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PRIMARY PRODUCTION AND CARBON ALLOCATION IN CREOSOTEBUSH: THE EFFECT OF CARBOHYDRATE LEVELS ON DARK CO$_2$ RELEASE

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ABSTRACT

The effect of substrate levels on the rate of dark respiration of shoots of the warm desert evergreen perennial, *Larrea tridentata* (creosotebush), was investigated. Measurements of dark CO_2 release were made on shoots of intact plants, using an open infrared gas analysis system. Levels of total nonstructural carbohydrates were measured at the beginning of an experiment and estimated during the course of an experiment from CO_2 exchange data. Rates of dark CO_2 release were compared to both the concentration of total nonstructural carbohydrates and the amount of CO_2 accumulated during the light period immediately preceding the dark CO_2 release measurements. It was found that the rate of dark CO_2 release is a function of total nonstructural carbohydrate concentration and not a function of CO_2 accumulated in the preceding light period except when total nonstructural carbohydrate concentrations are extremely low.

INTRODUCTION

Early attempts to develop models of the net production of plant communities assumed that dark respiration was a function only of plant biomass and environmental conditions (Duncan et al. 1967). It is becoming apparent, however, that dark respiration is also a function of the levels of photosynthetically produced respiratory substrates (McCree 1970). Our attempts to develop a computer model simulating carbon gain and allocation in the widespread desert perennial, *Larrea tridentata* (creosotebush), have shown that model outputs are very sensitive to predicted rates of dark respiration. It also appears that net production is very much underestimated if dark respiration is assumed to be only a function of plant biomass and environmental conditions (i.e., temperature and water status). This underestimate of net production apparently results from overestimation of dark respiration caused by a failure to include the possibility of substrate limitations to dark respiration in the model (Reynolds and Cunningham, in prep.).

McCree (1970) has shown that the dark respiration rate of *Trifolium repens* L. is correlated with the amount of net photosynthesis which occurs during the previous light period. It remains an open question, however, as to whether dark respiration rates are dependent on photosynthate accumulated only during the previous light period or are dependent upon the total nonstructural carbohydrate levels in the plant. We therefore investigated this question for *Larrea tridentata* by measuring rates of dark respiration and expressing them as a function of both net photosynthesis during the previous light period and total nonstructural carbohydrate (TNC) levels within the plant.

METHODS

Field transplants of small (height < 20 cm) *Larrea tridentata* plants were established in native soil in quart pots. Plants and soil were both obtained from Dona Ana County, New Mexico. Following establishment, the plants were transported to the Duke University Phytotron, Durham, North Carolina, where they were barerooted and repotted in 1-quart containers with a 50:50 v:v mixture of sterilized vermiculite and gravel. The plants were then maintained in a controlled-environment room for a minimum of 10 weeks before measurements of dark respiration rates were made. Conditions in the controlled environment room were: photoperiod and thermoperiod 16:8 hr day:night; temperature 30:20 C day:night; irradiance 550 $\mu E \cdot m^{-2} \cdot s^{-1}$ PhAR.

The plants were watered every other day, alternating with distilled water and one-half strength Hoagland's solution. Three plants were used for the experiments. The shoot of each plant was subsampled after removal from the controlled environment room for analysis of TNC levels (Smith 1969). Three subsamples of each tissue harvested were used and each of these was analyzed by three separate titrations. TNC levels were expressed as a percentage of tissue dry weight. The plant was then placed in the measurement cuvette of an open, infrared gas analysis system for evaluation of net CO_2 exchange rates. The gas analysis system, techniques of operation and methods of calculation were essentially the standard ones described by Šesták et al. (1971). Outside air was drawn into the system and humidified to a dew point of 11 C before entering the cuvette. The difference between CO_2 concentrations in the inlet and outlet air streams of the cuvette was measured with a Beckman 215B Differential Infrared Gas Analyzer. Interfering water vapor was removed from the air streams entering the IRGA by magnesium perchlorate. The measurement cuvette was a 23.8-liter Plexiglas box with an internal heat exchanger and fan to provide temperature control and a constant air flow over the shoot. The roots were isolated from the air stream measuring shoot CO_2 by sealing the pot in a second smaller cuvette located inside the first. An air flow around the pot was maintained through the inner root cuvette so that CO_2 efflux from the roots could be measured. Irradiance was provided by a 300-watt incandescent lamp (G.E. PAR 56/2MFL). A 15% copper sulfate solution was used to filter out excess longwave radiation. Irradiances were measured at the height of the top of the pot, using a Lambda quantum sensor. All temperatures were measured using copper-constantan thermocouples.

The first plant (A) remained in the dark for 104 hr at 20 C after being placed in the measurement cuvette. Following this dark period a 16:8 hr day:night photoperiod was reestablished along with the original 30:20 C day:night thermoperiod. During the first light period, irradiance was maintained at 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. During each subsequent light period it was raised by 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ giving 800, 1200, 1600 and 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$ on days 6, 7, 8 and 9, respectively. The second plant (B) was treated similarly except that the initial dark period was reduced to 56 hr. The third plant (C) was not given an extended dark period but maintained on the 16:8 hr day:night photoperiod. For plant C, irradiance was 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$ during the first light period and was reduced in each subsequent light period by 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ until it was 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ on the last day.

RESULTS AND DISCUSSION

Rates of net CO_2 exchange from the shoot during the 10 days of observation are shown for plant A in Figure 1. During the 104 hr in the dark, the rate of CO_2 release under constant environmental conditions tended to decrease with time (after approximately 50 hr), thus indicating a possible decrease in dark respiration as carbohydrate reserves were depleted. In subsequent dark periods the rate of CO_2 release increased with increasing net CO_2 uptake in the previous light period, resulting from the increased irradiance during each subsequent light period. This relationship between dark CO_2 release and CO_2 uptake during the previous light period is shown more clearly in Figure 2. When net CO_2 release in the dark was plotted as a function of net CO_2 uptake in the previous light period, a linear relationship ($r^2 = 0.85$, $P < 0.005$) was obtained. Plant B, which was maintained in the dark for only 56 hr before the first light period, did not show as strong a linear correlation between net CO_2 uptake in the light and net CO_2 release in the subsequent dark period ($r^2 = 0.40$, $P < 0.3$). For plant C, which was placed directly in the light and irradiance decreased rather than increased with each successive light period, no linear correlation was observed between dark net CO_2 release and net CO_2 uptake in the previous light period. These results indicate rates of

dark respiration in *Larrea* are more closely correlated with net CO_2 uptake in the previous light period following extended periods of net CO_2 release by the plant. This leads one to conclude that the nonstructural carbohydrate accumulated during the previous light period is important only in controlling rates of dark respiration when total nonstructural carbohydrate levels have been depleted to some extent. This, of course, indicates total nonstructural carbohydrates as the rate-controlling substrate, not simply carbohydrate produced during the previous light period.

This is shown more clearly in Figure 3 where rate of net CO_2 release in the dark is plotted as a function of percent total nonstructural carbohydrate. The CO_2 release rate values were taken every hour during the dark periods on each of the three plants. The percent TNC value for each CO_2 release rate observed was calculated by adding the carbohydrate equivalent of CO_2 taken up in the light or subtracting the carbohydrate equivalent of CO_2 released in the dark from the previous value of TNC calculated for the plant. For each plant the initial values of percent TNC are given in Table 1. An analysis of variance indicated no significant differences in percent TNC between stems and leaves so a mean of the stem and leaf value was used for each plant. Carbohydrate
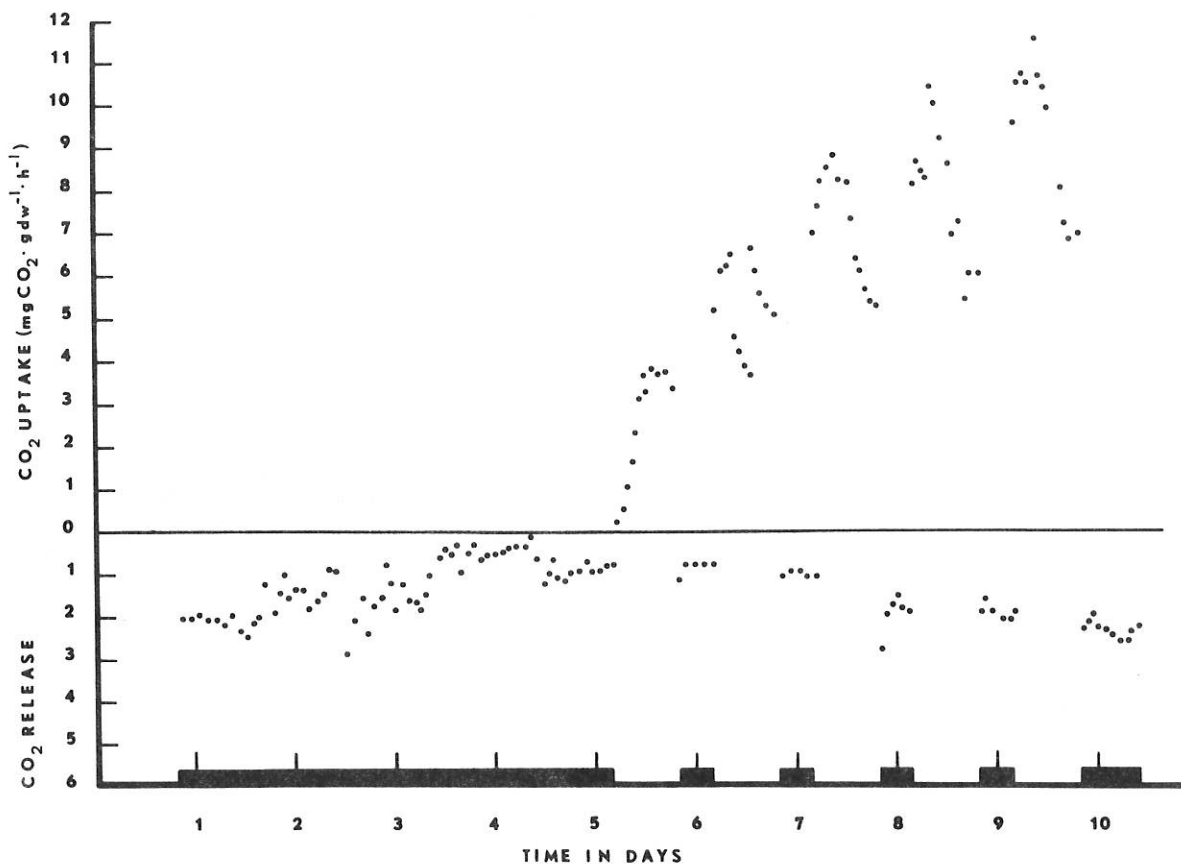

Figure 1. Course of net CO_2 exchange rates during the experimental treatment of plant A. Details of the protocol are given in the text. Bars along the abscissa indicate dark periods.
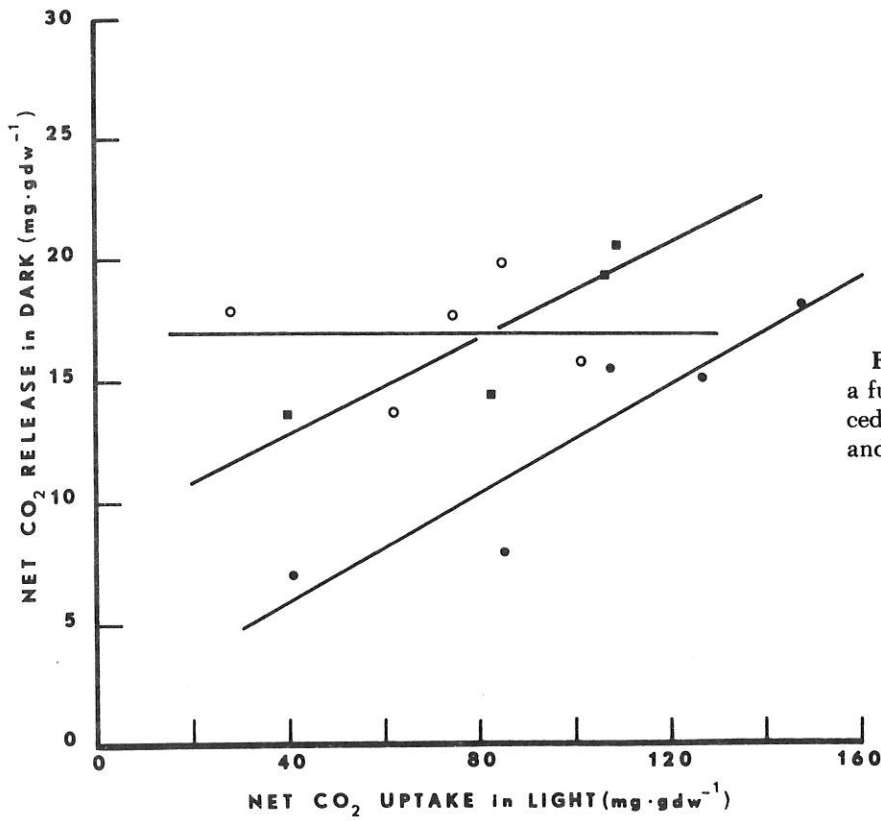
Figure 2. Net CO_2 release in the dark as a function of net CO_2 uptake in the preceding light period for plants A (•), B (■) and C (o).
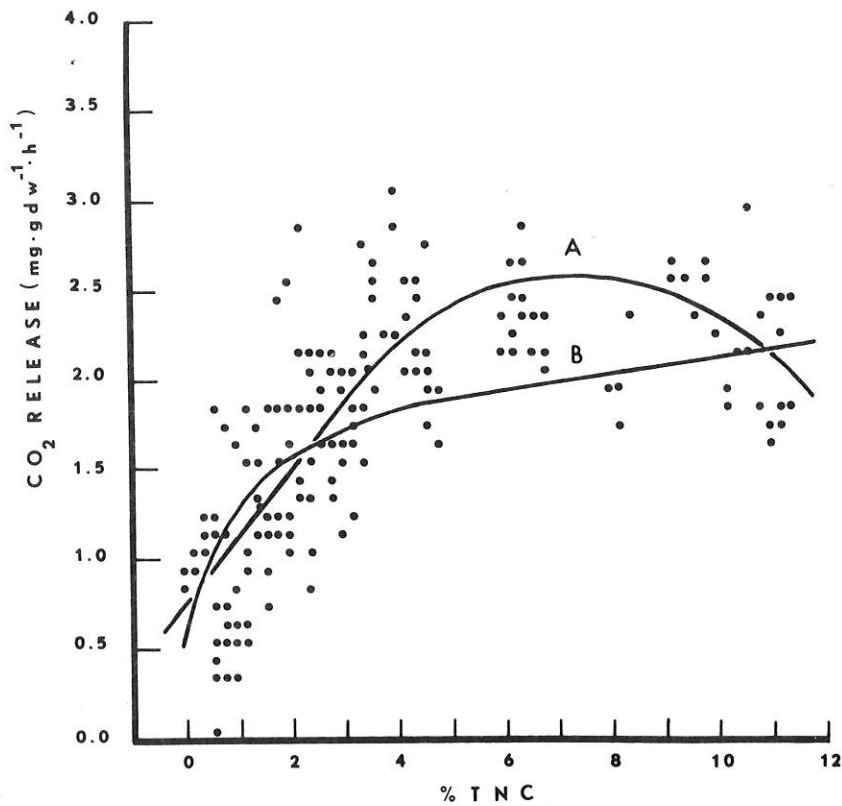

Figure 3. Rate of net CO_2 release in the dark as a function of estimated levels of total nonstructural carbohydrates (TNC) in percentage of dry weight. Lines representing the logarithmic (A) and quadratic (B) regression models are also shown.

equivalents of CO_2 lost by root respiration were also subtracted from the TNC value, assuming roots were drawing upon leaf and stem carbohydrate reserves to meet respirational demands. The actual number of data pairs represented on the graph is 292, but data pairs with identical coordinates are shown by only a single point.

The data appear to fit the logarithmic relationship that would be expected if substrate can become the limiting factor controlling rate of net CO_2 release. This relationship can be described:

$$F = k_1 + e^{k_2}S$$

where

F = rate of net CO_2 release (mg $CO_2 \cdot gdw^{-1} \cdot hr^{-1}$)
S = total nonstructural carbohydrates (%)
e = base of the natural logarithm
k_1 and k_2 = constants

This equation was linearized to the form $F = k_1 + k_2 \ln S$ and used as a regression model. A significant regression was obtained ($r^2 = 0.49$, $P < 0.001$). Therefore, the hypothesis that the data fit the logarithmic model cannot be rejected. Closer inspection of the data indicates there may be a tendency for the rate of net CO_2 release to be depressed at the highest TNC percentages. If this is the case, the data would be expected to fit a quadratic relationship of the form $F = k_1 + k_2 S + k_2 S^2$. When this equation was used as the regression model, a significant regression was also obtained ($r^2 = 0.68$, $P < 0.001$); the hypothesis that the data fit a quadratic equation cannot be rejected. Thus, it appears that there may be an inhibition of net CO_2 release at substrate levels above about 9% TNC. It must be remembered, however, that the values of percent TNC given were calculated from initial measured values and carbohydrate equivalents of CO_2 taken up or released by the plant. Therefore, we are not certain that TNC levels actually reach these higher values. It may be that nonstructural carbohydrate was converted to structural materials, unavailable for respiratory substrate, before it accumulated to 10-12% of dry weight. The fact that we have never measured TNC greater than 8.6% in *Larrea* indicates that this may be true. (Data are stored under DSCODE A3UCL01.)

CONCLUSIONS

The results presented show that rates of net CO_2 release in the dark from shoots of *Larrea tridentata* vary over a wide range, even when air temperature and, presumably, leaf temperature are constant. Plants which have had their nonstructural carbohydrate reserves reduced to low levels by being maintained in the dark exhibit a linear increase in dark CO_2 release with increasing net CO_2 uptake during the preceding light period. If, however, nonstructural carbohydrate levels are not depleted, net CO_2 release in the dark is not a linear function of net CO_2 uptake in the previous light period. This, coupled with the fact that up to 68% of the variation in net CO_2 release in the dark (at a constant

Table 1. Total nonstructural carbohydrate content (TNC) in percent dry weight for leaves and stems of the three experimental plants at the beginning of CO_2 exchange measurements. Values given are means of nine observations as explained in the text. 1 SD = 1.40

	Plant		
	A	B	C
Leaves	4.67	4.23	7.67
Stems	4.70	5.05	8.63

temperature) can be accounted for by the percent total nonstructural carbohydrate in the plant, leads to the conclusion that rates of net CO_2 release in the dark are a function of total nonstructural carbohydrate levels as well as environmental conditions. Therefore, the effect of total nonstructural carbohydrate levels on net dark CO_2 release must be included in models which attempt to simulate *Larrea* production. Our results indicate that either of the regression models used will provide an adequate prediction of net dark CO_2 release if the total nonstructural carbohydrate levels in the plant are below approximately 9%, which in our experience they always are.

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