Environmental Influences on Photosynthesis and Carbon Export in Greenhouse Roses during Development of the Flowering Shoot

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ADDITIONAL INDEX WORDS. carbon fixation, irradiance, translocation, respiration, sucrose, greenhouses

ABSTRACT. Photosynthesis and concurrent export rates of expanded leaves on the flowering shoot of *Rosa hybrida* L. 'Samantha' were measured at three stages of shoot and flower bud development. At 35 and 90 Pa CO₂ photosynthesis and concurrent export rates of the upper expanded leaves were greater at Stage 3 (i.e., when petal color of the flower bud was visible) than at the two earlier stages of shoot and flower development. The optimum for leaf photosynthesis and concurrent export at ambient CO₂ and saturating irradiance were $\approx 25^{\circ}\text{C}$. Export was more sensitive to increased temperature than was carbon fixation. For example, at 40°C photosynthesis was 40% lower while the export rate during photosynthesis was reduced by 80%. Increasing the photon fluence flux rate from 200 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR increased the photosynthetic rate and the concurrent export rate at 35 and 90 Pa CO₂, but the increase in export was proportionally greater than that of photosynthesis. At 35 Pa CO₂, the rate of C export during photosynthesis increased from 31 to 59% of the concurrent C fixation rate. At 90 Pa CO₂, export during photosynthesis increased from 38 to 62% of the photosynthesis rate. The importance of irradiance on translocation processes was further demonstrated by comparing the disappearance of label during the feed period and during an extended night period. Plants grown at each CO₂ level exported about three times as much of the ¹⁴C fixed during a 2-hour feed period in the light as during a subsequent 15-hour dark chase period. The nighttime export and respiration rates of leaves which had been exposed to elevated CO₂ levels during the feed were higher than those rates observed at ambient CO₂. However, at the end of the chase period, the leaves of plants which had been exposed to CO₂ enrichment during the feed also retained more ¹⁴C than did the leaves of the plants which were at ambient CO₂. Thus, although more ¹⁴C was fixed and exported under high CO₂, the same proportion of labelled assimilates were exported, respired, and retained in the dark as at ambient CO₂.

The primary functions of a source leaf are to provide photoassimilates and energy required for plant growth. Translocation as well as photosynthesis must be viewed as a major process occurring in leaves. Photosynthetic and export capacities of leaves are affected by many variables including the age of the plant and the stages of leaf development (Giaquinta, 1978; Ho and Shaw, 1977; Silvius et al., 1978; Turgeon and Webb, 1973). Also, whereas leaf photosynthesis occurs only during the light period, photoassimilate partitioning and translocation are processes that occur in the light and in the dark (Geiger and Servaities, 1994). Carbon assimilation rates and export are influenced by the environmental conditions affecting the source leaves (Grodzinski et al., 1998; Ho, 1976; Ho et al., 1977; Jiao and Grodzinski, 1996) and by the demand for photosynthates in the sinks (Farrar, 1988; Wardlaw, 1990). Although the major biochemical and physiological processes of C assimilation are well studied, the factors regulating and thus controlling C partitioning and translocation are still less clearly understood (Farrar, 1988; Geiger and Servaities, 1994; Patrick, 1988; Wardlaw, 1990).

The importance of irradiance, CO₂ concentration, and leaf temperature on production of greenhouse roses is well documented

(Hand and Cockshull, 1975a, 1975b; Jiao et al., 1991c; Mattson and Widmer, 1971; Mortensen et al., 1992; Zieslin et al., 1972). Because light is the major limiting factor in greenhouse rose production at northern latitudes, many commercial growers in North America and Europe use artificial lighting to supplement crop production (Mortensen et al., 1992; Tsujita, 1987). Irradiance, CO₂ concentration, and temperature account for 70%, 20%, and 5%, respectively, of the variance in whole plant net carbon exchange rate (NCER) in Samantha roses plants (Jiao et al., 1991c). Compared with the data available on the response of individual leaves in the canopy (Pasian and Lieth, 1989) measurements of whole-plant gas exchange have the advantage of automatically accounting for the problems associated with estimating the effects of mutual shading on photosynthesis (Jiao et al., 1991a, 1991b, 1991c). Although whole-plant photosynthesis and respiration data are useful in modelling and in the development of software for control systems, knowledge of gas exchange by itself reveals little about C partitioning in the plant, any alteration in the harvest index, or any change in the quality of flowers produced (Jiao et al., 1991c; Leonardos et al., 1994). There are very little data available on the effects of irradiance, CO₂, and temperature on C partitioning and export from source leaves of rose plants during photosynthesis which could be used to construct better models of rose growth and development under commercial conditions.

It appears that leaves on the flowering shoot generally become source leaves just after the visible bud stage (Mor and Halevy, 1979). Studies with radioisotopes (i.e., ¹⁴C, half-life of 5370 y, and ¹¹C, half-life of 20.4 min) showed that upper leaves on the flowering shoot exported assimilates mainly to the flower bud and to the upper shoot, whereas the lower leaves allocated proportionally more C basipetally (Jiao et al., 1989; Mor and Halevy, 1979). Growth temperature during the night altered transport and ¹⁴C partitioning in rose plants (Khayat and Zieslin, 1986; Khayat et al.,

Received for publication 5 Dec. 1997. Accepted for publication 18 June 1998. Grants to B.G. from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Ontario Ministry of Agriculture Food and Rural Affairs (OMAFRA), Flowers Canada (On) Ltd., the Cecil Delworth Foundation, the Centre for Research in Environmental and Space Technologies (CRESTech), and an Ontario-Québec Exchange Fellowship are all gratefully acknowledged. We thank George Lin for able technical assistance and Demos Leonardos, Arend Librande, John T.A. Proctor, and Dennis Murr for comments on an earlier version of this manuscript. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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Fig. 1. (A) Total C fixation, retention, and export from a mature rose leaf during a 2-h $^{14}\text{CO}_2$ feeding at 35 Pa CO_2 , 25 °C and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Total C fixation (dashed line) was calculated from IRGA data. Retention of ^{14}C in the leaf was measured nondestructively with a GM detector continuously (solid line), and in a set of leaves by destructive analysis (U). Export during steady-state $^{14}\text{CO}_2$ feeding (dotted line) was estimated as the difference between total fixation and ^{14}C retention in the leaf. (B) Partitioning of ^{14}C in the total ethanol soluble fraction (S), in the sugar fraction (I) and in starch (n). (C) Accumulation of ^{14}C sucrose in the source leaf. (D) Specific activity of ^{14}C sucrose pool in the 2-h feeding period. Each point is a mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3 (Table 1).

1988). Darkening the shoot resulted in decreased allocation of ^{14}C to the shoot tip and had a detrimental effect on growth and flowering of the shoot (Mor and Halevy, 1980). These studies demonstrate the importance of export and allocation of assimilates in roses during daytime periods.

The objectives of this study were to 1) develop a protocol for measuring the export rate from source leaves of 'Samantha' roses during steady-state photosynthesis; 2) examine leaf photosynthesis and concurrent export capacity during flower shoot development; 3) examine the effect of irradiance on photosynthesis and concurrent export capacity at the growth temperature; 4) investigate the effect of acclimation to CO_2 enrichment on photosynthesis and concurrent export; and 5) relate export during photosynthesis to the subsequent export and respiration of the newly fixed C during the nighttime.

Materials and Methods

PLANT MATERIALS. Rooted cuttings of *Rosa hybrida*, L. 'Samantha' were planted in PROMIX-BX (Les Tourbières Premir LTÉE, Rivière du Loup, Que., Canada) in 14-cm-diameter (1.4-L) pots and a single flowering stem was allowed to develop on each plant as described previously (Jiao et al., 1991a). Plants were grown at 24/18 °C day (16 h)/night (8 h) under either ambient (35 Pa) CO_2 or enriched (95 $\pm$ 5 Pa) CO_2 during irradiance. The photon fluence rate was maintained above 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR during irradiance.

LEAF PHOTOSYNTHESIS, EXPORT, AND STORAGE OF ASSIMILATES DURING PHOTOSYNTHESIS. Steady-state gas-exchange measurements were conducted on an attached intact leaflet of the compound leaf using an open-flow system described previously (Jiao and

Grodzinski, 1996). Plants were irradiated with Sylvania metal halide lamps (1000 W) that provided a maximum of $\approx 1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR at the leaf level. A Geiger-Muller (GM) detector was mounted in the lower half of the leaf cuvette (Jiao and Grodzinski, 1996) to monitor radioactivity (i.e., ^{14}C accumulation) in the source leaves continuously as described by Geiger and Fondy (1979). In rose plants, sucrose is the major phloem mobile sugar (Jiao et al., 1989). To establish the time required to reach isotopic equilibrium of ^{14}C sucrose, leaves were fed with $^{14}\text{CO}_2$ of known specific activity from 0 to 120 min. During the entire feeding period the net CO_2 assimilation and ^{14}C accumulation rates were monitored continuously with an infrared gas analyzer (IRGA) and a GM detector, respectively. After each feeding period, the feed leaf was extracted with boiling 80% ethanol and the major ^{14}C -labelled assimilates were analyzed as described previously (Jiao and Grodzinski, 1996). Photosynthetic irradiance response curves were generated by shading the plant chamber with a series of neutral density shade screens. The CO_2 concentration in the leaf cuvette was controlled and maintained at either 35 or 90 Pa. Unless otherwise stated, whole plant and leaf temperature was maintained at $25 \pm (\text{SE}) 1^\circ\text{C}$. Humidity levels were routinely 60% to 70%.

NIGHTTIME ^{14}C EXPORT AND LEAF DARK RESPIRATION. Leaves were fed with $^{14}\text{CO}_2$ for 2 h as outlined above. To estimate the capacity to export previously fixed C at night, the disappearance of ^{14}C from the source leaf was continuously monitored during a 15-h chase during which the gas stream entering the leaf cuvette did not contain $^{14}\text{CO}_2$. The export of ^{14}C in the dark was then corrected for loss of $^{14}\text{CO}_2$ due to dark respiration. Respiratory release of $^{14}\text{CO}_2$ was determined by trapping the gas in 20% KOH (mass/v) and counting radioactivity by liquid scintillation counting (Leonardos et al., 1996).

Results

ESTABLISHMENT OF ISOTOPIC EQUILIBRIUM OF EXPORTED SUCROSE. Total cumulative fixation increased linearly with time because steady-state photosynthetic conditions were maintained during the 2-h feed period (Fig. 1A). The difference between the total net C fixation rate and the ^{14}C retention rate was used to calculate the export (Fig. 1A). The major labelled photoassimilates accumulated in the rose leaf in the light period were sucrose and starch (Fig. 1 B and C). The specific activity of the sucrose pool remained unchanged after 60 min (Fig. 1D). This labelling pattern, which indicates that isotopic equilibrium of ^{14}C sucrose, was reached within ≈ 1 h (Fig. 1D). The ^{14}C retention rate (Fig. 1A) was also linear after this period. The concurrent export rate was routinely calculated as the difference between the rate of steady-state photosynthesis and the rate of ^{14}C retention in the leaf between the 90- to 120-min period.

Table 1. Characteristics of Samantha roses at three stages of development of a single-stemmed flowering shoot. At stage 1 of shoot development the flower bud was formed but it was not visible. Only five leaves on the flowering shoot had unfolded. At stage 2, leaf expansion was $\approx 90\%$ complete and the developing flower bud was ≈ 1 cm in diameter. At stage 3, all leaves were fully expanded, and the red petal color was visible. Mean values are those of 15 plants $\pm$ SE.

Stage	Leaf area		Shoot length	Bud diam
	(cm 2)	Expansion (%)	(cm)	(mm)
1	209 $\pm$ 13	32	25.9 $\pm$ 0.8	Not visible
2	621 $\pm$ 32	94	46.6 $\pm$ 2.3	8.53 $\pm$ 0.3
3	659 $\pm$ 33	100	54.9 $\pm$ 2.0	20.12 $\pm$ 0.3

Fig. 2. Gas exchange profiles of individual leaves on a single-stemmed rose plants grown at ambient CO_2 . Measurements were made at three stages of shoot development at 35 Pa CO_2 , 25 °C leaf temperature and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Leaf numbers were assigned from the oldest leaf at the bottom of the flowering shoot in an acropetal direction. (A, C, and E) Photosynthetic rates. (B, D, and F) Transpiration rates. Each point is a mean $\pm$ SE of four leaves from four different plants.

LEAF PHOTOSYNTHESIS AND EXPORT DURING SHOOT DEVELOPMENT. At stage 1 of shoot development the flower bud was formed but it was not visible (Jiao et al., 1989; Table 1). Only five leaves on the flowering shoot had unfolded and the total leaf area of the flowering shoot was about one-third of its final leaf area (Table 1). The leaves which had expanded were photosynthetically active, but the C fixation rates of the upper, younger leaves (Fig. 2 A) were lower than those of leaves at stage 2 (Fig. 2 B) and stage 3 (Fig. 2 C). At stage 1 of shoot development, the youngest leaves and stem tissue were still active sinks for photoassimilates. At stage 2, leaf expansion was $\approx 90\%$ complete and the developing flower bud was ≈ 1 cm in diameter (Table 1). At this stage, photosynthetic rates of the lower leaves were slightly greater than those of the upper leaves (Fig. 2 C). At stage 3, all leaves were fully expanded, and the red petal color was visible (Table 1). Leaf photosynthetic rates of the upper (i.e., younger) leaves were slightly higher than those of the lower, older leaves (Fig. 2 E). There was a strong correlation between net photosynthesis (Fig. 2 A, C, and E) and transpiration (Fig. 2 B, D, and F) in individual leaves ($r = 0.81$). By stage 3, the stomatal opening and the capacity for gas exchange were similar in all the leaves (Fig. 2 E and F).

To study the export capacity of leaves at ambient and enriched CO_2 as it related to development of the flowering shoot, gas exchange and concurrent export of only the expanded individual leaves were compared at the three stages of development (Fig. 3). The uppermost unfolded leaf at stage 1 had a relatively high photosynthetic capacity (Fig. 3 A). However, it retained more newly fixed ^{14}C and exported proportionally less ^{14}C than did a leaf at a similar position at a later developmental stage of the shoot (Fig. 3 B and C). At stage 2, the leaf photosynthetic rates were similar to those of the leaves at stage 1 (Fig. 3 A), but export rates during photosynthesis were slightly higher (Fig. 3 B and C). Leaf photosynthesis and concurrent export rates were highest at stage 3. For plants growing at high CO_2 , similar patterns of leaf photosynthesis and export rates during shoot development were observed (Fig. 3).

However, compared to leaves developed at ambient CO_2 , the photosynthetic rates of leaves developed at high CO_2 were 55% and 81% higher at stage 1 and stage 3, respectively (Fig. 3 A). The concurrent export rates from leaves of plants grown at high CO_2 were higher than those of leaves of ambient grown plants (Fig. 3 B), indicating a higher relative efflux rate of C from leaves maintained at high CO_2 (Fig. 3 C).

EFFECT OF TEMPERATURE ON PHOTOSYNTHESIS AND CONCURRENT EXPORT. At ambient CO_2 (i.e., 35 Pa), photosynthesis increased from 8.3 to 10.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ when the leaf temperature was increased from 15 to 25 °C (Fig. 4 A). At 35 °C, leaf photosynthesis was still $\approx 90\%$ of that at 25 °C. At 40 °C, photosynthesis was 40% lower than that measured at 25 °C (Fig. 4 A). Export rate increased from 2.8 to 6.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ as leaf temperature increased from 15 to 25 °C (Fig. 4 B). However, the rates of export were 40% and 80% lower at 35 and 40 °C, respectively (Fig. 4 B). The relative efflux rate, which is the export rate expressed as a percentage of the C fixation rates (Fig. 4 C), was significantly reduced below (i.e., 15 °C) and above (e.g., 35 °C) the optimal temperature. Throughout this paper the C fixation and export rates are compared for leaves fed $^{14}\text{CO}_2$ at 25 °C only (Fig. 4).

EFFECT OF IRRADIANCE. At ambient CO_2 , leaf photosynthesis was saturated at $\approx 500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR (Fig. 5 A). However, for plants grown and assayed at 90 Pa CO_2 , the leaf photosynthetic rate was 50% higher when irradiance was increased from 500 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR (Fig. 5 A). Enrichment with CO_2 increased leaf photosynthesis by 20% at the lowest irradiance tested (i.e., 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR). Photosynthesis was further increased by $\approx 35\%$ between 300 and 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR, and by $>80\%$ at the higher light levels (i.e., 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR).

Export rates during steady-state photosynthesis also increased with increasing PAR under ambient and high CO_2 conditions (Fig. 5 B). Increasing irradiance altered the photosynthesis rate and the concurrent translocation rate differently (Fig. 5). For example, at ambient CO_2 , when PAR was increased from 200 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthesis increased 2-fold (Fig. 5 A), whereas the concurrent export rate increased by a factor of three (Fig. 5 B). When the photon fluence rate was increased from

Fig. 3. Leaf photosynthesis (A), concurrent export rate (B), and relative export flux during photosynthesis (C) of rose plants grown at 35 Pa (○) or 90 Pa (●) CO_2 at three stages of shoot development. Photosynthesis and export measurements were made at 25 °C leaf temperature, 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR and at CO_2 concentrations in which the plants were maintained during the photo-period. Each point is a mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3 (Table 1).

Fig. 4. Effect of leaf temperature during a 2-h assay on the rate of steady-state leaf photosynthesis (A), the concurrent export rate (B) and the relative export flux expressed as a percentage of the photosynthesis rate (C). Plants were grown at ambient CO_2 concentration and measurements were made at $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR and 35 Pa CO_2 concentration. Each point is a mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3 (Table 1).

500 to $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, leaf photosynthesis increased by only 10% (Fig. 5A), but the concurrent export rate was increased by 50%, from 4.1 to $6.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 5B). Similarly, at 90 Pa CO_2 , when the light intensity was raised from 200 to $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, leaf photosynthesis increased 3-fold while concurrent export rate increased 5-fold (Fig. 5B).

The relative efflux rate, which is a measure of export capacity expressed as a percentage of the influx of newly fixed C, increased with increasing irradiance under both CO_2 conditions (Fig. 5C). For example, at ambient CO_2 when PAR was raised from 500 to $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, leaf photosynthesis increased from 9.4 to $10.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while the export rate of the newly fixed C increased from 4.1 to $6.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 5B). This represented an increase in the relative efflux rate from 44% to 59% (Fig. 5C).

Because the relative efflux rate or percentage of ^{14}C being exported immediately increased with increasing irradiance at both CO_2 levels (Fig. 5C), proportionally less ^{14}C was being retained during the 2-h feed period (Fig. 6A). However, in absolute terms, the total μmol of ^{14}C retained in the leaf increased with increasing PAR (Fig. 6B). At high CO_2 leaves accumulated more ^{14}C than at ambient CO_2 , particularly at the higher irradiances (Fig. 5A). Label was partitioned into starch at both CO_2 levels, but at a much lower rate than into sugars (Fig. 6C). Over 90% of the ^{14}C in the sugar fraction was ^{14}C sucrose (Fig. 6C).

EFFECT OF SHORT-TERM AND LONG-TERM CO_2 ENRICHMENT. Leaves of plants which were acclimated to each CO_2 regime were fed $^{14}\text{CO}_2$ at 35 and 90 Pa CO_2 (Table 2). Short-term CO_2 enrichment (i.e., during the feed period only) resulted in an 80% increase in photosynthesis in leaves grown at ambient CO_2 (Table 2). However, the photosynthetic rates of leaves of the high CO_2 grown plants were 25% lower than were those of the ambient grown plants when they were measured at the ambient CO_2 level (i.e., 35 Pa; Table 2). When measured at 90 Pa CO_2 , there was no reduction or loss of photosynthetic capacity in leaves of high CO_2 grown plants compared with that of the plants grown at the ambient CO_2 level and assayed at the high CO_2 level (Table 2).

The effect of short-term and long-term CO_2 treatments on the export capacity during steady-state photosynthesis were similar to those on the photosynthesis rates (Table 2). Leaves that had developed in, and therefore, were acclimated to CO_2 enrichment

had high export rates during photosynthesis, but only when they were assayed at high CO_2 (Table 2). The absolute export rate and relative efflux rates were lower when leaves grown at high CO_2 were measured at ambient CO_2 , and when these values were compared to those of leaves grown and measured at ambient CO_2 (Table 2).

EFFECT OF CO_2 ENRICHMENT ON ^{14}C PARTITIONING AND SUBSEQUENT NIGHTTIME EXPORT. Export capacity in the light (i.e., during the feed period) was compared to that during a 15-h nighttime chase period. Sugars were the major newly fixed ^{14}C products that accumulated in the source leaves exposed to the different CO_2 combinations (Table 2). The sugar-to-starch ratio was ≈ 7 to 1 for plants tested at ambient and enriched CO_2 levels. The fate of these labelled pools of assimilates which accumulated during the 2-h feed was examined further. More ^{14}C was accumulated in the source leaves at high CO_2 (Fig. 7). Leaves of plants fed at high CO_2 exported approximately twice the amount of fixed C during irradiation and during darkness compared to plants fed at ambient CO_2 (Fig. 7, Table 3). Under both CO_2 conditions, C export during photosynthesis (i.e., calculated from the 90 to 120 min period of the feed) was three times greater than that exported during the 15-h dark chase period (Table 3). However, the patterns of disappearance of ^{14}C during the dark period were essentially similar for leaves of plants which were fed at high and low CO_2 levels (Fig. 7). The fastest decline in the radioactivity occurred in the first hour of the dark period. The nighttime respiratory loss of previously fixed ^{14}C was less than the amount of C exported during the chase. Respiratory loss of ^{14}C from leaves treated with high CO_2 was 40% greater than that from the leaves of plants which were at ambient CO_2 during the feed (Table 3). At the end of the 15-h chase period, leaves of high CO_2 grown plants retained about the same amount of ^{14}C assimilates as had been exported during the dark period. At the end of the entire 17-h experiment, leaves of high CO_2 treated plants retained more ^{14}C than did leaves of the plants treated at ambient CO_2 only (Table 3).

When daytime export, nighttime export, nighttime respiratory

losses, and the radioactivity remaining at the end of the entire chase period were expressed as percentages of the total amount of ^{14}C fixed during the feed, there was no significant difference in the allocation of label in leaves

Fig. 5. Effect of irradiance on the rate of steady-state leaf photosynthesis (A), the concurrent export rate (B) and the relative export flux expressed as a percentage of the photosynthesis rate (C) of plants grown at ambient (○) or 90 Pa (●) CO_2 . Each point is a mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3 (Table 1).

Fig. 6. Effect of irradiance on the total ^{14}C accumulated in the feed leaf during a 2-h feed period. Total retention was expressed (A) as a percentage of the total fixed during the 2-h feed, (B) as the absolute amount of carbon retained, and (C) the amount of newly fixed C partitioned into the sugar and the starch fraction after 2 h of steady-state $^{14}\text{CO}_2$ labeling. Plants were grown and measured at 35 Pa ($\circ$) or 90 Pa ($\bullet$) CO_2 concentrations as described in Fig. 5. Each value is a mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3 (Table 1).

of plants at the ambient versus the high CO_2 treatment (Table 3). In both sets of leaves $\approx 75\%$ of that C which was exported during the entire experiment, was actually translocated during the 2-h feed during irradiance indicating the importance of export during photosynthesis regardless of the CO_2 level (Table 3). The major difference in photosynthesis and export in the light was that more ^{14}C was reduced, and therefore, more ^{14}C was exported in total from the leaf which had fixed the ^{14}C at 90 Pa CO_2 (Table 3).

EXPORT DURING PHOTOSYNTHESIS. When the data for photosynthesis and concurrent export were pooled from all conditions (i.e., the three stages of shoot development and the varying environmental conditions which were tested), there was a strong linear correlation ($r = 0.96$) between photosynthetic rate and concurrent export rate (Fig. 8A), indicating that the concurrent export rate was primarily determined by the rate of C fixation during photosynthesis. When export rates in the light at ambient and high CO_2 were pooled and plotted against ^{14}C sugar accumulation in the fed leaves (Fig. 8B), a relationship between the two values existed, but with a lower linear correlation coefficient ($r = 0.65$).

LEAF PHOTOSYNTHESIS AND EXPORT DURING SHOOT DEVELOPMENT. The transition from sink to source status is characterized by a rapid decrease in C import with a concomitant onset of export ability which, in many dicot plants, occurs when the leaf is $\approx 50\%$ fully expanded (Giaquinta, 1978; Milthorpe and Moorby, 1969; Turgeon and Webb, 1973; Wardlaw 1990). Leaves of 'Forever Yours' roses attained their maximum photosynthetic capacity shortly after the red color disappeared from the underside of the leaf, and subsequently declined until the flower developed on the shoot (Aikin and Hanan, 1975). Photosynthetic rates of the cultivar 'Cara Mia' were similar for all leaves which were 10 to 40-d-old (Pasian and Lieth, 1989). Bozarth et al. (1982) reported slightly lower rates of photosynthesis in lower leaves of a flowering shoot of 'Samantha', which was at a stage similar to our stage 2 (Table 1). During development the flower bud receives most of its assimilates from the leaves on that shoot (Jiao et al., 1989). The contribution of each leaf to shoot and flower development is primarily determined by the irradiance intercepted by that leaf and the export capacity of that leaf. With the exception of the very young leaves at stage 1, most leaves on the flowering shoot of 'Samantha' roses had similar photosynthetic capacities at all three stages of development (Fig. 2). At stage 1 leaves retained more newly fixed C for growth, exporting at slightly lower rates than did leaves at later stages (Fig. 3 B and C). The higher export rates of leaves at stage 2 and stage 3 of shoot development would be due to the further development of the laminar tissues and the increased sink strength created by the growth of the developing flower bud (Table 1).

Older leaves near the base of the shoot at stage 3 had relatively high photosynthetic rates. Due to mutual shading in the canopy these leaves usually do not achieve their full photosynthetic and export potential (Jiao et al., 1991b). However, after harvesting of the flowering shoot, the bottom leaves which are frequently left on the mother plant receive more light and can serve as major source leaves for the new axillary bud growth particularly at early stages of development of new shoots (Mor and Halevy, 1979).

TEMPERATURE AND TRANSLOCATION. Photosynthesis in leaves at ambient CO_2 and saturating PAR were optimal at the growth temperature of $\approx 25^\circ\text{C}$ (Fig. 4A). Interestingly, export was inhibited more at high leaf temperature than was C fixation (Fig. 4 B and C). Most commercial growers of 'Samantha' roses are unable to sustain high rates of production when temperatures in the greenhouse rise above 30°C , even with CO_2 enrichment to suppress photorespiration. An inhibition of translocation can in part explain

Table 2. The effects of acclimation to long-term exposure during growth at 35 Pa and 90 Pa CO_2 levels versus short-term exposure of the leaf to either 35 Pa or 90 Pa CO_2 during the assay of leaf photosynthesis, export and partitioning after a 2-h $^{14}\text{CO}_2$ feeding period. Each value is the mean $\pm$ SE of measurements of four expanded leaflets of four different plants. Each leaflet was part of the third most expanded leaf counting down from the top of the flowering shoot of a plant at stage 3.

Growth (Pa CO_2)	35	35	90	90
Assay (Pa CO_2)	35	90	35	90
Photosynthesis ^a ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	11.4 $\pm$ 0.8	19.3 $\pm$ 0.4	7.9 $\pm$ 0.5	18.9 $\pm$ 0.9
Export during the 90 to 120 min period ^b ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	6.7 $\pm$ 0.7	10.9 $\pm$ 0.4	3.8 $\pm$ 0.4	11.7 $\pm$ 0.7
Relative export rate ($\text{b} \cdot \text{a}^{-1} \times 100\%$)	58.7 $\pm$ 2.2	56.7 $\pm$ 2.1	47.7 $\pm$ 3.1	62.3 $\pm$ 1.8
^{14}C partitioning after the 2-h feed period ($\text{mmol} \cdot \text{m}^{-2}$)				
Total retained	40.1 $\pm$ 4.0	65.8 $\pm$ 4.0	34.8 $\pm$ 2.7	57.2 $\pm$ 4.0
Sugars	33.1 $\pm$ 2.6	53.3 $\pm$ 3.3	29.3 $\pm$ 1.7	48.6 $\pm$ 3.1
Starch	4.8 $\pm$ 1.3	9.3 $\pm$ 1.6	2.2 $\pm$ 0.4	6.1 $\pm$ 0.5
Others	2.2 $\pm$ 0.3	3.2 $\pm$ 0.1	3.3 $\pm$ 0.3	2.5 $\pm$ 0.3

Fig. 7. Effects of CO_2 concentration (35 Pa and 90 Pa CO_2) on the pattern of ^{14}C accumulation during the 2-h feed in the light and the subsequent disappearance of radioactivity from the same leaflets during a 15-h chase period in the dark as monitored nondestructively with a GM detector. Plants grown at 35 Pa CO_2 were labelled with $^{14}\text{CO}_2$ at 35 Pa CO_2 for a 2-h period at 25 °C and 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Plants grown at high CO_2 were labelled at 90 Pa CO_2 . During the dark chase period, CO_2 and leaf temperature were maintained at 35 Pa and 25 °C, respectively, for ambient and high- CO_2 -grown plants. Each trace represents a typical analysis profile obtained from a single leaflet. The experiment was repeated four times with the expanded leaflet of four different plants. The leaflet which was measured in each case was part of the third most expanded leaf counted downward from the top of the flowering shoot of a plant at stage 3 as outlined in Fig. 1.

the poor quality of roses produced under high daytime temperatures. Earlier studies with two other ornamental crop species, *Alstroemeria* sp. (Leonardos et al., 1996) and *Salvia splendens* L. (Jiao and Grodzinski, 1996) demonstrated that export during photosynthesis was generally more sensitive to changes in leaf temperature than photosynthesis *per se*. In *salvia*, leaf export rates decreased rapidly when the leaf temperature was changed from 35 to 40 °C. The decrease in the export rate was not simply due to lower photosynthetic rates. When photosynthetic rates were maintained at 40 °C with CO_2 enrichment and low O_2 levels to suppress photorespiration, export was still inhibited (Jiao and Grodzinski, 1996). As the canopy temperature rises the possibility of blockage of the transport pathway and/or inhibition of vein loading, due to callose formation, for example, can be a possible cause of the reduced export (Jiao and Grodzinski, 1996). The extent to which translocation processes in roses are temperature sensitive processes merits further analysis.

EFFECT OF IRRADIANCE ON PHOTOSYNTHESIS AND CONCURRENT EXPORT. In this study the PAR saturation level for 'Samantha' roses was similar to that reported earlier (Bozarth et al., 1982). At ambient CO_2 , photosynthesis was maximal at $\approx 500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. When photorespiration was reduced by exposure to 90 Pa CO_2 , photosynthesis was not saturated below 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR (Fig. 5A). To our knowledge, there has been no study on the effect of varying PAR on C export rates from source leaves in roses.

In 'Marimba' roses, irradiance increases the capacity of the young flowering shoot to import ^{14}C , but the enhancement of the import rate was independent of photosynthesis in the sink (Mor and Halevy, 1980). The effect was attributed to an effect of light quality, possibly mediated by the action of phytochrome on shoot sink activity which increased the unloading processes (Mor et al., 1980). In 'Samantha' roses the export rates of the source leaves increased with increasing light intensities up to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR at both CO_2 levels (Fig. 5C). Collectively our data (Figs. 5A–C, 6A, and 8) show clearly that the effect of light on export during

photosynthesis is not a low PAR phenomenon as suggested by Hartt (1965). Increased irradiance increased the export rate from leaves of *Lycopersicum esculentum* Mill. (Ho, 1976). PAR probably affects export rates during photosynthesis in a number of ways. Most importantly in 'Samantha', PAR stimulated the concurrent export rate by stimulating the leaf photosynthetic rate (Figs. 5A–C, 6A, and 8A) and the mass flow of C into sucrose synthesis (Fig. 8B). However, PAR could also have affected the flux of C out of the mesophyll and into the phloem in another manner. For example, phloem loading and export require energy (Giaquinta, 1972; Hendrix and Grange 1991). It is possible that during irradiance, reducing power is more readily available for these processes than it is in the dark (Côté et al., 1992). The mechanisms by which PAR can, directly or indirectly, regulate C export processes are not known. Since export continues at night, light energy *per se* is not required for export to occur. Nevertheless, the data show that in roses high irradiances sustain maximum C fixation rates and facilitate rapid export of the newly fixed C (Fig. 5). In fact, of the C fixed, >75% of the total C that was exported from the leaf during the total 17-h experiment was mobilized during the 2-h feed period in the light (Table 3). These observations underscore the importance of irradiance and C export during photosynthesis, on greenhouse rose production.

NIGHTTIME EXPORT AND RESPIRATION. Export in the dark requires additional energy which can only be derived from existing photoassimilates. As much as a third of the C stored in starch might be lost through dark respiration in support of the energy requirements for mobilization and export (Bouma et al., 1995). In *Gossypium* plants, nighttime export was highly correlated with starch levels at the end of the photoperiod and with nighttime respiration rates (Hendrix and Grange, 1991). In sugar beet (*Beta vulgaris* L.), it has been shown that during the first 2 to 3 h in the dark the source of C for export was from the sucrose pool which was accumulated during the light period and the concentration of sucrose was an important factor controlling the rate of translocation during this dark period (Geiger and Batey, 1967). Thereafter, polysaccharide was broken down to form sucrose for translocation. In rose plants the ^{14}C sucrose accumulated during the feed period (Fig. 1C) probably served as the primary source of ^{14}C during the nighttime chase. Interestingly, during the first hours of the dark period, the

Table 3. Summary of the effects of CO_2 enrichment on C allocation towards export in a source leaf during a 2-h period of irradiance, and, during a subsequent 15-h dark period at ambient CO_2 as described in Fig. 7. Each value is the mean and the standard error of measurements of four expanded leaflet of four different plants. The values in parenthesis are the mean values expressed as a percentage of the total amount of C which was fixed during the initial 2-h photosynthetic period (i.e., 100%). Export during the 2-h irradiance period in which photosynthesis was constant was derived based on the rate of concurrent export determined for the 90- to 120-min period of the $^{14}\text{CO}_2$ feed (see Table 2). The leaflet which was measured was one on the third most expanded leaf from the top of the flowering shoot of a plant at stage 3, which had been grown and assayed at the same CO_2 level (i.e., grown in 35 Pa and assayed in 35 Pa CO_2 or grown in 90 Pa and assayed at 90 Pa CO_2).

	35 Pa (mmol·m ⁻²)	90 Pa (% of total fixed)
Growth/assay CO_2		
Total C fixed	82.8 ± 6.8 (100%)	137 ± 12 (100%)
Exported during irradiance	48.1 ± 4.0 (59%)	85.8 ± 5.8 (62%)
Exported in the dark	14.8 ± 1.2 (18%)	26.1 ± 2.8 (19%)
Respired in the dark	6.1 ± 0.8 (7%)	7.3 ± 1.3 (6%)
Retained in the leaf	14.1 ± 1.5 (16%)	16.9 ± 1.8 (13%)

Fig. 8. Relationships between (A) concurrent export rate and leaf photosynthetic rate and (B) concurrent export rate and sugar accumulation in the source leaves. Photosynthesis and export of leaves during different stages of shoot development and under different light, temperature conditions and two CO₂ levels, 35 Pa (○) or 90 Pa CO₂ (●) were pooled.

rate of loss of ¹⁴C was fastest (Fig. 9). This seems to be the case in leaves exposed to either ambient or high CO₂ treatments during the feed (Fig. 6C, Table 2). The slightly higher dark respiration rates observed in the leaves treated at high CO₂ (Table 3) may be due simply to the fact that in these leaves there was more carbohydrate available for export during the night period (Drake et al., 1997; Grodzinski, 1992). The increased respiration rates may therefore reflect the increased demand for energy to sustain nighttime export. Rose leaves that had fixed the ¹⁴C under CO₂ enrichment had higher nighttime export rates (Table 3). These data are important since they indicate that in spite of the fact that during CO₂ enrichment more C was initially available for export, the relative distribution and use of the reduced ¹⁴C in the leaves were the same in the two CO₂ conditions. Greenhouses normally receive CO₂ enrichment only during the day (Porter and Grodzinski, 1985). In these experiments CO₂ enrichment was not supplied during the dark chase period in an attempt to mimic the nighttime growth conditions. Taken together, the data show that the primary difference between the high and ambient CO₂ conditions was the amount of ¹⁴C initially fixed (Table 3), and not the proportional amounts of ¹⁴C being exported during irradiance versus in the dark (Table 3).

ACCLIMATION TO CO₂ ENRICHMENT: EFFECTS ON LEAF PHOTOSYNTHESIS AND EXPORT. In commercial greenhouses equipment for supplying and maintaining high CO₂ levels can fail. It is noteworthy therefore that when attached source leaves of 'Samantha' roses which were acclimated to growth at 90 Pa CO₂ were challenged to fix and export C at a lower CO₂ level (i.e., 35 Pa) photosynthesis and translocation rates were lower than rates for leaves of plants acclimated to growth at ambient CO₂ (Table 2). However, even though there was a reduction in photosynthesis and export of attached leaves of plants acclimated to 90 Pa CO₂ when assayed at 35 Pa rather than at 90 Pa, there can be no doubt that the rates of C fixation and export at the higher CO₂ level (i.e., 90 Pa) were greater than those of the leaves assayed and grown at 35 Pa CO₂ (Table 3).

Several researchers have noted a decline in leaf photosynthetic activity in some herbaceous, C₃ species when grown at high CO₂ (Besford et al., 1990; Porter and Grodzinski, 1984; Sage et al., 1989; Yelle et al., 1989). In several species there are reductions in extractable leaf protein, and more specifically, decreases in the *in vitro* activities of one or more key enzymes (e.g., RUBISCO, RUBISCO activase and carbonic anhydrase, CA) which are associated with photosynthetic carbon fixation (Bowes, 1993; Grodzinski, 1992; Stitt, 1992). In leaves of *Rosa hybrida* 'Red

Success' (Beeson and Graham, 1991) observed that following several weeks of growth at high CO₂ the RUBISCO and CA levels were not depressed as was the case with leaves of a number of C₃ species. In leaves of 'Samantha' roses grown at 150 Pa CO₂ for 6 weeks there was a small reduction of 10% and 30% in the activity of RUBISCO and CA respectively (data not shown). Whether or not these small decreases in extractable, enzyme activities could account for the slight decrease in C fixation and export rates in attached source leaves of plants acclimated to high CO₂, but assayed at 35 Pa (Table 2) remains to be determined. What is important with the data for 'Samantha' is the observation that when assayed at the CO₂ level under which the roses were growing (i.e., 90 Pa CO₂), attached source leaves fixed and exported more C than did leaves of plants which were maintained at ambient CO₂.

The increases in photosynthetic and export rates during CO₂ enrichment reported here are the primary physiological reasons for increased shoot biomass and crop productivity observed in commercial greenhouse roses during production under CO₂ enrichment. It has been suggested that the depression of photosynthesis in some species under long-term CO₂ enrichment can be due to the failure of the demand for C export to keep up with the supply of photoassimilates (Wardlaw, 1990 and references therein). As in many other woody species (Kozlowski, 1992), a large amount of dry matter is partitioned in rose plants into the stem tissue. Therefore, in addition to the flower bud, the stem tissue is a major sink for the allocation of assimilates. In 'Samantha' roses we observed that CO₂ enrichment increased stem length and diameter, even though the dry mass of the flower was not markedly increased (Jiao et al., 1991a).

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