A close relationship between the 2 species is suggested by the number and types of compounds common to both. Although variation is seen in the glycosidic types especially of the flavones, the aglycones are the same. The major difference appears to be the presence of scutellarein glucoside in *B. vittata* and apigenin 7-apiosylglucoside in *A. glomerata*. The only report on some of the chemical constituents of the *Bromeliaceae* is that by Hegnauer (11). Our investigation on the flavonoid composition of 2 taxa of *Bromeliaceae* suggests that a detailed analysis of the flavonoids of various species in both genera would be of taxonomic value.

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# Photosynthesis in the Rose; Effect of Light Intensity, Water Potential and Leaf Age[1]


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*Abstract:* The net rate of $^{14}CO_2$ uptake was determined on individual leaves of *Rosa hybrida*, cv. 'Forever Yours', budded on *Rosa manetti* and grown in gravel. Rose leaves were found to reach an average peak of 11 mg $CO_2$ $dm^{-2}$ $hr^{-1}$ about 6 days after the red color disappeared on the leaf underside, or 32 days after harvesting the previous flower on the parent cane. Thereafter, $CO_2$ uptake declined during 14 days to 5 to 6 mg $CO_2$ $dm^{-2}$ $hr^{-1}$. At ambient $CO_2$ concentrations of 500 ppm, the maximum net uptake was near 3400 ft-c. However, internal plant water potential influenced the $CO_2$ uptake by reducing it at each increase of radiant energy. This resulted in light saturation at lower energies the lower the plant water potential. Radiant energy affected both net $CO_2$ uptake and water potential. Wilting was generally observed to occur at about −13 bars, and maximum rates of $CO_2$ uptake were found at potentials of −8 bars or higher, over a range of 350 to 450 microeinsteins, or 3000 to 3500 ft-c.


There is inadequate information on basic physiological processes in the rose. In order to intelligently manipulate environment for maximum production, one of the important factors to elucidate is how the rate of photosynthesis may vary with changes in the environment. Provided sufficient, accurate information is obtained, it may be possible to predict the environment required for the rose to produce at its genetic potential. This study reports on effects of radiant intensity, water potential, and changes in net $CO_2$ uptake with leaf age.

## Materials and Methods

*Rosa hybrida*, cv. 'Forever Yours', budded on *R. manetti*, were established in a granitic gravel in 15 liter, plastic containers, and grown in a fiberglass-covered greenhouse. Temperatures were 16.7°C nights and 22.2°C days. Forced-air ventilation began between 25.6 and 26.7°C. The total ventilation time during this study (October to May), was less than 20 hours. Relative humidity during the daylight hours was maintained near 70% with high pressure mist. $CO_2$ was injected at the same time at sufficient rates to maintain 500 ppm under conditions of maximum solar radiation when the ventilation system was off. The plants were automatically irrigated 2 to 5 times daily, depending upon the season, using a nutrient solution devised by Sadisaviah (9).

*Technique.* The net $CO_2$ uptake determination method we used has been described by Shmishi (8). Briefly, leaf sections were exposed to flowing $^{14}CO_2$, total $CO_2$ level 500 ppm, for about 30 seconds. One cm diameter leaf sections were excised, digested to remove the $^{14}C$, and the resultant activity determined by liquid scintillation counting. The method was deliberately chosen for its versatility in the field, although precision may be decreased. Supplemental studies included examination of radiation differences within the greenhouse as the result of location, calibration for the loss of counting sensitivity ("quenching") due to the technique used for incorporating $^{14}C$ in the scintillation fluid, radiation transmittance through the plastic $^{14}CO_2$ leaf applica-


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[2] Graduate Assistant and Professor respectively. This paper presents a portion of the thesis for the M.S. degree by the senior author, and supported by Roses, Inc. and the Joseph H. Hill Foundation. Published with the approval of the Director, CO State Univ. Agr. Expt. Sta., Ft. Collins, as Scientific Series No. 2054.

[3] Model 756, Weston Instrument Co., Monterey Park, CA.

[4] Lampda Instrument Co., Lincoln, NE., Sensor Mod. No. L1-190S.

[5] Model IT-2, Barnes Engineering Co., Stamford, CN.

tor device, and relationships between internal plant water potential ($\psi$) and solar radiation. Untreated leaf samples were taken before and after any series of determinations in order to assess possible $^{14}C$ contamination.

*Leaf age.* Observation showed that leaf age could not be reliably determined by leaf size, since leaf size varies markedly at maturity. Immature 'Forever Yours' rose leaves are red on the underside, and this red color gradually disappears as the leaf matures. Leaves become fully green at a fairly uniform age, and this date was designated as "day zero" when relating $^{14}CO_2$ uptake to leaf age. The first 5-leaflet leaf from the base of a flowering stem was sampled.

*Radiant energy.* Initial studies employed a color-corrected, non-cosine corrected, illumination meter calibrated in ft-c[3]. The instrument was held horizontally above the selected leaf prior to sampling. The instrument had the advantage of ease of handling. Later studies used a cosine corrected photometer[4], with a much smaller sensor, calibrated in microeinsteins in the photosynthetic wavelengths of 400 nm to 700 nm. Positioning was similar to that described for the illumination meter.

*Water potential.* Determinations of internal water potential of cut shoots followed procedures described by Scholander et al. (7) and Boyer (1) for the pressure chamber. The shoot was cut immediately after $^{14}CO_2$ exposure, and taken directly to the pressure bomb. In any given series of measurements, sampling was generally begun prior to sunrise, and continued at regular intervals to about 1300. Cloudy days were avoided unless the sky was uniformly overcast.

## Results and Discussion

*Effect of leaf age.* Maximum net $CO_2$ uptake occurred about 8 days after the red color disappeared from the leaf underside (Fig. 1), or approximately 36 days after cutting the previous flower from the parent cane. Leaves 6 to 8 days older had $CO_2$ uptake of 75% of the peak, and this declined to 50% of the maximum after another 6 to 8 days. At 40 to 50 days after the red color disappeared, the flower was fully open, and the entire stem was removed. Higher values were obtained before "day zero" because of difficulties with small and tender leaves. The clamping technique caused young leaves to fold in the exposure chamber, resulting in more tissue being exposed to $^{14}CO_2$.

The results were consistent with those reported in the literature (e.g. 4, 10). About 40 to 50 days were required between initiation of the flowering stem from its parent cane and cutting of the flower for sale.

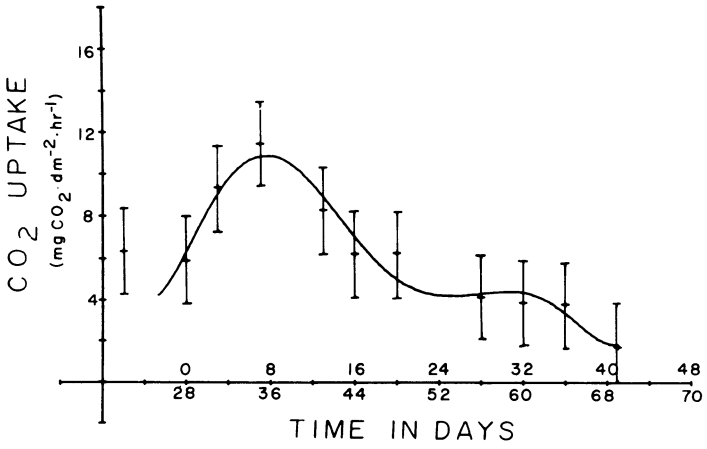


Fig. 1. $^{14}CO_2$ uptake in 'Forever Yours' rose leaves at 500 ppm $CO_2$ concentration as a function of leaf age. Bottom scale on the abscissa is time in days since the last flower was cut. Means are averages of 7.2 samples for each data point from the first 5-leaflet leaf from the base of the flowering stem. The data were subjected to analysis of variance. The error mean square from this analysis was used to calculate the HSD confidence interval shown by the vertical bars at a 5% probability level. The curve was then fitted to the means by the least squares method, r = 0.976.

This would appear to be sufficient time for all leaves on the stem to have reached a maximum rate of $CO_2$ uptake before the stem was cut for sale. Green leaves remaining on the rose stem after harvesting the flower likely assimilate at less than half of their original maximum. It can be appreciated that leaf age, as well as environmental effects, influence the photosynthetic rate.

*Effect of light intensity.* At 500 ppm $CO_2$, maximum $CO_2$ uptake was found to occur at about 3400 ft-c (Fig. 2). The rate of uptake per increment of energy ($\Delta$ $CO_2$ uptake/$\Delta$radiation), gradually declined with increasing energy, reaching zero about 3400 ft-c. At intensity levels below 200 to 300 ft-c, assimilation increased with each 100 ft-c of light 0.5 mg $CO_2$ $dm^{-2}$ $hr^{-1}$. Above 2000 ft-c, the added increment per 100 ft-c was less than 0.1 mg $CO_2$. A change of 100 ft-c between 400 and 500 ft-c resulted in a 29% increase in $CO_2$ uptake, but only an 8% increase between 1000 and 1100 ft-c. In recent years, considerable interest has been generated in supplemental irradiation for roses (e.g. 3, 6). Our data suggest that above 1000 ft-c of solar radiation, the electrical power and installation expense for high intensity, supplemental lighting is probably not warranted on the basis of increases in photosynthetic rates.

The higher than normally quoted saturation light intensity for individual leaves, of 2000 to 2500 ft-c (5, 10), was expected with the elevated $CO_2$ concentration used in this study. As shown by Gaastra's work (4), high assimilation rates with elevated $CO_2$ levels require higher energy levels for saturation. Thus, $CO_2$ injection may not be as effective in climatic areas with low solar radiation as compared to those having a high radiant regime.

*Effect of water potential and radiation.* Preliminary studies of water potential ($\psi$) in rose stems showed considerable variation, depending upon stage of maturity. Stages 1 and 4 had average water potentials different from Stages 2 and 3 (Fig. 3). Stage 4 had a mean value of about $-10$ bars, whereas stage 1, under similar conditions, had a mean of about $-4$ bars. Stages 2 and 3 were usually selected for $^{14}C_2$ treatment.

Response to increasing solar radiation was less as internal plant water potential decreased (Fig. 4), and light saturation occurred at a lower level. A $\psi$ of $-4$ bars was never observed in Stages 2 and 3 at light intensities approaching 5000 ft-c.

Light intensity and $\psi$ were found to be closely correlated. Technically, one assumes in statistical analyses that the data are randomly distributed about the mean, and in multiple linear analyses, the

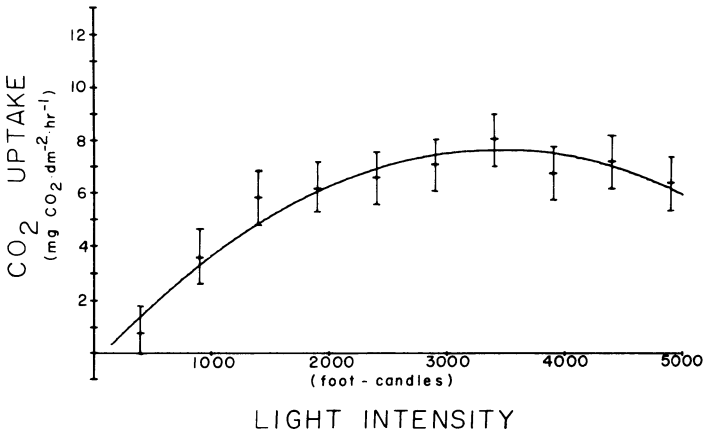


Fig. 2. Effect of light intensity on $^{14}CO_2$ uptake in mature 'Forever Yours' rose leaves at 500 rpm $CO_2$ concentration. The average number of samples per mean was 10.8, and the means subjected to an analysis of variance. The error mean square from this analysis was used to calculate the HSD confidence interval shown by the vertical bars at a 5% probability level. Curve was fitted to the means by the least squares method:

$$CO_2 \text{ uptake} = -0.3239 + 0.004668X - (6.8 \times 10^{-7})X^2,$$

where

X = light intensity: Correlation (r) = 0.968.

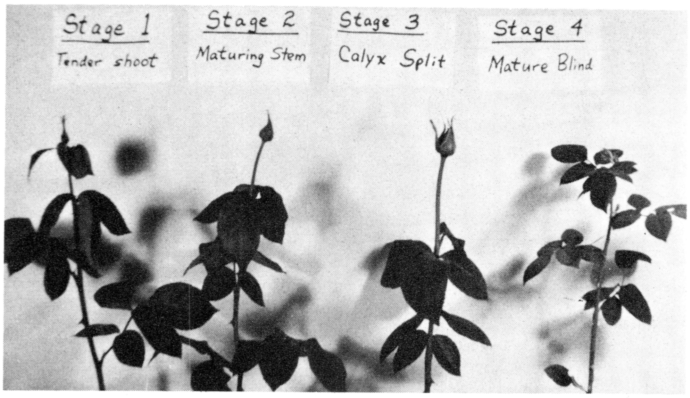


Fig. 3. Four developmental stages of 'Forever Yours' roses selected for determining average water potential in the stem under equal conditions of water supply and radiant intensity.

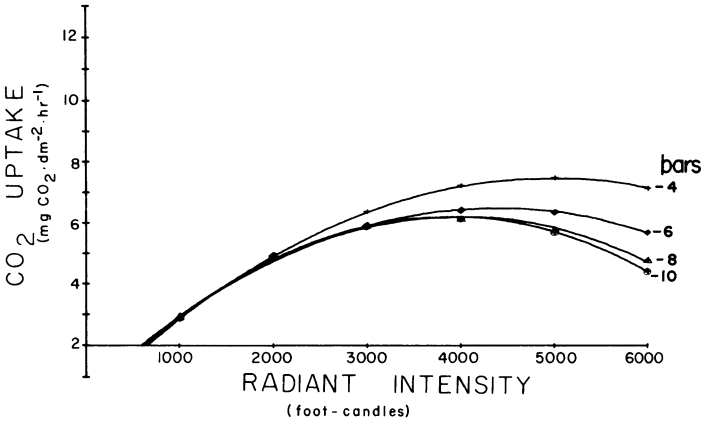


Fig. 4. $^{14}CO_2$ uptake in mature 'Forever Yours' rose leaves at 500 ppm concentration as a function of light intensity with internal water potential held constant. Note that the curves were adjusted to a common point on the abscissa.

variables are independent. However, it is acceptable procedure to compensate for lack of independence and non-linearity by generating new variables that express the interrelationships between the original variables (Fig. 5). This often may be a matter of trial and error. In this instance, simple correlation coefficients ranged from 0.71 to 0.91. The effect of potential on net $CO_2$ uptake in the rose was similar to that obtained by Boyer (2) for other species. Under our conditions, decreasing potentials: 1) decreased the light saturation point, and 2) decreased the rate at which $CO_2$ uptake changed with increasing radiant energy (Figs. 4, 5). The trend of the surface contour plot (Fig. 5) suggests that there may be an optimum radiant energy level, for maximum assimilation, at $\psi$'s of $-4$ bars or higher.

These data deal with the net $CO_2$ uptake of roses under conditions approximating commercial conditions. The technique requires large samples with particular attention paid to leaf exposure, age of leaf and internal water potential. The resultant variability may have accounted for the fact that we were unable to include leaf temperature in

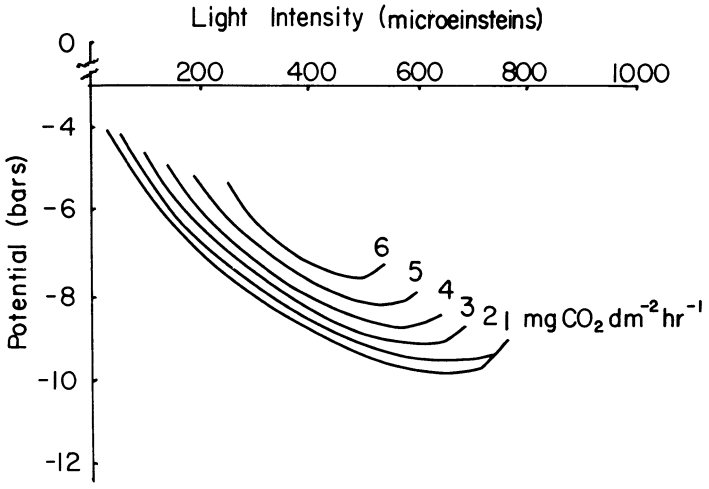


Fig. 5. Response surface plot of $^{14}CO_2$ uptake of mature 'Forever Yours' fose leaves at 500 ppm $CO_2$ concentration as a function of water potential and radiant energy. Curves connect points to equal $^{14}CO_2$ uptake. Formula for plot construction:

$$^{14}CO_2 \text{ uptake} = -9.22443 - 0.00747X_1 \pm 5.73419X_2 - 0.00009X_1^2 - 0.87206X_2^2 + 0.01268X_1X_2$$

where $X_1$ and $X_2$ are radiant energy and water potential respectively, r = 0.942.

multiple variable equations to help express photosynthetic behavior with greater accuracy. Several trials were made using leaf temperatures as determined with an infrared thermometer[5]. Or, the temperature range might not have been sufficient to markedly effect assimilation rate as compared to radiant energy and $\psi$.

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