Carbon use efficiency depends on growth respiration, maintenance respiration, and relative growth rate. A case study with lettuce

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ABSTRACT

Carbon use efficiency (C_{UE}, the ratio between the amount of carbon incorporated into dry matter to the amount of carbon fixed in gross photosynthesis) is an important parameter in estimating growth rate from photosynthesis data or models. It previously has been found to be relatively constant among species and under different environmental conditions. Here it is shown that C_{UE} can be expressed as a function of the relative growth rate (r_{GR}) and the growth (g_r) and maintenance respiration coefficients (m_r): $1/C_{UE} = 1 + g_r + m_r/r_{GR}$. Net daily carbon gain (C_{dg}), r_{GR}, and C_{UE} were estimated from whole-plant gas exchange measurements on lettuce (*Lactuca sativa* L.) ranging from 24 to 66 d old. Carbon use efficiency decreased from 0.6 to 0.2 with increasing dry mass, but there was no correlation between C_{UE} and C_{dg}. The decrease in C_{UE} with increasing dry mass was correlated with a simultaneous decrease in r_{GR}. From the above equation, g_r and m_r were estimated to be 0.48 mol mol^{-1} and 0.039 g glucose g^{-1} dry matter d^{-1}, respectively. Based on the g_r estimate, the theoretical upper limit for C_{UE} of these plants was 0.68. The importance of maintenance respiration in the carbon balance

of the plants increased with increasing plant size. Maintenance accounted for 25% of total respiration in small plants and 90% in large plants.

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INTRODUCTION

Photosynthesis is the basic process driving plant growth, but obtaining accurate estimates of plant growth from photosynthesis measurements can be difficult. To do so, one needs to know how efficiently carbohydrates are converted into structural dry matter (Amthor 1994). Convenient parameters in this regard are carbon use efficiency (C_{UE}, the ratio between the amount of carbon incorporated into dry matter to the amount of carbon fixed in gross photosynthesis), and the ratio between daily respiration and daily gross photosynthesis ($R : P = 1 - C_{UE}$). Cannell & Thornley (2000) suggested that C_{UE} varies within a limited range (approximately 0.4–0.6), when averaged over weeks or longer and that mechanistic models should predict limited variation in C_{UE}. This argument is based on reports that the C_{UE} of various species and under different environmental conditions is relatively constant (Gifford 1994, 1995; Ryan, Lavigne & Gower 1996; Goetz & Prince 1998; Monje & Bugbee 1998; Reich *et al*. 1998a, b; Ziska & Bunce 1998). Probably the most convincing evidence for limited variation in C_{UE} was presented by Gifford (1994), who reported that the C_{UE} of plants was remarkably constant (about 0.6) among seven diverse species, with dry masses ranging over two orders of magnitude. Growing temperature (from 15 to 30 °C) affected C_{UE} only slightly. Using a mechanistic model of short-term carbon dynamics, Dewar, Medlyn & McMurtrie (1998) found that C_{UE} is approximately constant under variable light conditions, when averaged over days to weeks. A sudden change in temperature only has a short-term effect (2–3 d) on C_{UE} (Gifford 1995).

However, others have shown that C_{UE} can vary greatly, either among or within species. For example, Ryan *et al*. (1997) found that the C_{UE} of pine (*Pinus*) stands can vary from 0.36 to 0.68. The C_{UE} of wheat is relatively constant throughout much of the life cycle, but decreases rapidly near the end of the life cycle, as photosynthesis declines more rapidly than respiration after anthesis (Monje & Bugbee 1998). Similarly, Winzeler, Hunt & Mason (1976) found large ontogenetic changes in the C_{UE} of barley (*Hordeum vulgare* L.), which increased early in the life cycle, and decreased again during the second half of the life cycle. Carbon use efficiency of vinca (*Catharanthus roseus* (L.) G. Don) was negative shortly after transplanting of bare-rooted seedlings, because of a sharp increase in dark respiration, but subsequently increased to 0.7 with increasing plant size and age (van Iersel 1999). Amthor (1989) argued that C_{UE} should decline throughout the vegetative growth phase, because an increasing fraction of total respiration is associated with maintenance, leaving a smaller fraction for growth and growth respiration. Finally, Amthor (2000) showed in a literature review that there are large differences in C_{UE}, both among and within species. Based on the respiratory needs for growth and maintenance, he estimated that C_{UE}, averaged over long periods (i.e. a growing season), may vary from 0.2 to 0.65.

Although there is substantial evidence that changes in C_{UE} are fairly small under some circumstances, it is not clear by which physiological mechanism plants would be able to maintain C_{UE} at a specific level. A constant C_{UE} suggests that plants always respire the same fraction of the carbohydrates fixed in gross photosynthesis (P_g). To get a better understanding of how C_{UE} is determined, it is useful to separate respiration into growth (R_g) and maintenance respiration (R_m) (Cannell & Thornley 2000; see Amthor (2000) for an in-depth discussion of different growth and maintenance respiration paradigms). Growth and maintenance respiration cannot be clearly separated at the biochemical level, because they share certain biochemical pathways [i.e. for the production of ATP and NAD(P)H, Amthor (2000)]. Nonetheless, this concept has proven useful for modelling growth and respiratory processes in plants (Heuvelink 1995; Marcelis & Baan Hofman-Eijer 1995 , Amthor 2000, Thornley & Cannell 2000).

For C_{UE} to remain constant throughout the life cycle of a plant, R_g and/or R_m would have to vary in some specific limited ways in response to changes in P_g. Although growth, and therefore R_g, clearly depends on the amount of carbohydrates fixed in P_g, there has not been a physiological explanation of how plants would maintain their C_{UE} at a certain constant level. Based on the concept of growth and maintenance respiration, a constant C_{UE} throughout plant development appears unlikely. Carbon use efficiency can be defined as:

$$C_{UE} = C_{dg}/P_{g,day} \quad (1)$$

where C_{dg} is the net daily carbon gain and $P_{g,day}$ is the total gross photosynthesis of a plant during that same day. Since all carbon either remains in the plant (C_{dg}) or is respired, and respiration can be separated into R_g and R_m, Eqn 1 can be rewritten as:

$$C_{UE} = C_{dg}/(C_{dg} + R_t) \quad ((2a))$$
$$= C_{dg}/(C_{dg} + R_g + R_m) \quad ((2b))$$

where R_t is the total daily respiration.

Growth respiration can be calculated as the product of the growth coefficient (g_r) and the growth rate, and R_m equals the maintenance coefficient (m_r) × plant size (Amthor 2000), where dry mass (M_d) is a commonly used measure of plant size. Note that g_r and m_r do not necessarily have to be constant throughout plant development, although they often are assumed to be (e.g. McCree 1974; Hansen & Jensen 1977). Since C_{dg} can be used as a measure of the growth rate of a plant, it follows from Eqn 2b that:

$$C_{UE} = C_{dg}/[C_{dg} \times (1 + g_r) + m_r \times M_d] \quad (3)$$

or

$$1/C_{UE} = [C_{dg} \times (1 + g_r) + m_r \times M_d]/C_{dg} \quad ((4a))$$
$$= 1 + g_r + m_r \times M_d/C_{dg} \quad ((4b))$$

since C_{dg}/M_d is the relative growth rate [r_{GR}, in moles of C per gram dry matter (DM) per day], this can be further simplified to:

$$1/C_{UE} = 1 + g_r + m_r/r_{GR} \quad (5)$$

Note that the only assumption used in deriving Eqn 5 is that respiration can be divided into growth and maintenance components. No assumptions are made about which energy-requiring processes are related to growth and which are related to maintenance (see Cannell & Thornley 2000 for a review).

Equation 5 indicates that C_{UE} depends on the ratio of growth rate to plant size (r_{GR}), and thus on the ratio of R_g to R_m. To maintain a constant C_{UE} throughout plant development or under different environmental conditions, either r_{GR} has to be constant (i.e. exponential growth), or g_r and/or m_r have to change in accord with r_{GR}. Although exponential growth can occur during the seedling stage, when there is no intra- or inter-plant competition for light, r_{GR} decreases as plants get larger (Květ *et al.* 1971). Since g_r and m_r should be considered to be variables (Amthor 2000), they may change during plant development. The growth coefficient depends on which chemical compounds are produced (Penning de Vries, Brunsting & van Laar 1974), and therefore may change if the chemical composition of a plant changes during its development. Plant composition also affects m_r, because certain plant compounds require little or no maintenance (e.g. lignin, cellulose), and other compounds (e.g. proteins) require a relatively large amount of maintenance (Penning de Vries 1975; Johnson 1990). If the ratio between these compounds changes (e.g. during secondary growth or lignification), m_r will be

affected as well. Thus, relatively constant C_{UE} during plant development likely results from a decrease in r_{GR}, accompanied by a simultaneous decrease in g_r and/or m_r.

The objective of this research was to determine how P_g, net photosynthesis (P_n), dark respiration (R_d), R_g, R_m, C_{dg}, and C_{UE} change throughout plant development, and to determine how changes in C_{UE} are related to these other physiological parameters. Lettuce (*Lactuca sativa* L.) was chosen as a model crop, because it grows relatively fast, has little lignification, and produces mainly leaves during the vegetative part of its life cycle. Thus, it seems unlikely that there would be large changes in g_r and m_r during its vegetative growth phase, which makes it an ideal crop to determine possible ontogenic changes in C_{UE}. The hypothesis behind this research was that C_{UE} of plants decreases as r_{GR} decreases, because R_m will become a larger fraction of total respiration, thus reducing the amount of carbohydrates available for growth and R_g.

MATERIALS AND METHODS

Plant material

Seeds of lettuce (*Lactuca sativa* L.) 'Grand Rapids' were seeded in 1.5 L pots (15 cm diameter) filled with **diatomaceous earth (Isolite CG-2; Sundine Enterprises, Thornton, CO, USA)** every 3 to 5 d for 3 weeks. Seeding was done at six different times to assure that plants of different size and growth rate would be available for CO_2 exchange measurements. Plants were drip-irrigated with a fertilizer solution containing nitrogen at 100 mg L^{-1}. The fertilizer solution was made using a commercially available water-soluble fertilizer (Miracle-Gro Excel 15-5-15 Cal-Mag; The Scotts Co, Marysville, OH, USA). Plant density was approximately 15 plants m^{-2}. Air temperature in the greenhouse averaged 25.0 °C, relative humidity averaged 73%, and daily photosynthetic photon flux averaged 10.5 mol m^{-2} d^{-1}.

Gas exchange measurements

Gas exchange data were collected once a week for 4 weeks, starting 24 d after seeding of the last crop. On each measurement day, six groups of six plants each (one group of six plants from each seeding date) were measured, resulting in a total of 24 crops having ages ranging from 24 to 66 d during the 4 week measurement period. Younger seedlings were not included in the measurement, because of the difficulties associated with obtaining accurate measurements from very small plants. The six groups of six plants were placed in a whole-plant gas exchange system (van Iersel & Bugbee 2000), consisting of eight acrylic chambers (0.32 m × 0.50 m × 0.60 m; w × l × h), placed inside one of two growth chambers. Two empty chambers were used to check and correct for possible zero drift of the differential infra-red gas analyser (IRGA: model LI-6262; Li-Cor Inc., Lincoln, NE, USA). Ambient air, with a CO_2 concentration of approximately 370 μmol mol^{-1}, was blown into the gas exchange chambers with a rotary vane blower. The actual CO_2 concentration inside the gas exchange chambers depended on the CO_2 exchange rate of the plants, and ranged from 280 to 365 μmol mol^{-1} during the photosynthesis measurements. Although these differences in CO_2 concentration may have affected the CO_2 exchange rate, these effects probably were small, because the low photosynthetic photon flux (PPF) level during the measurements (200 μmol m^{-2} s^{-1}) probably was the main factor limiting canopy photosynthesis. For example, P_n of *Alstroemeria* did not change appreciably with an increase in CO_2 concentration from 280 to 365 μmol mol^{-1}, when the PPF level was 200 μmol m^{-2} s^{-1}, but increased by approximately 25% at a PPF level of 1200 μmol m^{-2} s^{-1} (Leonardos *et al.* 1994).

Flow rate through the chambers (approximately 0.6 L s^{-1}) was measured continuously, and the difference in the CO_2 concentration between the incoming and outgoing air of each chamber was measured with an IRGA for 30 s every 10 min. Water vapour was removed from the air before measuring the CO_2 concentration by passing the air through a 4 °C condenser. The CO_2 exchange rate (μmol s^{-1}) was calculated as the product of mass flow

of air through the chambers (mol s^{-1}) and the difference in CO_2 concentration between the incoming and outgoing air (μmol mol^{-1}).

To minimize the effects of acclimation on the gas exchange measurements, environmental conditions in the gas exchange chambers were set to mimic greenhouse conditions. Temperature was controlled with resistance heaters mounted in each gas exchange chambers and maintained at 25 °C. Temperature fluctuations were within 0.5 °C of the set point. The PPF at the top of the canopies was 200 ± 5 μmol m^{-2} s^{-1}, resulting in a total PPF of 10 mol for the entire 14 h photoperiod, similar to the average daily PPF in the greenhouse. Light was provided by a mixture of fluorescent and incandescent lights. During the next 10 h, R_d was measured. Gross photosynthesis (P_g) was calculated as the sum of the average values for P_n and R_d, based on the assumption that the respiration rates (excluding photorespiration) were similar in the light and dark. This assumption also was used to calculate total daily respiration ($R_{d,day}$).

After the gas exchange measurements, leaf area (LA) and dry mass (M_d, shoots and roots) of the plants were determined. To adjust for differences in plant size, gas exchange rates not only are expressed on a whole plant basis (P_g, P_n, and R_d), but also per unit leaf area or M_d ($P_{g,LA}$, $P_{n,LA}$ and $R_{d,M}$). Both photosynthesis and respiration data are expressed as positive values, even though they represent CO_2 fluxes in opposite directions.

Calculations and data analysis

The gas exchange measurements were used to calculate C_{dg}(g d^{-1}), which is a direct measure of growth rate:

$$C_{dg} = (P_{n,light} - R_{d,dark}) \times 12 \quad (6)$$

where $P_{n,light}$ is the total net photosynthesis during the 14 h light period, $R_{d,dark}$ is the total respiration during the 10 h dark period and 12 is the molecular mass of C.

Carbon use efficiency of the plants was calculated from [Eqn 1](#) (with C_{dg} in units of mol d^{-1}) and r_{GR} of the plants was calculated as:

$$r_{GR} = C_{dg}/M_d \quad (7)$$

Note that r_{GR} is expressed in units of g C g^{-1} DM d^{-1}, and not in the more traditional units of g DM g^{-1} DM d^{-1}.

Gas exchange data also were used to estimate g_r and m_r using several different methods. Traditionally, g_r and m_r often have been estimated from the correlation between the specific respiration rate and r_{GR} ([Hesketh, Baker & Duncan 1971](#); [Amthor 1984](#); [Amthor & Cumming 1988](#) , [Wullschleger & Norby 1992](#)):

$$R_{d,day}/M_d = m_r + g_r \times r_{GR} \quad (8)$$

where $R_{d,day}$ is expressed in grams of glucose per day. Thus, g_r is in units of grams of glucose respired per gram of carbon incorporated into plant dry matter and m_r is in units of grams of glucose per gram DM per day. Similarly, g_r and m_r can be estimated directly from $R_{d,day}$, growth rate (C_{dg}) and M_d ([Amthor 1994](#)):

$$R_{d,day} = m_r \times M_d + g_r \times C_{dg} \quad (9)$$

where g_r and m_r have the same units as in [Eqn 8](#). Although [Eqn 8](#) can be derived by dividing [Eqn 9](#) by M_d, they do not necessarily results in identical estimates of m_r and g_r, because the division by M_d changes the distribution of the data points. One disadvantage of [Eqn 9](#) is the lack of an intercept, which makes the calculation of an R^2-value impossible. Finally, g_r and m_r were estimated from [Eqn 5](#), which results in different units for g_r

(mol C respired mol^{-1} C incorporated) and m_r (g C respired g^{-1} DM d^{-1}). Estimates of m_r and g_r were obtained from [Eqns 5, 8, and 9](#) by regression analysis across plants of different ages. Thus, these methods for estimating g_r and m_r assume that both are constant throughout plant development. Estimates of g_r and m_r subsequently were used to estimate R_g and R_m (g glucose d^{-1}) as $g_r \times C_{dg}$ and $m_r \times M_d$, respectively. To determine the importance of R_m in the carbon balance of the plants, R_m as a fraction of total respiration ($R_m/R_{d,day}$) was calculated and plotted versus both M_d and r_{GR}. The dependence of $R_m/R_{d,day}$ on r_{GR} can be described as:

$$R_m/R_{d,day} = R_m/(R_m + R_g) = m_r \times M_d/(m_r \times M_d + g_r \times C_{dg}) = m_r/(m_r + g_r \times C_{dg}/M_d) = m_r/(m_r + g_r \times r_{GR})$$
$$= 1/(1 + r_{GR} \times g_r/m_r) \quad (10)$$

Relationships between other parameters of interest were determined using both linear and non-linear regression equations.

To determine whether the different atmospheric CO_2 concentrations during the measurements may have affected the main conclusions from this research, its potential effect on the calculated r_{GR} and C_{UE} was estimated. For these calculations, it was assumed that for every 4 μmol mol^{-1} decrease in atmospheric CO_2, P_n was reduced by 1%. This assumption was used to estimate what P_n would have been at an atmospheric CO_2 concentration of 365 μmol mol^{-1}, and r_{GR} and C_{UE} were recalculated accordingly. For these calculations, it was assumed that R_d would not have been affected by the higher, recalculated P_n. The assumptions of a strong dependence of P_n on atmospheric CO_2 and independence between P_n and R_d, were used because they result in the largest possible effects on r_{GR} and C_{UE}, and thus represent a worst-case scenario.

RESULTS AND DISCUSSION

Gas exchange and plant growth

The response of photosynthesis to increasing leaf area depended greatly on whether it was expressed on a whole plant basis or per unit leaf area. Both P_g and P_n increased asymptotically with increasing leaf area ([Fig. 1](#)), presumably because of the asymptotic increase in canopy light interception with increasing leaf area ([Monsi & Saeki 1953](#)). In contrast, $P_{g,LA}$ and $P_{n,LA}$ decreased linearly with increasing leaf area ([Fig. 2](#)). Such a decrease is expected, due to increased intra- and inter-plant competition, which decreases the amount of light intercepted per unit leaf area. Whole-plant R_d also increased with increasing plant size ([Fig. 1](#)), whereas $R_{d,M}$ initially decreased rapidly with an increase in M_d from 0 to 5 g, but was similar (0.02 ± 0.005 μmol g^{-1} s^{-1}) for plants with a M_d of 5 g per plant or more ([Fig. 2](#)). Such a decrease in specific respiration with increasing mass has been reported previously, for example in barley (*Hordeum vulgare* L.) ([Winzeler *et al.* 1976](#)).

Figure 1.

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Carbon exchange rate of lettuce as a function of plant size. Gross and net photosynthesis are plotted as a function of leaf area, whereas dark respiration is shown as a function of dry mass. All data are expressed on a per plant basis.

Figure 2.

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Carbon exchange rate of lettuce as a function of plant size. Gross and net photosynthesis are expressed per unit leaf area, and plotted as a function of leaf area, whereas dark respiration is expressed per unit dry mass, and shown as a function of dry mass.

Daily carbon gain increased sharply as plant mass increased from 0 to approximately 5 g, whereas C_{dg} tended to decrease for plants with a mass> 5 g ([Fig. 3]). However, there was a poor correlation between C_{dg} and mass for plants with a mass> 5 g. The decrease in C_{dg} with increase in mass (>5 g) was the result of the increased importance of R_m in the carbon balance of the plants (see discussion of $R_m/R_{d,day}$ below). Relative growth rate decreased exponentially with increasing plant size ([Fig. 3]). Such a decrease in r_{GR} with increasing plant size is typical, and results from increasing inter- and intra-plant competition for light ([Kvǩt *et al.* 1971]).

Figure 3.

Relative growth rate and daily carbon gain of lettuce as function of plant dry mass. Daily carbon gain was calculated from 24 h gas exchange measurements, and relative growth rate was calculated as daily carbon gain divided by dry mass.

Carbon use efficiency, growth respiration and maintenance respiration

Carbon use efficiency of the plants decreased linearly with increasing M_d, from 0.5 to 0.6 for small plants (M_d of 0–3 g) to 0.2–0.3 for large plants (M_d of 10–16 g, [Fig. 4]). Thus, the fraction of carbohydrates fixed in P_g that was lost through R_d increased with increasing plant size. There was no correlation between C_{UE} and C_{dg}, whereas $1/C_{UE}$ was closely correlated with $1/r_{GR}$ ($r = 0.97$, [Fig. 4]). Based on this correlation, g_r and m_r were estimated to be 0.48 ± 0.08 mol mol^{-1} and 15.5 ± 0.7 mg C g^{-1} DM d^{-1} (estimate $\pm$ se) or 39 mg glucose g^{-1} DM d^{-1}, respectively. A direct conversion of the g_r estimate to the conventional units of grams of glucose per gram of new plant material is not possible, because it depends on the carbon content of the plant material. However, plants generally have a carbon content of approximately 0.4 g g^{-1} ([Hadley & Causton 1984]) as does glucose, and the value of g_r therefore is similar when it is expressed in units of mol mol^{-1} or g g^{-1}.

Figure 4.

Carbon use efficiency (C_{UE}) as a function of daily carbon gain (C_{dg}, a measure of growth rate) and plant dry mass. Although there was a highly significant correlation between C_{UE} and dry mass, there was a much better correlation between the inverse of C_{UE} and the inverse of relative growth rate (dry mass divided by C_{dg}). The Y-intercept of this regression is an estimate of $1 + g_r$, while the slope of the regression estimates m_r. The dashed line shows the estimated correlation between $1/C_{UE}$ and $1/r_{GR}$ ($1/C_{UE} = 1.44 + 1.24/r_{GR}$, $r = 0.96$), after recalculating the data based on the assumption that every 4 μmol mol^{-1} decrease in atmospheric CO_2 decreased net photosynthesis by 1%.

As it cannot be ruled out that the collected P_n data were affected by differences in atmospheric CO_2 concentrations among different groups of plants, the potential effect of atmospheric CO_2 on C_{UE} and r_{GR} was

estimated as outlined in the materials and methods. These calculations indicate that low CO_2 concentrations may have resulted in underestimation of both C_{UE} and r_{GR}. Since both C_{UE} and r_{GR} would have been affected similarly, the basic relationship between these two parameters was only marginally affected by these recalculations (Fig. 4). Recalculated estimates for g_r and m_r were 0.44 mol mol^{-1} and 37 mg glucose g^{-1} DM d^{-1}, respectively.

One of the most common methods to estimate g_r and m_r is by linear regression of specific respiration versus r_{GR} (Eqn 8, Fig. 5; Chiariello, Mooney & Williams 1989), which resulted in estimates of 1.55 ± 0.15 g glucose g^{-1} C and 31 ± 5 mg glucose g^{-1} DM d^{-1} for g_r and m_r, respectively ($r = 0.91$). Assuming a carbon content of 0.4 g g^{-1}, this estimate of g_r is equivalent to 0.62 g glucose g^{-1} DM. Finally, g_r and m_r also were estimated by modelling them as a function of growth rate and plant size, respectively (Eqn 9), resulting in estimates of 1.00 ± 0.14 g glucose g^{-1} C incorporated (or 0.40 g glucose g^{-1} DM, assuming a carbon content of 0.4) for g_r and 38.1 ± 1.7 mg glucose g^{-1} DM d^{-1} for m_r.

Figure 5.

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The correlation between the specific respiration rate and relative growth rate of lettuce. The *Y*-intercept of the regression line is an estimate of m_r, while the slope is an estimate of g_r.

The different methods for determining g_r and m_r resulted in different estimates, even though they were based on the same data. Estimates of g_r ranged from 0.40 to 0.62 g g^{-1}, while estimates for m_r ranged from 31 to 39 mg g^{-1} d^{-1}. These differences are due to differences in which data points have relatively more effect on the regression results. For example, plants with a high r_{GR} (small plants) have a relatively strong effect on the slope of the regression (g_r) of r_{GR} versus specific respiration, whereas plants with a low r_{GR} have a relatively strong effect on the estimate of the slope of the regression of $1/C_{UE}$ versus $1/r_{GR}$ (m_r). These estimates are all based on the assumption that g_r and m_r were constant for plants of different size. Although this assumption resulted in a good fit of the data (especially in the case of $1/C_{UE}$ versus $1/r_{GR}$), this does not necessarily mean that g_r and m_r were indeed constant in this trial. It cannot be ruled out that there were concomitant, and offsetting changes in g_r and m_r.

Other literature values for g_r generally are close to 0.43 g g^{-1} (McCree 1982; Penning de Vries *et al.* 1989; Cannell & Thornley 2000; van Iersel & Seymour 2000). Thus, g_r estimates from Eqn 5 (0.48 mol mol^{-1}) and 9 (0.40 g glucose g^{-1} DM) are close to generally accepted values, while the estimate based on Eqn 8 (0.62 g g^{-1}) may be unrealistically high. Literature values for m_r are much more variable than those of g_r, and generally range from 3 to 50 mg g^{-1} d^{-1} (Hesketh, Alberte & Jones 1980). The variability in estimates of m_r is at least partly due to changes with plant age and environmental conditions (Walker & Thornley 1977; Mariko & Koizumi 1993). All estimates of m_r of lettuce from the current data are well within the normal range.

Growth and maintenance respiration rates were estimated based on the g_r and m_r-values estimated from Eqn 5 (Fig. 4), since it had the best fit, and resulted in estimates consistent with other literature values. Since m_r was assumed to be constant, R_m increased linearly with increasing plant size, whereas R_g increased with increasing plant size from 0 to 3 g, but there was no clear correlation between R_g and plant size for larger plants. Maintenance accounted for only 25% of total respiration in small plants, but for 90% in large plants (Fig. 6). This is consistent with the assertion that C_{UE} should decrease with increasing plant size due to the increased importance of R_m (Amthor 1989). The increasing importance of R_m in the carbon balance of the plants explains the tendency for C_{dg} to decrease with increasing $M_d(> 3$ g). For plants with a M_d of more than 7 g, more carbon was lost in maintenance than was incorporated into the plants (Figs 3 & 6), indicating that the maintenance

demand for carbon greatly reduced growth. As expected, R_m accounted for more of the total respiration with decreasing r_{GR}, because r_{GR} is the ratio between C_{dg} and M_d and thus directly related to the ratio between R_g and R_m (Eqn 10; Fig. 6).

Figure 6.

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Growth and maintenance respiration of lettuce as a function of dry mass (top). Maintenance as a fraction of total respiration increases with increasing plant dry mass (middle), but decreases with increasing relative growth rate (r_{GR}).

Because g_r is a measure of the biochemical efficiency with which plants convert carbohydrates into biomass, it can be used to calculate a theoretical upper limit for C_{UE} (i.e. C_{UE} when R_m accounts for a negligible fraction of the overall carbon balance) as $1/(1 + g_r)$. Using an estimate of 0.48 mol mol^{-1} for g_r of lettuce, this implies that the maximum possible C_{UE} is 0.68 mol mol^{-1} and the difference between this theoretical maximum and the actual C_{UE} is due to R_m.

Ontogenic changes in g_r, m_r, and C_{UE}

Ontogenic changes in g_r and m_r have not been studied in much detail, at least partly because of the difficulty in estimating g_r and m_r without assuming that they are constant. Since g_r depends on the chemical composition of the biomass that is being produced (Penning de Vries *et al.* 1974), changes in g_r during plant development would be expected, especially in crops with an abrupt transition of vegetative to reproductive growth. For example, wheat produces roots, leaves and stems during its vegetative growth period, but a large amount of starch during seed fill. Since the production of starch is very energy efficient, g_r would be expected to be low during seed fill. Similarly, many fruits contain large amounts of organic acids, whose production also requires little growth respiration (Penning de Vries *et al.* 1974). Thus, g_r is likely to decline during periods of seed fill or fruit growth in such crops (in contrast to oil crops, which produce large amount amounts of fatty acids, which require relatively much growth respiration).

Despite these potential changes in g_r, experimental estimates from a variety of studies suggest that g_r is similar (generally differing by less than 10%) among plant parts, species, and growing conditions (Cannell & Thornley 2000). The growth yield (Y_g, grams of dry matter produced per gram of glucose utilized for growth, thus excluding glucose used for maintenance needs) generally is close to 0.7 g g^{-1} (McCree 1982; Penning de Vries *et al.* 1989; Cannell & Thornley 2000). Since $g_r = 1/Y_g - 1$ *(when both are expressed in units of g g^{-1}, Johnson 1990)*, this corresponds to a g_r of 0.43 g g^{-1} and a theoretical maximum C_{UE} of 0.70.

Changes in m_r during development likely are larger than changes in g_r, especially if m_r is expressed per unit total M_d. For example, a linear relationship between R_m and M_d did not describe the respiration of barley (Winzeler *et al.* 1976) or chrysanthemum (*Dendranthema × grandiflorum* Kitam.; Hughes 1973) adequately, especially early in the life cycle. This suggests that there were ontogenic changes in m_r, which may be related to plant composition. Certain plant compounds require little or no maintenance (e.g. lignin, cellulose), whereas other compounds (e.g. proteins) require a relatively large amount of maintenance (Johnson 1990; Amthor 1994). In growth models, this can be accounted for by separating biomass into non-degradable and degradable fractions, with only the degradable fraction requiring maintenance (Thornley 1977). However, often it is simpler to not make this distinction, and plants that undergo a significant amount of lignification or wood formation during their development are likely to have a decrease in m_r (per unit total M_d). Since secondary growth alters the ratio of degradable to non-degradable biomass, large changes in m_r are more likely in woody than in herbaceous

plants. A decrease in m_r during plant development will help to minimize changes in C_{UE}, since it counteracts the effect of decreasing r_{GR} on C_{UE}. This may at least partly explain the relatively constant C_{UE} during the life cycle of wheat (Monje & Bugbee 1998). Wheat straw has high concentrations of both lignin and cellulose (Rahn & Lillywhite 2002), and m_r of wheat thus likely decreases during its life cycle. In addition, wheat produces mainly starch during grain fill, which requires little growth respiration (Penning de Vries *et al.* 1974) and thus reduces g_r. The combined effects of decreasing g_r and m_r during plant development may explain the relatively small changes in C_{UE} of wheat. Lettuce, on the other hand, does not have significant lignification or secondary growth, and its m_r is likely to be much more stable than that of wheat, causing C_{UE} to decrease throughout the growing period. Clearly, potential changes in C_{UE} depend at least partly on changes in the chemical composition of plants throughout ontogeny and are likely to be species-specific.

Plants grown under near-optimal conditions (high light and CO_2 concentrations, e.g. Monje & Bugbee 1998), likely will have smaller changes in C_{UE} than plants grown under poor conditions (e.g. the low light intensity in this study), because r_{GR} will be higher under near-optimal conditions, minimizing the effect of m_r on C_{UE}. Moreover, m_r generally is decreased under high atmospheric CO_2 (Gifford 1995; Wullschleger *et al.* 1997), further reducing its effect on C_{UE}. For example, the C_{UE} of lettuce decreases faster under low atmospheric CO_2 (approximately 300 μmol mol^{-1}) than under high CO_2 (approximately 1200 μmol mol^{-1}) (Frantz, van Iersel & Bugbee, unpublished results), presumably because of a combination of a lower r_{GR} and higher m_r at low CO_2.

CONCLUSIONS

Carbon use efficiency can be expressed as a simple function of g_r, m_r and r_{GR}. Based on this function it can be concluded that: (1) the decrease in C_{UE} of lettuce from 0.6 to 0.2 during development could be explained based on the decrease in r_{GR} and the resulting increase in importance of maintenance respiration in the carbon balance of the plants; (2) based on the respiratory requirements for growth, the theoretical upper limit for C_{UE} of the lettuce in this experiment was 0.68; (3) ontogenic changes in C_{UE} likely are more pronounced under poor growing conditions, because a low r_{GR} increases the importance of m_r in determining C_{UE}; (4) a decrease in r_{GR} will result in a decrease in C_{UE}, unless g_r and/or m_r change concurrently with r_{GR}. In many species, especially those with extensive lignification or secondary growth, changes in m_r (expressed per unit total M_d) are likely, because of changes in the ratio between degradable and non-degradable biomass. Large changes in g_r appear to be less common, but may occur when the composition of newly produced biomass changes, e.g. during the transition from vegetative to reproductive growth.

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