

Growth Respiration, Maintenance Respiration, and Carbon Fixation of Vinca: A Time Series Analysis

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ADDITIONAL INDEX WORDS. photosynthesis, dark respiration, carbon use efficiency, conversion efficiency, glucose requirement, maintenance coefficient, *Catharanthus roseus*

ABSTRACT. Respiration is important in the overall carbon balance of plants, and can be separated into growth (R_g) and maintenance respiration (R_m). Estimation of R_g and R_m throughout plant development is difficult with traditional approaches. Here, we describe a new method to determine ontogenic changes in R_g and R_m . The CO_2 exchange rate of groups of 28 'Cooler Peppermint' vinca plants [*Catharanthus roseus* (L.) G. Don.] was measured at 20 min intervals for 2 weeks. These data were used to calculate daily carbon gain (DCG, a measure of growth rate) and cumulative carbon gain (CCG, a measure of plant size). Growth and maintenance respiration were estimated based on the assumption that they are functions of DCG and CCG, respectively. Results suggested a linear relationship between DCG and R_g . Initially, R_m was three times larger than R_g , but they were similar at the end of the experiment. The decrease in the fraction of total available carbohydrates that was used for R_m resulted in an increase in carbon use efficiency from 0.51 to 0.67 $\text{mol} \cdot \text{mol}^{-1}$ during the 2-week period. The glucose requirement of the plants was determined from R_g , DCG, and the carbon fraction of the plant material and estimated to be 1.39 $\text{g} \cdot \text{g}^{-1}$, while the maintenance coefficient was estimated to be 0.031 $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ at the end of the experiment. These results are similar to values reported previously for other species. This suggests that the use of semicontinuous CO_2 exchange measurements for estimating R_g and R_m yields reasonable results.

Carbon accumulation is the primary process for plant biomass production, and depends both on photosynthesis and respiration. The relationship between photosynthesis and plant growth has been studied extensively, but the importance of respiration is commonly underestimated, even though respiration is very important in the overall carbon balance of plants (Jiao et al., 1996). The carbon use efficiency of plants (CUE, the amount of carbon incorporated into dry matter divided by the total amount of carbon fixed in the photosynthetic process) is normally only 50% to 70% (Amthor, 1989). This implies that the other 30% to 50% of the carbohydrates fixed in photosynthetic processes are respired.

Carbon fixation by plants can be measured as their CO_2 exchange rate. These measurements yield net photosynthesis (P_n) during the light period and dark respiration (R_d) during the dark period. Gross photosynthesis (P_g) is calculated as $P_n + R_d$, based on the common assumption that respiration is similar in the light and in the dark (e.g., Gifford, 1995; McCree, 1982; van Iersel and Bugbee, 2000). Dark respiration of plants can be divided into two different physiological processes: growth respiration (R_g) and maintenance respiration (R_m). Growth respiration is defined as the amount of carbohydrates respired in processes that result in a net gain in plant biomass. This includes the production of ATP and reductant for biosynthetic processes, transport processes, and nutrient uptake and reduction (Chiariello et al., 1989). Maintenance

respiration is defined as the respiration needed to provide the energy for all plant processes that do not result in a net increase in plant dry matter, such as maintenance of ion gradients across membranes and the resynthesis of degraded organic compounds (Chiariello et al., 1989).

Growth respiration can be used to calculate the conversion efficiency [Y_g ($\text{g} \cdot \text{g}^{-1}$), the amount of plant dry matter (g) produced from 1 g of glucose], while R_m is used to determine the maintenance coefficient [the amount of glucose respired for maintenance per unit dry weight (DW) per d, $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$]. Both the conversion efficiency and the maintenance coefficient are important parameters in crop growth models (Gifford et al., 1995; Heuvelink, 1995).

Growth respiration (R_g) and R_m are difficult to separate, because there is no clear distinction at the biochemical level and both processes result in a CO_2 efflux from plants. Therefore, they cannot be measured separately and are estimated commonly using physiological models (McCree, 1982; Thornley, 1970; Thornley and Johnson, 1990). In these models, it is normally assumed that R_g is proportional to the growth rate of the plants, while R_m is proportional to the DW of the plant (Chiariello et al., 1989). This last assumption is especially questionable, since R_m depends not only on the weight, but also on the chemical composition of the plant. Plants contain a significant amount of nonbiodegradable compounds (e.g., lignin), that do not require maintenance (McCree, 1982), while proteins require a relatively large amount of maintenance (Johnson, 1990; Thornley, 1977). The fractions of nonbiodegradable biomass and proteins may change during plant development, which would likely affect R_m and the maintenance coefficient. In addition, many current approaches to estimating R_g and R_m rely on occasional, infrequent measurement of respiration. Because there are distinct daily fluctuations in the respiration rate of plants (Seymour, 1999; van Iersel and Bugbee, 2000), these measurements may not be an accurate estimate of the respiration rate throughout the day.

Received for publication 17 Dec. 1999. Accepted for publication 19 June 2000. We thank Keven Calhoun and Larry Freeman for technical assistance and The University of Georgia Research Foundation for financial support. Mention of brand names is for information only and does not constitute an endorsement to the exclusion of other products that may also be suitable. 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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Other approaches for estimating R_g and R_m are based on the chemical composition of the plant material (Penning de Vries et al., 1974) or the heat of combustion and organic nitrogen content of the plant tissue (Williams et al., 1987). These methods require destructive sampling, and are thus not well-suited to determining developmental changes in the conversion efficiency or maintenance coefficient.

There has been little improvement in techniques for studying R_g and R_m since the initial work by McCree (1974), Penning de Vries et al. (1974), and Thornley (1970). Studying changes in R_g and R_m throughout plant development has been difficult. Using a combination of semicontinuous, whole-plant CO_2 exchange measurements and time series analysis (a new statistical approach to analyzing this type of data; Seymour, 1999), we describe a nondestructive approach for determining R_g and R_m throughout plant development. Our approach does not assume linear relationships between growth rate and R_g , or plant DW and R_m , making it easier to detect changes during plant development. This new approach is based on the premise that the CO_2 exchange rate of plants can be used as a measure of the growth rate, while the total amount of carbon in the plant can be used as a measure of plant size. Indeed, it has been argued that expressing plant weight in terms of carbon equivalents is a convenient approach to whole-plant respiration and growth research (Thornley and Johnson, 1990).

Materials and Methods

PLANT MATERIAL. 'Cooler Peppermint' vincaseeds (*Catharanthus roseus*) were planted in a peat-based growing mix (Redi-Earth; The Scotts Co., Marysville, Ohio) and germinated in the dark at 20 °C. The seedlings were subsequently transferred to a double-layer polyethylene greenhouse and grown until the second pair of true leaves appeared. Temperature set points for the greenhouse were days/nights of 23/18 °C. The seedlings were then transplanted into cell packs (166 mL/cell) filled with diatomaceous earth (Isolite CG-2; Sundine Enterprises, Arvada, Col.). During transplanting, most of the growing mix was removed from the root system by dipping the roots in water. Diatomaceous earth was used as a posttransplant growing medium in this experiment, because it is easy to remove from the root system and thus facilitates accurate plant DW measurements. Diatomaceous earth is a chemically inert growing substrate consisting mainly of SiO_2 (78%), Al_2O_3 (12%), and Fe_2O_3 (5%), with a low cation exchange capacity ($<0.02 \text{ meq} \cdot \text{g}^{-1}$).

Eight groups of 28 seedlings were placed in watertight trays and transferred to transparent acrylic chambers ($3.2 \times 5 \times 6 \text{ dm}^3$), which were placed inside two larger growth chambers (model E-15; Conviron, Asheville, N.C.). The plants were watered as needed with a complete 20N-4.4P-16.6K water-soluble fertilizer (20-10-20 Peat-Lite Special; The Scotts Co.), containing N at $100 \text{ mg} \cdot \text{L}^{-1}$. Environmental conditions inside the chamber were 14 h days/10 h nights of 22/18 °C, and a photosynthetic photon flux of $425 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at the canopy level. This resulted in a total daily photon flux of $21.4 \text{ mol} \cdot \text{m}^{-2}$. Relative humidity inside the acrylic chambers was $\approx 75\%$ during the light period and 100% at night.

CARBON DIOXIDE EXCHANGE MEASUREMENTS. Whole-plant carbon exchange rate (CER) of each group of 28 plants was measured with an open CO_2 exchange system (van Iersel and Bugbee, 2000). Ambient air was blown into the acrylic chamber and air flow was measured with mass flow meters (GFM37-32; Aalborg Instruments and Controls, Monsey, N.Y.). The difference in the CO_2 concentration of the air entering and exiting the chamber was measured with an infrared gas analyzer (LI-6251; LI-COR, Lincoln, Nebr.). Whole

chamber CER ($\mu\text{mol} \cdot \text{s}^{-1}$) was calculated as the product of mass flow ($\text{mol} \cdot \text{s}^{-1}$) and the difference in CO_2 concentration ($\mu\text{mol} \cdot \text{mol}^{-1}$). Gas exchange data of each group of plants were collected at 20 min intervals until 26 d after transplanting. Both P_n and R_d data are reported as positive quantities and all data represent the CER of groups of 28 plants. To give the plants ample time to get established and adjust to the conditions in the gas exchange system, the data from the first 12 d of the experiment were not used for analysis.

Since whole plants, including the containers, were enclosed in the gas exchange chamber, CER measurements included root-zone respiration. Root-zone respiration consists of respiration by the roots and by microorganisms in the growing medium. Since root respiration is part of the whole plant metabolism, this should be included in whole plant CER measurements. Microbial respiration resulting from the breakdown of organic products leaking from plant roots also should be included in whole plant net CER measurements, since the carbon in these compounds was originally fixed in the photosynthetic process but is no longer available for plant growth after it leaks from the roots (van Iersel and Bugbee, 2000).

DATA ANALYSIS. Growth rates in the eight gas exchange chambers differed because of experimental treatments (van Iersel, 1999). To assure that comparisons among plants from different chambers were meaningful, we selected data from three chambers with similar growth rates for determination of R_g and R_m .

The interpretation of continuous CER data is difficult with standard statistical techniques, because the data are both serially and periodically correlated. Serial correlation means that an observation at any given time are correlated with the prior observations, while periodic correlation means that the data at any given time are correlated with data from the same time during prior days (i.e., there are regular daily patterns in the CER of plants). This type of data cannot be analyzed adequately with standard regression techniques, but periodic time series analysis has been developed to analyze this type of periodically correlated data (Seymour, 1999). Time series techniques were used to fit regression curves to long-term P_n and R_d data, resulting in estimates P_n^* and R_d^* ($\text{mol} \cdot \text{s}^{-1}$), respectively. These estimates were used to calculate the gross photosynthesis, growth rate or daily carbon gain, cumulative carbon gain, and carbon use efficiency:

$$P_g^* = P_n^* + R_d^* \quad [1]$$

$$\text{DCG} = (t_{\text{light}} \times P_n^*) - (t_{\text{dark}} \times R_d^*) \quad [2]$$

$$\text{CCG} = \int \text{DCG} \, dt \quad [3]$$

$$\text{CUE} = \text{DCG} / (t_{\text{light}} \times P_g^*) \quad [4]$$

where P_g^* = estimated gross photosynthesis ($\mu\text{mol} \cdot \text{s}^{-1}$); P_n^* = estimated net photosynthesis ($\mu\text{mol} \cdot \text{s}^{-1}$); R_d^* = estimated dark respiration ($\mu\text{mol} \cdot \text{s}^{-1}$); t_{light} = duration of the light period ($\text{s} \cdot \text{d}^{-1}$); t_{dark} = duration of the dark period ($\text{s} \cdot \text{d}^{-1}$); DCG = daily carbon gain ($\text{mol} \cdot \text{d}^{-1}$); CCG = cumulative carbon gain (mol C); and CUE = carbon use efficiency ($\text{mol} \cdot \text{mol}^{-1}$, calculated according to van Iersel and Bugbee, 2000).

Note that CCG is a measure of carbon or biomass accumulation since the start of the experiment; a CCG of zero does not indicate that the plant DW was zero, but rather that there was no increase in the amount of C in the plant since the start of the CER measurements.

Since growth respiration (R_g) is a function of the growth rate, and maintenance respiration (R_m) a function of plant size, dark respiration (R_d) can be expressed as a function (f_1) of growth rate plus a function (f_2) of plant size:

$$R_d = R_g + R_m = f_1(\text{growth rate}) + f_2(\text{plant size}) \quad [5]$$

These functions are not necessarily linear, and their shape can be determined from the data. In this case, we found that a modified Richards function described the data accurately ($R^2 > 0.99$):

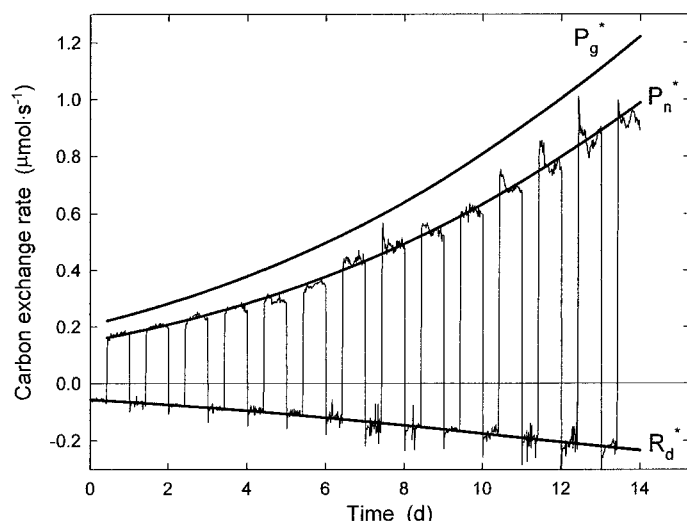


Fig. 1. Carbon exchange rate of a group of 28 vinca plants during a 14-d period. The bold lines indicate the estimated net photosynthesis (P_n^*), dark respiration (R_d^*), and gross photosynthesis (P_g^*) using time series analysis. Note that R_d^* has a negative value in this figure, because it relates to the CO_2 exchange rate of the plants. In the rest of this paper, R_d^* refers to the CO_2 efflux from the plants and has a positive value.

$R_d^* = R_m + R_g = x_0 + x_1 \times (1 + e^{(x_1 - x_2 \times \text{CCG})})^{x_3} + y \times \text{DCG}$ [6]
where x_0 , x_1 , x_2 , x_3 , and y are regression coefficients; R_m = maintenance respiration ($\mu\text{mol}\cdot\text{s}^{-1}$); R_g = growth respiration ($\mu\text{mol}\cdot\text{s}^{-1}$); R_d^* = estimated dark respiration ($\mu\text{mol}\cdot\text{s}^{-1}$); DCG = daily carbon gain ($\text{mol}\cdot\text{d}^{-1}$); and CCG = cumulative carbon gain (mol C). This modified Richards function is flexible and was fitted with the nonlinear regression procedure (PROC NLIN) of SAS (SAS Inst., Inc., Cary, N.C.).

When the growth rate (or DCG) is zero, growth respiration (R_g) is by definition zero, thus:

$$R_m = x_0 + x_1 \times (1 + e^{(x_1 - x_2 \times \text{CCG})})^{x_3} \quad [7]$$

$$R_g = y \times \text{DCG} \quad [8]$$

These two functions were chosen based on a preliminary analysis of data from eight gas-exchange chambers (van Iersel, 2000). That analysis indicated there was a linear relationship between R_g and DCG , but not between R_m and CCG .

Growth respiration can be used to calculate the conversion efficiency (Y_g) and the glucose requirement [$1/Y_g$ ($\text{g}\cdot\text{g}^{-1}$), the amount of glucose needed to produce 1 g of plant material] of the plants. Because the conversion efficiency and the glucose requirement are used as indicators of the biochemical efficiency of the conversion of glucose into new plant material, the glucose lost in R_m is normally not included in these estimates. Thus, the glucose requirement ($1/Y_g$) can be calculated as the sum of the amount of glucose used in R_g to produce new plant material and the amount of glucose needed to provide the carbon for the new plant material.

$$1/Y_g = [(30 \times F_c \times R_g)/(\text{DCG} \times 12)] + (30 \times F_c/12) \quad [9a]$$

$$= 2.5 \times F_c \times [(R_g/\text{DCG}) + 1] \quad [9b]$$

where F_c = carbon fraction of the plants ($\text{g}\cdot\text{g}^{-1}$); R_g = growth respiration (for simplicity now expressed in units of $\text{mol}\cdot\text{d}^{-1}$, instead of $\text{mol}\cdot\text{s}^{-1}$); DCG = daily carbon gain ($\text{mol}\cdot\text{d}^{-1}$); 30 ($\text{g}\cdot\text{mol}^{-1}$) converts moles of CO_2 to grams of glucose; and 12 ($\text{g}\cdot\text{mol}^{-1}$) converts moles of C to grams of C. The first part of Eq. [9a] determines how much glucose is respired $[(30 \times F_c \times R_g)/(\text{DCG} \times 12)]$, while the second part of the equation calculates the amount of glucose needed to provide the carbon for the new plant material ($30 \times F_c/12$).

In this experiment, F_c of the plants was only determined at the end of the experiment, since destructive sampling would have interfered with the CER measurements. Therefore, it is assumed that F_c was constant. This same assumption has been made previously in similar research (e.g., Monje and Bugbee, 1998).

Results and Discussion

Both P_n and R_d of the plants increased during the 14-d period. Example data from one of the groups of plants are illustrated in Fig. 1. The increase in P_n was likely the result of increased light interception by the expanding canopy, while R_d increased because of increasing R_m and R_g as the plants became larger and the growth rate increased. The plants never became large enough to intercept all the radiation, at which point P_n would be expected to reach a maximum.

Carbon use efficiency of the plants also increased from 0.51 to 0.67 $\text{mol}\cdot\text{mol}^{-1}$ over time and with increasing plant size (Fig. 2A and B), which is within the range of normal values for CUE (Amthor, 1989). This increase in CUE is consistent with the finding of Winzeler et al. (1976) that the ratio of respiration to photosynthesis of young unculm barley (*Hordeum vulgare* L.) plants decreases during the first few weeks of plant development. An increase in CUE indicates that a smaller fraction of the carbohydrates fixed in the photosynthetic process was lost by respiration as the plants became larger. This more efficient use of carbohydrates suggests that there was a fundamental change in the fraction of carbohydrates allocated to respiratory processes (R_m and/or R_g) in the plants.

The estimates for R_m and R_g are illustrated in Fig. 3A, together with R_d^* . Both R_m and R_g increased throughout the experiment. Initially, R_m was much larger than R_g and accounted for 76% of R_d^* (Fig. 3B). Growth respiration increased more rapidly than R_m and at the end of the 14-d period, R_m accounted for 55% and R_g for 45% of R_d^* .

The regression results indicate that the relationship between DCG and R_g was linear (Eq. [8], Fig. 4). The slope of the regression line of R_g versus DCG was 2.69 ± 0.93 ($\mu\text{mol}\cdot\text{s}^{-1}$)/($\text{mol}\cdot\text{d}^{-1}$), or 0.232 ± 0.080 $\text{mol}\cdot\text{mol}^{-1}$ (mean \pm SE). This indicates that R_g accounted for 0.232 mol of CO_2 /mol of C that was incorporated into the plants. This value can be used to calculate a theoretical maximum value for the CUE of these plants, which is achieved when R_m is a negligible

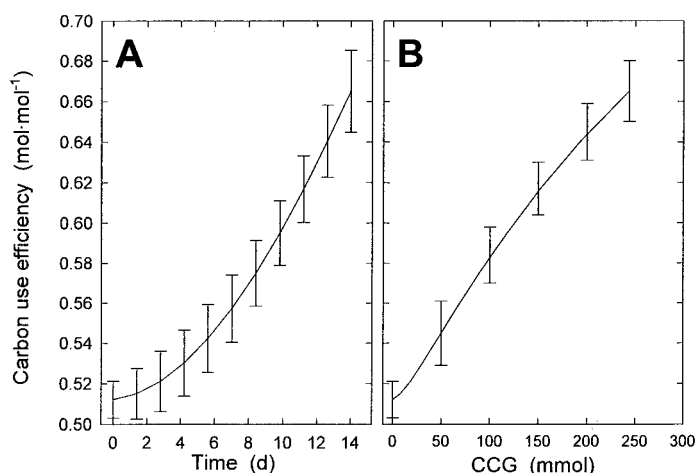


Fig. 2. Carbon use efficiency (mean \pm SE) of three groups of 28 vinca plants as a function of (A) time and (B) cumulative carbon gain (CCG), a measure of plant size.

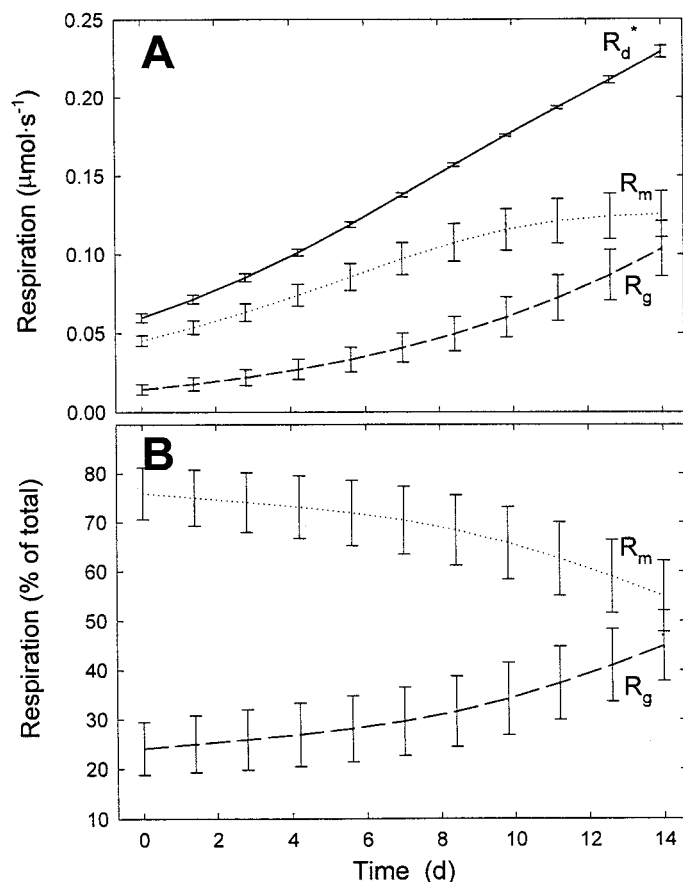


Fig. 3. Estimated dark (R_d^*), growth (R_g), and maintenance respiration (R_m) of three groups of 28 vinca plants during a 14-d period (mean \pm SE). Estimates of R_g and R_m were based on the assumption that R_g is a function of the growth rate and R_m is a function of the plant size. The respiration data are shown both as (A) their actual rate and as (B) a percentage of total dark respiration.

part of total respiration (i.e., all respiration is R_g). To add 1 mol of C to the plant, a total of 1.232 mol C is needed (1 mol that is incorporated into the plant plus 0.232 mol that is respired), so the maximum CUE that these plants could reach was 0.812 mol·mol⁻¹ (1/1.232). Carbon use efficiency was lower than this theoretical maximum, because a significant fraction of the available carbohydrates was used for R_m (Fig. 3).

Since both the growth rate and R_g of the plants are known, the conversion efficiency (Y_g) of the plants can be calculated using Eq. [9b]. The carbon fraction of the plants at the end of the experiment was 0.45 and was assumed to have been constant throughout the 14-d growing period. Since R_g /DCG also was constant throughout the experiment (Fig. 4), the glucose requirement (1/ Y_g) of the plants was constant and estimated to be 1.39 ± 0.05 g of glucose per g of newly produced biomass (mean \pm SE). This estimate is very close to the commonly used values of 1.39 and 1.45 g·g⁻¹ for leaves and stems of nonleguminous species, respectively (Penning de Vries et al., 1989). It is also close to the 1.34, 1.54, and 1.46 g·g⁻¹ reported for whole soybean [*Glycine max* (L.) Merr.] and sorghum [*Sorghum bicolor* (L.) Moench] plants (Amthor et al., 1994), and leaves of yellow-poplar [*Liriodendron tulipifera* L.] (Wullschlegel et al., 1997), respectively. A glucose requirement of 1.39 g·g⁻¹ yields a conversion efficiency of 0.72 g·g⁻¹, which is well within the normal range of 0.6 to 0.8 g·g⁻¹ (McCree, 1982).

The maintenance coefficient was also close to previously reported values. At the end of the experiment, the DW of the plants was

10.6 \pm 0.7 g, while the final R_m was 0.125 ± 0.015 μmol·s⁻¹. Thus, maintenance respiration was 0.012 ± 0.002 μmol·g⁻¹·s⁻¹, resulting in a maintenance coefficient of 0.031 ± 0.004 g·g⁻¹·d⁻¹. Most previously reported values range from 0.003 to 0.050 g·g⁻¹·d⁻¹ (Hesketh et al., 1980). The maintenance coefficient of plants is much more variable than the conversion efficiency, because it depends on the age of the plant and the environmental conditions, especially temperature (Mariko and Koizumi, 1993; Walker and Thornley, 1977).

The overall distribution of the available carbohydrates among growth, R_g , and R_m during this 14-d experiment is shown in Fig. 5. Based on the results of this analysis, it is evident that CUE increased throughout the 14-d period, because a smaller fraction of the total available carbohydrates was used for R_m as the plants became larger. Thus, a larger fraction of the carbohydrates was available for growth and R_g , increasing CUE.

The comparison of our estimates of R_g and R_m with previously reported values suggests that our approach results in reasonable estimates. However, an important difference between our approach and previous research is that we did not have to assume a linear relationship between growth and R_g or between plant size and R_m . Indeed, we found that the relationship between plant size and R_m was not linear (Eq. [7]). This is consistent with previous work: based on CO₂ exchange measurements throughout the life cycle of barley, Winzeler et al. (1976) found that a linear relationship between R_m and plant DW did not describe the experimental data adequately, especially early in the life cycle. Similarly, Hughes (1973) found that a linear model resulted in a negative R_m during the early development of chrysanthemum (*Dendranthema ×grandiflorum* Kitam.). The findings of Hughes (1973) and Winzeler et al. (1976) indicate that modeling R_g and R_m as linear functions of growth rate and DW respectively, is an oversimplification of the whole-plant carbon balance. It seems likely that R_g , R_m , the conversion efficiency, and the maintenance coefficient depend on tissue, organ, and plant age (Gary et al., 1998b; Thornley and Johnson, 1990), as well as many physiological and environmental factors (Amthor, 1989). For example, a high mineral content of plant material can result in an increase in the conversion efficiency, because of the relative dilution of the organic matter in the plant (Gary et al., 1998a). The main reason that the assumption of linear relationships between growth rate and R_g and between plant weight and R_m is commonly made appears to be its simplicity. It allows for estimating

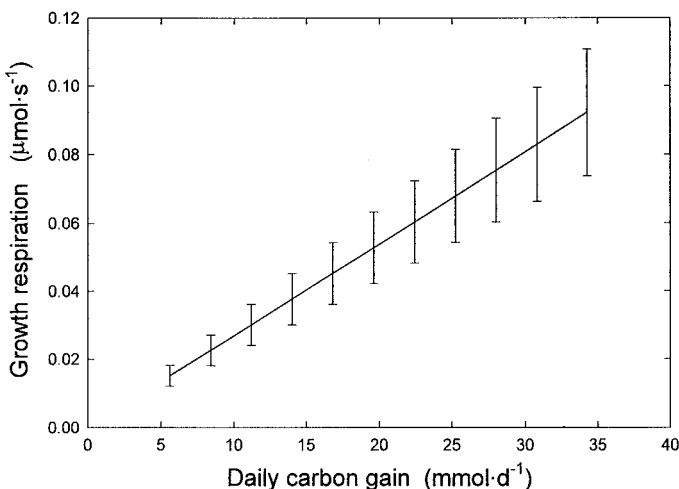


Fig. 4. Estimated growth respiration as a function of daily carbon gain (a measure of growth rate) of three groups of 28 vinca plants during a 14-d period (mean \pm SE).

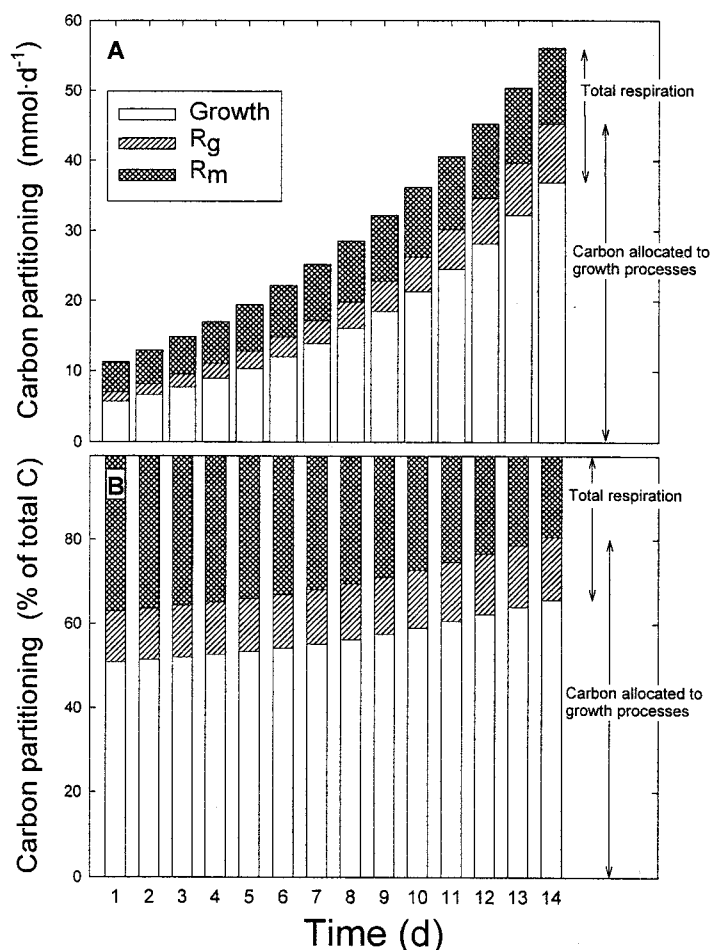


Fig. 5. Distribution of the total available carbohydrates among growth, growth respiration (R_g), and maintenance respiration (R_m) during a 2-week period, expressed as (A) their actual rate and as (B) a percentage of the total amount of available carbohydrates. Note that the fraction of carbohydrates allocated to R_m decreases, even though R_m increases with increasing plant age.

R_g and R_m from CO_2 exchange measurements of plants with different growth rates (Chiariello et al., 1989).

Using semicontinuous CER measurements, we have developed a technique to estimate R_g and R_m that does not depend on the assumption of linear relationships between growth rate and R_g or between plant weight and R_m . This makes it feasible to determine changes in R_g and R_m during plant development. Comparisons of our estimates of the conversion efficiency and maintenance coefficient indicate that this approach results in realistic estimates. This approach can be used to quantify the effects of cultural and environmental factors on R_g and R_m .

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