER of the hybrids were consistently higher compared with the midparent values and in some cases, they were higher than the high parent. These results suggest that the introgression of lower-ploidy *Fragaria* species into the cultivated strawberry (*Fragaria* ×*ananassa*) may lead to increased NCER and light adaptability.

The cultivated strawberry was originally derived from the accidental hybridization of two wild, octoploid species, *Fragaria chiloensis* and *Fragaria virginiana* (Darrow, 1966). The resulting octoploid hybrid, *Fragaria* ×*ananassa*, is the basis for the modern strawberry cultivar. The discovery of the narrow genetic base of the cultivated strawberry (Sjulin and Dale, 1987) has led to a renewed interest in the use of wild *Fragaria* species in breeding. High photosynthetic rate is one of the many interesting characteristics observed in some of the wild species and may be exploited to improve photosynthetic rates of the cultivated strawberry (Hancock et al., 1989a). Reported net carbon exchange rate for the cultivated strawberry ranges from 15 to 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Hancock et al., 1989b; Schaffer et al., 1986); light saturation for strawberry cultivars is between 800 and 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Cameron and Hartley, 1990; Ferree and Stang, 1988). Source-sink ratio can cause photosynthetic rates to fluctuate with sink demand (Iglesias et al., 2002). Strawberry fruit is a large sink and can account for 40% to 50% of total plant dry matter accumulation (Forney and Breen, 1985) and the presence of fruit increases NCER when compared with nonfruiting plants (Forney and Breen, 1985; Schaffer et al., 1986; Strik, 1987). In the strawberry cultivar Brighton, the photosynthetic capacity of the plant was not sufficient to meet sink demands during fruiting so translocation of reserve carbohydrates took place to meet demands of the developing fruit (Forney and Breen, 1985).

Two avenues to improve photosynthetic capacity are increasing the maximum photosynthetic rates under full light conditions and improving the stability of photosynthetic rates under a variable range of conditions. There has been limited success in yield improvement through selection for high photosynthetic rates (Hancock et al., 1989a) despite evidence that up to 90% of plant dry matter is accumulated through photosynthesis (Zelitch, 1982). The increases in yield over the last century have been largely the result of increases in harvest index and light interception; however, the role that photosynthesis has played is not completely understood (Richards, 2000). In several grain crops, maximum harvest indices are being approached and the need to increase the photosynthetic capacity may become necessary to realize further yield improvements (Richards, 2000). If genes for desirable photosynthetic characteristics can be incorporated into strawberry cultivars, there may be an opportunity to increase yield potential through increased dry matter accumulation and partitioning to fruit and storage organs. With adequate nitrogen (N) supply and light, increasing the amount of carbon assimilated per unit of N in the leaf could lead to increased biomass (Lawlor, 2002).

The use of wild *Fragaria* species to increase NCER has been investigated using the octoploid species, *F. chiloensis,* which has been shown to have 20% to 70% higher NCER than the strawberry cultivars (Cameron and Hartley, 1990). Hancock et al. (1989a) conducted a study to determine if these higher NCERs would be observed in *F. chiloensis* × cultivar hybrids and found that mean NCERs of hybrids were positively correlated with percent *F. chiloensis* germplasm incorporated into the hybrid; i.e., as the proportion of *F. chiloensis* increased,

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NCER also increased. These findings suggested that the high photosynthetic capacity of *F. chiloensis* was heritable and appeared to be quantitatively controlled because the relationship between NCER and gene composition was linear.

A second avenue to improve plant productivity is by increasing photosynthetic adaptability over a range of light conditions. Hancock et al. (1989b) suggested that it is the stability of NCER over the growing season and during critical periods of development that are associated with yield and found a positive correlation between the seasonal stability of NCER and yield in strawberry. Strik (1987) measured NCER for strawberry cultivars throughout the season and found that it was positively related to the harvest index but not to yield. Crown dry weight, leaf dry weight, and leaf area during flower bud initiation (FBI) were correlated with yield the next season indicating the importance of vegetative growth during FBI in determining yield potential (Strik, 1987; Strik and Proctor, 1986). In perennial crops such as strawberry in which competing sinks (e.g., fruiting and vegetative growth) are constantly present, high photosynthetic rates at critical times will help to ensure that demands for carbohydrates can be met. Single leaf photosynthetic measurements can be a useful measure of photosynthetic potential (Hancock et al., 1989b) for this type of measurement.

Most of the interest in using wild species germplasm to improve the cultivated strawberry has been focused on the progenitor species, *F. chiloensis* and *F. virginiana.* NCERs for strawberry cultivars are intermediate to its progenitor species, *F. virginana* and *F. chiloensis* (Hancock et al., 1989a). Previous research has reported NCER for *F. virginiana* of $\approx$7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Jurik, 1983; Jurik et al., 1979). In comparison, Hancock et al. (1989a) found mean maximum rates for five *F. chiloensis* clones to be 21.5 and 15.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the field and greenhouse, respectively. In a study that compared NCER of *F. chiloensis* with the cultivar Totem, *F. chiloensis* had rates that were 20% to 70% higher (Cameron and Hartley, 1990). In addition to the octoploid species, several lower-ploidy *Fragaria* species (2×, 4×, and 6×) have desirable characteristics such as extreme vigor (Harbut et al., 2009), unique flavors, disease resistance (Xue et al., 2005), and temperature adaptability (Harbut et al., 2010) that hold great potential as breeding germplasm (Harbut and Sullivan, 2004; Xue et al., 2005). The lower-ploidy species are found in a wide range of habitats including temperate, Mediterranean, grassland, and subtropical environments (Darrow, 1966; Hancock, 1990, 1999), which may influence photosynthetic capacity. Some of the species such as *F. orientalis* (4×) are found primarily in alpine forests and cold, dry areas in Asia, whereas *F. moschata* (6×) is found in heavily shaded forest habitats (Darrow, 1966). *F. vesca* (2×) is the most widely adapted species in the genus and inhabits regions of North America, South America, Europe, Asia, and Hawaii (Hancock, 1990, 1999). This species is found in a range of habitats including cool, high-light alpine conditions, shaded forests, and humid, temperate coastal habitats and is considered both heat- and cold-tolerant (Darrow, 1966; Staudt, 1989). If these *Fragaria* species have undergone ecotypic differentiation, adaptive traits such as photosynthetic rates, shade, and heat tolerance will be genetically based and therefore can be exploited through breeding to improve the adaptive strategies of the cultivated strawberry.

Attempts to carry out interspecific hybridizations have been made over several decades and were met with limited success resulting in the lower-ploidy species being largely overlooked for breeding purposes (Sangiacomo and Sullivan, 1994). Efforts to develop a method to incorporate lower-ploidy *Fragaria* species were started at the University of Guelph by Evans (1982) and were continued by Bors (2000) and Bors and Sullivan (1998). This method led to the creation of *Fragaria* species hybrids or synthetic octoploids. Each SO is a complex interspecific hybrid composed of at least two *Fragaria* species and can be easily crossed with the cultivated strawberry. The yield and vegetative growth of three lower-ploidy *Fragaria* species, SOs, F_1 hybrids with the cultivated strawberry, were evaluated in field trials in Ontario, Canada (Harbut et al., 2009). SOs had high vegetative vigor and the F_1 hybrids were also vigorous with a high flower number. The vegetative vigor and reproductive potential suggested high photosynthetic rates. The effect of temperature on NCER and dry matter partitioning has been addressed (Harbut et al., 2010). In the present study the photosynthetic characteristics of the lower-ploidy species, the SOs with breeding potential and the early generation progeny of SOs, and the cultivated strawberry are evaluated. The effect of ecological background on photosynthetic characteristics is also evaluated.

Materials and Methods

Plant material. The genotypes included in this study can be classified into five groups as outlined in Table 1. All runners, except those of the *Fragaria* species, were collected from existing field trials at the Cambridge Research Station, Cambridge, Ontario, Canada (lat. 43°27′N, long. 80°23′W) and established in the greenhouse during June and later planted in Aug. 2002. Greenhouse temperatures were 24 ± 2 °C with no supplemental light provided. The runner plants were 11 weeks old when transplanted to the field at Elora. The five groups of plants used in the study were: *Fragaria* species, strawberry cultivars, SOs (interspecific hybrids containing two or more *Fragaria* species), F_1 hybrids (first generation hybrids between cultivars and SOs), and outcross hybrids (crosses between F_1 hybrids and strawberry cultivars). Two elite selections, SJ8 and SJ9, from the Agriculture and Agri-Food Canada breeding program in Quebec, Canada, were included under the cultivar section. The SO, F_1, and OC1 hybrids are expected to have 100%, 50%, and 25% wild species germplasm, respectively. Species hybrids (SO, F_1, and OC1) were previously selected at their respective locations for yield, fruit quality, fertility, and horticultural characteristics. This research was conducted in a field trial in Elora, Ontario, Canada, and a greenhouse trial in Guelph, Ontario, Canada.

Elora field trial. This trial was carried out at the Elora Research Station in Elora, Ontario, Canada (lat. 43°29′N, long. 80°25′W). Planting occurred on 19 Aug. 2002 into single rows with 0.3 m between plants and 1 m between rows. A randomized complete block design was used with four replications each with 24 plants. Plants were covered with straw in late Nov. 2002 for winter protection. Straw was removed in late Apr. 2003 and plants were derunnered throughout the season to maintain uniform density. Plants were watered with a solid set irrigation system to provide 2.3 cm of water per week. Photosynthetic data (see NCER measurements subsequently) were collected at fruiting (defined as $\approx$25% ripe fruit) and flower bud initiation on 4 July 2003 and 26 Sept. 2003, respectively. The daylength and temperature conditions were appropriate for flower bud initiation at this latitude (Hancock, 1999).

Table 1. Genotype, parentage, and source of *Fragaria* species, cultivars, synthetic octoploids (SOs), and hybrids included in this study.

Genotype (ploidy)	PI[z] or cross	Source[y]	Trial[x]
Species			
F. moschata (6×)	PI 551750	NGR	G, E
F. nilgerrensis (2×)	PI 616602	NGR	G
F. nubicola (2×)	PI 551853	NGR	G, E
F. orientalis (4×)	PI 602942	NGR	G
F. vesca (2×)	PI 651550	NGR	G, E
Cultivars and selections			
'Allstar'		UG	G, E
'Camerosa'		UG	G, E
'Honeoye'		UG	G, E
'Jewel'		UG	G, E
'Latestar'		UG	G
SJ8		AAFC	G, E
SJ9		AAFC	G, E
'Sparkle'		UG	G, E
'Sweet Charlie'		UG	G
Synthetic octoploids			
SO 8183	*F. vesca* × (*F. nubicola* × *F. moschata*)	UG	G, E
SO 8132	(*F. moshcata* × *F. nubicola*) × (*F. nubicola* × *F. moschata*)	UG	G, E
SO 8212	*F. orientalis* × (*F. nubicola* × *F. moshcata*)	UG	G, E
SO 8223	(*F. vesca* × *F. nubicola*) × (*F. vesca* × *F. pentaphylla*)	UG	G, E
SO 8228	(*F. vesca* × *F. nilgerrnesis*) × *F. orientalis*	UG	G, E
SO 8231	(*F. vesca* × *F. nubicola*) × (*F. nubicola* × *F. moschata*)	UG	G, E
SO 8280	(*F. moschata* × *F. viridis*) × (*F. nubicola* × *F. moschata*)	UG	G, E
SO 8245	(*F. vesca* × *F. nilgerrensis*) × *F. orientalis*	UG	G, E
F_1 hybrids (SO × cultivar)			
00-28	'Sparkle' × 8245	UG	G, E
00-29	'Sparkle' × 8243	UG	G, E
00-38	SJ9 × 8245	UG	G, E
00-44	SJ8 × 8245	UG	G, E
00-53	SJ9 × 8280	UG	G, E
AEW-4	'Chandler' × 800	UM	G, E
AFA-4	'Honeoye' × 8183	UM	G, E
AFB-2	'Idea' × 8183	UM	G, E
AFG-1	847 × 'Seneca'	UM	G. E
OC1 hybrids (F_1 × cultivar)			
00-34	AFA-4 × 'Sparkle'	UG	G
00-56	SJ8 × AFB-2	UG	G, E
CFG	'Redcrest' × AEW-22	UM	G, E
CJA	AFG-1 × 'Jewel'	UM	G, E
CLE	'Quinault' × AFA-4	UM	G, E
CN	AAD-1 × AFA-4	UM	G

[z]Plant introduction no.
[y]NGR = National Germplasm Respository (Corvallis, OR); UG = University of Guelph program (Guelph, Ontario, Canada); AAFC = Agriculture and Agri-Food Canada (St. Jean-sur-Richelieu, Quebec, Canada); UM = University of Maryland (College Park, MD).
[x]G = Greenhouse trial; E = Elora (Ontario, Canada) field trial.

Greenhouse trial. The greenhouse trial was conducted on the same plants measured in the field and provided another set of measurements in a controlled environment. Twelve plants of each genotype from the Elora field trial were dug in late Nov. 2003 after the onset of dormancy and cold-stored at 4 °C for 6 weeks to complete dormancy requirements. Plants were potted into 18-cm-diameter containers in PRO-MIX® 'BX' media (Les Tourbières Premier, Rivière-du-Loup, Quebec, Canada) and placed on greenhouse benches on 19 Dec. 2003 in a randomized complete block design with four replications each containing three plants. Trickle irrigation was installed and used to supply water at a rate of 500 $mL \cdot d^{-1}$. The temperature in the greenhouse was maintained at 23/18 °C (day/night) and high-pressure sodium lights were used to provide a 14-h photoperiod with ≈500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Photosynthetic measurements were taken at flowering and fruiting stages.

Net carbon exchange rate measurements. Photosynthetic data were collected using a portable photosynthesis system (LI-6400; LI-COR®, Lincoln, NE). This is an open system with an integrated light source to maintain constant light, temperature, and CO_2 during measurements. Light response curves were generated using light levels between 100 and 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 100-$\mu mol \cdot m^{-2} \cdot s^{-1}$ intervals. Single leaflet measurements were made on the center leaflet of the last fully expanded leaflet at three stages of development; i.e., 1) flowering (greenhouse trial only); 2) fruiting; and 3) flower bud initiation (Elora field trial only). Measurements were taken between the hours of 0900 and 1500 HR at saturating photosynthetic photon flux (1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and CO_2 concentration was set at 400 $\mu mol \cdot mol^{-1}$ with a flow rate of 0.5 $L \cdot min^{-1}$. Individual genotypes were randomized to time periods (blocks) for measurement. Blocks were not significant in the analysis of variance (ANOVA). Leaf temperature in the cuvette was maintained at 23 ± 1 °C. Response curves represent the mean of measurement from three plants in each replication at each stage of development.

Statistical analysis. All procedures were carried out in SAS (Version 9.1; SAS Institute, Cary, NC). The Type I error rate was set at 0.05 for all analyses. Normality of data was determined using the Shapiro Wilkes statistic and test of assumptions was carried out using residual analysis. ANOVAs for NCER data were carried out using the Proc Mixed procedure. Light response curves were generated according Proctor et al. (1976) using nonlinear regression models in the form:

$$Y = a - be^{-cx}$$

where a = asymptote, b = intercept, c = rate of approach to asymptote, and x = x-axis value. The r^2 values were calculated by dividing the model sums of squares by the corrected total sums of squares (Steel et al., 1997).

Results

All genotypes were not included in the two trials, so each trial was analyzed separately. Where genotype × stage of growth interactions were significant, stages of growth were presented separately. Where no significant difference within genotypic groups was observed, group means are presented.

Net carbon exchange rate. NCER was lower in the greenhouse trial compared with the Elora field trial as a result of the lower ambient light levels; however, responses of genotypic groups were similar in both trials (Table 2). Generally, the mean NCERs of the *Fragaria* species, F_1 hybrids, and OC1 hybrids were significantly higher than the mean of the cultivars at all stages of development (Table 2). Synthetic octoploid NCERs were higher compared with cultivars in all trials except during fruiting in the greenhouse (Table 2). There was little or no significant difference between mean values for SOs, F_1 or OC1 hybrids, or species, but all were higher than the cultivars.

In the greenhouse, the *Fragaria* species showed the greatest range in maximum NCER with rates between 11.8 and 21.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table 2). A narrower range was observed in the Elora field trial, because the three species included were shade species with similar leaf characteristics. *F. nilgerrensis* had the highest NCER in the greenhouse trial at both flowering and fruiting (21.9 and 19.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2, respectively) compared with all other genotypes (Table 2).

F_1 hybrids (50% cultivar) had significantly higher average NCER than cultivars in both trials (Table 2). For example, mean NCER of F_1s during fruiting and FBI in the Elora field trial were 20% and 43% higher than the cultivar mean, respectively. To test for heterosis, the NCER value of the hybrid was compared with the midparent value. NCERs of the F_1 hybrid 00-29 at fruiting and FBI (24.3 and 24.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively) were 15% and 37% higher than the calculated midparent values (mean NCER of parental genotypes) at fruiting and FBI stages, respectively (Table 3). OC1 hybrids (75% cultivar) had mean NCERs during fruiting in both trials that were 24% and 22% higher than the cultivar mean in the Elora field trial and greenhouse trial, respectively (Table 2). The higher rates observed in the hybrids were most evident in the Elora field trial during fruiting, where five hybrids had 5% to 31% higher NCER compared

Table 2. Net carbon exchange rate (NCER) at flowering, fruiting, and flower bud initiation (FBI) stages of *Fragaria* species, synthetic octoploids (SO), cultivars, F_1 (SO – cultivar), and first outcross [OC1 (F_1 × cultivar)] hybrids grown in the greenhouse at Guelph, Ontario, Canada, 2004 and in the field at Elora, Ontario, Canada, in 2003.

	Greenhouse trial			Elora field trial	
	NCER [mean ± SE ($\mu mol \cdot m^{-2} \cdot s^{-1}$)]			NCER [± SE ($\mu mol \cdot m^{-2} \cdot s^{-1}$)]	
	No.	Flowering	Fruiting	No.	Fruiting	FBI
Species						
F. moschata		13.1 d[z]	13.3 d		23.9 a[z]	20.3 a
F. nilgerrensis		21.9 a	19.0 ab		—	—
F. nubicola		11.8 d	15.6 bcd		20.6 a	20.2 a
F. orientalis		16.1 bcd	18.5 abc		—	—
F. vesca		12.9 d	13.8 cd		22.6 a	20.8 a
Mean ± SE	25	15.2 ± 0.8	16.1 ± 0.8	15	22.4 ± 1.1	20.4 ± 1.1
SOs						
Mean ± SE	40	14.4 ± 0.8	14.3 + 0.8	35	22.2 ± 0.8	21.5 ± 0.8
F1 hybrids						
Mean ± SE	45	14.5 ± 0.7	15.5 ± 0.7	45	22.6 ± 0.8	22.6 ± 0.8
OC1 hybrids						
Mean ± SE	30	15.0 ± 0.8	16.6 ± 0.8	20	23.4 ± 0.9	20.2 ± 0.9
Cultivars						
Mean ± SE	45	11.8 ± 0.7	13.1 ± 0.7	35	18.8 ± 0.8	15.8 ± 0.8

[z]Means followed by the same letter are not significantly different using Tukey's multiple means comparison, $p<0.05$.

Table 3. Observed and calculated midparent net carbon exchange rate (NCER) at flowering, fruiting, and flower bud initiation (FBI) of *Fragaria* synthetic octoploids (SO), F_1 (SO × cultivar), and first outcross [OC1 (F_1 × cultivar)] hybrids grown in the greenhouse at Guelph, Ontario, Canada, in 2004 and in the field at Elora, Ontario, Canada, in 2003.

	NCER ($\mu mol \cdot m^{-2} \cdot s^{-1}$)			
	Flowering stage		Fruiting stage	
Genotype	Observed	Midparent	Observed	Midparent
	Greenhouse			
SOs				
SO 8132	16.0	12.8	14.3	13.9
SO 8183	16.7	12.9	14.5	13.7
SO 8212	14.8	14.5	16.2	16.0
SO 8228	9.7	16.8	12.1	17.5
SO 8231	14.6	12.6	14.0	14.3
SO 8245	14.7	16.8	15.8	17.5
Mean (n = 24)	14.4	14.4	14.5	15.5
F_1 hybrids				
OO-29 ('Sparkle' × 8245)	14.4	13.9	15.2	14.9
OO-44 (SJ8 × 8245)	12.9	12.4	17.6	14.6
OO-53 (SJ9 × 8280)	12.3	13.1	16.1	11.9
AFA-4 ('Honeoye' × 8183)	13.9	15.9	14.2	14.5
Mean (n = 16)	14.2	14.2	15.8	14.0
OC1 hybrids				
OO-34 (AFA-4 × 'Sparkle')	13.3	13.5	15.3	14.1
OO-56 (SJ8 × AFB-2)	17.3	13.2	18.1	15.2
CJA (AFG-1 × 'Jewel')	16.2	12.8	18.8	13.2
Mean (n = 12)	15.0	13.1	16.6	14.2
	Fruiting stage		FBI stage	
	Field			
F_1 hybrids				
OO-29 ('Sparkle' × 8245)	24.3	21.7	24.9	20.6
OO-44 (SJ8 × 8245)	24.4	21.9	23.5	20.5
OO-53 (SJ9 × 8280)	23.4	17.9	22.6	20.5
AFA-4 ('Honeoye' × 8183)	20.2	19.2	16.7	20.7
Mean (n = 16)	22.6	20.2	22.8	20.6
OC1 hybrids				
OO-56 (SJ8 × AFB-2)	24.8	21.4	21.2	21.6
Mean (n = 4)	24.8	21.4	21.2	21.6

with the calculated midparent values (Table 3). In the greenhouse trial, eight of 13 hybrids at flowering had between 2% and 31% higher NCERs compared with calculated midparent values for NCERs, and nine of 13 hybrids at fruiting had NCERs that were between 3% and 42% higher compared with calculated midparent values.

Species proportion and net carbon exchange rate. Regression analysis showed that there was no significant relationship between wild species proportion and NCER. However, all genotypes containing wild species germplasm had higher NCER compared with genotypes containing no wild species. OC1 genotypes composed of 25% wild species and 75% cultivar had the highest NCER, which was most evident when sink demand was high during fruiting in both trials (Table 2). However, this difference was not statistically significant.

Light response curves. Light response curves generated on greenhouse-grown plants demonstrated the variation in NCER of different species to changing light intensities (Fig. 1). Of the five species evaluated, the three shade species, *F. moschata, F. nubicola*, and *F. orientalis,* had the lowest light saturation points (≈600 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and maximum NCER ($P_{max}$) values (14.5, 15.1, and 18.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively). *F. nilgerrensis* (sun-adapted species) and *F. vesca* (sun- and shade-adapted species) reached light saturation at ≈800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and maintained high rates up to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. These two sun-adapted species had P_{max} values that were 47% and 33% greater than the mean P_{max} for the three shade species. *F. nilgerrensis* had the highest P_{max} value, 23.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 1), and also had the highest NCER in single leaflet measurements (Table 2).

Light response curves were also generated for species hybrids (SO, F_1, and OC1) and parental genotypes. Response curves for the F_1 hybrids, 00-29 (Fig. 2A) and 00-44 (Fig. 2B) and their respective parental genotypes, illustrate the increase in NCER in the hybrids over the parental genotypes. F_1 hybrid 00-44 had a NCER that was 23% and 61% higher than the SO8243 and SJ8 parents, respectively, at light levels as low as 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. P_{max} for 00-29 was 36% and 98% higher than the SO8243 and 'Sparkle' parents, respectively, and 32% and 49% higher, respectively, for 00-44.

Higher NCER in hybrids compared with the parental genotypes was also evident in the OC1 hybrids (Fig. 2C). For example, even at light levels as low as 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the NCER of 00-56 was 52% and 107% higher than parental F_1 hybrid (AFB-2) and SJ8, respectively, and remained higher at

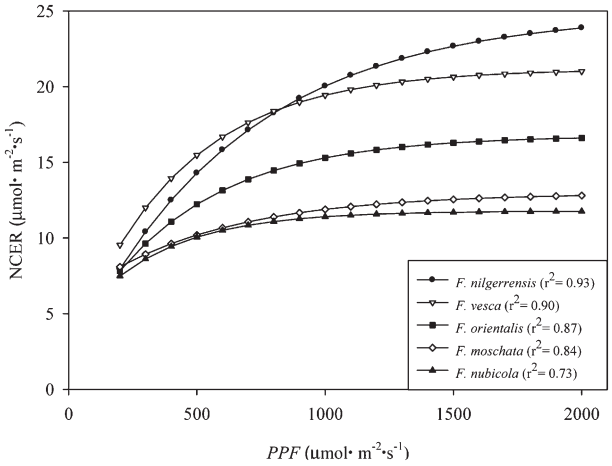

Fig. 1. Light response curves of net carbon exchange rate (NCER) of *Fragaria* species grown in the greenhouse at Guelph, Ontario, Canada, in 2004. Goodness of fit indicated by r^2 value.

all light levels. The P_{max} of 00-56 was 28% and 54% higher than parental F_1 hybrid (AFB-2) and SJ8 genotypes, respectively.

Discussion

The increase in photosynthetic capacity of the hybrids appears to be a heterotic effect. Results of the single leaflet measurements show that eight of 13 hybrids at flowering and nine of 13 hybrids at fruiting had NCER that exceeded midparent values with some hybrids having higher NCERs than the high parent. Heterotic responses in photosynthetic rates have been observed in several grain crops including rice [*Oryza sativa* (Sarker et al., 2001)] and maize [*Zea mays* (Giauffret et al., 1997)] but not in perennial fruit crops. This provides an excellent reason for the use of more wild species in strawberry cultivar development (Harbut and Sullivan, 2004). The increased photosynthetic capacity may be the result of several physiological factors including increased chlorophyll content, high stomatal conductance (Hancock et al., 1989a), and increased enzyme activity (Heath, 1994).

All genotypes that were introgressed with wild species germplasm, regardless of proportion, had higher NCER compared with the cultivars. When *F. chiloensis* was introgressed with the cultivated strawberry, NCER of the hybrids decreased linearly (i.e., each generation) as the proportion of species decreased (Hancock et al., 1989a). In the current study, it was the presence of the species germplasm that affected the NCER of hybrids and is likely responsible for the heterotic effect. The SOs evaluated in the current study were complex octoploid hybrids composed of two or more distantly related species differing in photosynthetic characteristics and ploidy level. The effect of heterosis increases with increased genetic distance between the parental genotypes (Melchinger, 1999) and the material used in this study is genetically diverse (Potter et al., 2000). *F. chiloensis* is a progenitor to the cultivated strawberry and therefore the genetic distance between it and cultivars would be far less compared with the lower-ploidy species that have not previously been used in breeding efforts (Potter et al., 2000).

The SOs (100% wild species) had vigorous vegetative growth with low yields resulting in a high source-sink ratio.

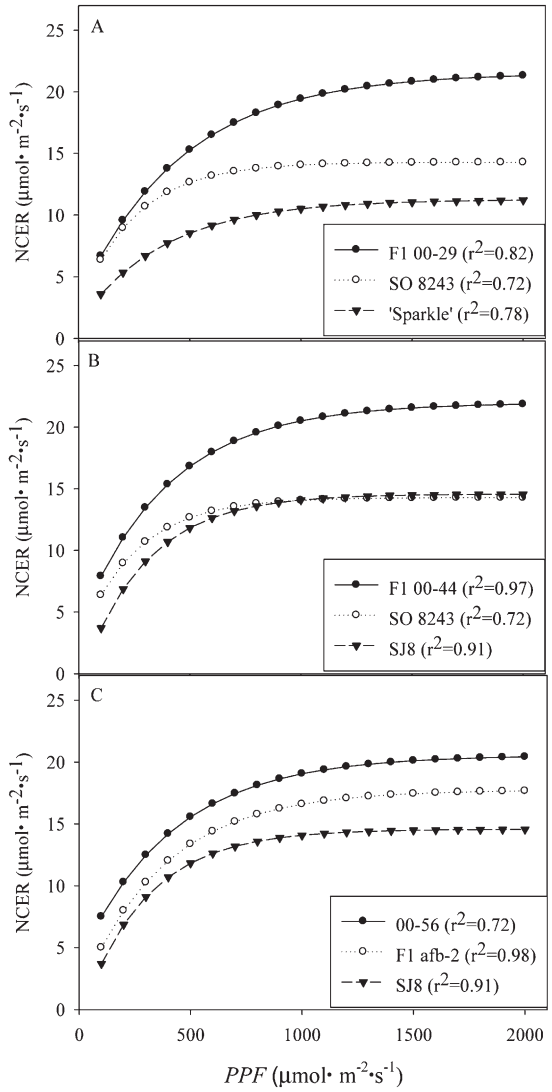

Fig. 2. Light response curves of net carbon exchange rate (NCER) of *Fragaria* hybrids and parental genotypes grown in the greenhouse at Guelph, Ontario, Canada, in 2004. (**A**) Parental cultivar (Sparkle), synthetic octoploid (SO8243), and F_1 hybrid (00-29). (**B**) Parental line (SJ8), synthetic octoploid (SO 8243), and F_1 hybrid (00-44). (**C**) Parent (SJ8), F_1 hybrid (AFB-2), and first outcross hybrid (00-56).

These data are reported in a recently published companion article (Harbut et al., 2009). Some of the vegetative vigor was reduced in the F_1 (50% wild species) and OC1 (25% wild species) hybrids with sink demand and NCER being greatest in OC1 hybrids. Increased sink demand (defined by yield) increases NCER in strawberry (Forney and Breen, 1985; Strik, 1987). Maximum photosynthetic potential of the SO and F_1 hybrids may not have been expressed as a reslt of high source-to-sink ratio. Cultivars had the lowest NCERs despite having the highest sink (Harbut et al., 2009) demand (i.e., yield potential), which may indicate that the maximum photosynthetic capacity of cultivars has been reached. These early-generation results suggest the introgression of SOs represents an excellent opportunity to improve NCER. The difference in yield among the SO, F_1, and OC1 generations (Harbut et al., 2009) suggests that by selecting for improved harvest index, the higher NCER rates could be effectively used.

The *Fragaria* species and species hybrids included in this study represent a wide diversity of ecological backgrounds and a broad genetic base compared with the progenitor species, *F. chiloensis* and *F. virginiana* (Potter et al., 2000). Ecotypic differentiation has been related to differences in photosynthetic response in other genera [*O. sativa* (Jiao and Li, 2001)] and differences in photosynthetic rates between species observed in this study were consistent with their respective ecological background. For example, *Fragaria* species such as *F. moschata* and *F. nubicola,* that are native to shade conditions, had lower NCER, light saturation points (LSP), and P_{max} compared with sun-adapted species such as *F. nilgerrensis* (Fig. 1), which had high LSP and a high P_{max}. *F. vesca* is a highly adaptable species that is native to a range of habitats in the temperate regions of the world (Darrow, 1966). This broad adaptability was reflected in the light response curves generated in this study. *F. vesca* had a high LSP ($\approx$800 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and also the highest NCER at lower light levels (200 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$) compared with the other species (Fig. 1). The potential of hybridizing genotypes adapted to different light environments has been exploited by rice breeders and the resulting hybrids can photosynthesize more efficiently under a broader range of light conditions than the parental genotypes (Jiao and Li, 2001). The results of the current study indicate that the diverse ecological distribution of the *Fragaria* species (Darrow, 1966) and the ecological differentiation within species that has been observed in previous studies (Hancock and Bringhurst, 1978) may be exploited to develop strawberry genotypes with a wider range of photosynthetic capacity.

The synthetic octoploids (Bors, 2000) are composed of two or more species that differ in ploidy level and ecological background. The mean NCER of the SOs was slightly lower than that of the parental species, but there are examples of hybrid combinations (i.e., F_1 and OC1) (Fig. 2) in which the NCERs were significantly higher than their respective parental genotypes. Despite the inclusion of shade-adapted species with low NCERs, the introgression of the species germplasm into the cultivated strawberry through the SO system led to substantially increased NCER and an increased range of light adaptability in the hybrids compared with the cultivars.

The value of the species germplasm is further highlighted by the light response curves of the F_1 and OC1 hybrids, which demonstrated that the introgression of *Fragaria* species increased the high and low light adaptability of the hybrids. The presence of the shade-adapted species in the pedigree did not appear to hinder the photosynthetic potential of the hybrids. This was encouraging given their low response to the higher light levels. The results indicated that the F_1 and OC1 hybrids measured (Fig. 2) can maintain rates even that are higher or at least equal to the parents at low light levels. Further investigation of quantum yield, dark respiration rates, and light compensation points would allow greater understanding of low light adaptability. The ability to efficiently photosynthesize under both high and low light levels is a beneficial trait in strawberry. In the northeastern United States and Canada, midsummer light levels in the field can reach up to 1600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Average LSP for strawberry cultivars is 800 to 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Cameron and Hartley, 1990), so the higher LSP and NCERs observed in the hybrids allows better use of light energy available under maximum intensity conditions. Low-light adaptability can be advantageous to strawberries grown in a matted row system, which is characterized by a dense canopy with mutual shading (Larson, 1994). Shading of lower leaves can lead to reduced whole plant photosynthesis, which in turn can decrease plant productivity (Strik and Proctor, 1988). The introgression of synthetic octoploids into the cultivated strawberry may be a valid strategy to increase NCER at low light levels, reduce the effect of canopy shading, and increase plant productivity. Increasing plant productivity is particularly important during the fall when lower light conditions are prevalent and yield potential is established through FBI (Strik and Proctor, 1988).

The results of this study have demonstrated that the ecological adaptability and the genetic diversity present in the genotypes that were evaluated can be exploited to improve the photosynthetic capacity of species hybrids and the cultivated strawberry. Even a small proportion of wild species (i.e., SO) germplasm made a positive contribution to the NCER of the hybrids. Although only one genotype of each species was evaluated in this study, the diversity in responses was positive and an indication that the broader variability within each *Fragaria* species is worth evaluating.

It appears that both the maximum NCER and the increased adaptability are potential avenues to explore. The diverse genetics in the SOs led to higher maximum NCERs, which appear to be the result of heterosis and hybridization of sun- and shade-adapted species resulted in hybrids that exhibited increased NCER under a range of light conditions. This is a significant finding for *Fragaria* breeding and perennial fruit crops in general. With increasing variability in climate and management systems, the ability for crops to adapt to a broad range of conditions will become essential. The lower-ploidy *Fragaria* species provide a source of genetic diversity that can continue to be used in developing the cultivated strawberry.

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