

A simple method for estimating gross carbon budgets for vegetation in forest ecosystems

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Summary

Gross carbon budgets for vegetation in forest ecosystems are difficult to construct because of problems in scaling flux measurements made on small samples over short periods of time and in determining belowground carbon allocation. Recently, empirical relationships have been developed to estimate total belowground carbon allocation from litterfall, and maintenance respiration from tissue nitrogen content. I outline a method for estimating gross carbon budgets using these empirical relationships together with data readily available from ecosystem studies (aboveground wood and canopy production, aboveground wood and canopy biomass, litterfall, and tissue nitrogen contents). Estimates generated with this method are compared with annual carbon fixation estimates from the Forest-BGC model for a lodgepole pine (*Pinus contorta* Dougl.) and a Pacific silver fir (*Abies amabilis* Dougl.) chronosequence.

Introduction

Many measurements of aboveground net primary production exist (O'Neill and DeAngelis 1981), but few studies have addressed gross carbon budgets for vegetation in ecosystems (Edwards et al. 1981). However, the components of net primary production, photosynthesis, respiration, and allocation, vary independently. For example, photosynthesis and respiration respond differently to variation in temperature and atmospheric CO₂ concentration (Larcher 1983, Ryan 1991), and differences in net production with ecosystem type or stand age may arise from differences in photosynthesis, respiration, or carbon allocation (Whittaker and Woodwell 1968, Edwards et al. 1981, O'Neill and DeAngelis 1981, Waring and Schlesinger 1985). A knowledge of gross carbon fluxes through vegetation is, therefore, essential to interpret current patterns and predict future trends in forest productivity. Parameterization and validation of simulation models also require information on gross C flux through vegetation in ecosystems.

Gross C budgets for vegetation are notoriously difficult to construct (Edwards et al. 1981). Direct measurements of photosynthesis and foliage respiration are not easily obtained because of the difficulty of controlling environmental conditions in gas-exchange chambers used in field measurements. Fine-root production estimates are challenging because of sampling difficulties. Estimating fine-root respiration directly is difficult because of problems in separating autotrophic and heterotrophic respiration. Even when direct measurements of C fluxes can be made, they usually represent small samples in space and time and must be scaled to provide ecosystem-level estimates. Errors in scaling can contribute as much uncertainty to large-scale estimates as errors in the original measurements. No direct method exists for measuring gross C flux for vegetation over large temporal and spatial scales.

Recently developed empirical relationships for estimating total belowground C allocation (Raich and Nadelhoffer 1989) and maintenance respiration (Ryan 1991) provide the tools necessary to generate estimates of gross C flux for vegetation in forest ecosystems. In this paper, I describe a simple method for estimating annual gross C budgets for vegetation in forest ecosystems from empirical relationships and data readily available from ecosystem studies. These gross C budgets are intended for use where no measurements exist and for comparison with traditional estimates of C flux. To evaluate and illustrate the utility of the method, I compared estimated annual C budgets with the annual total of net daily canopy fixation simulated with the Forest-BGC model (Running 1984, Running and Coughlan 1988) for a Pacific silver fir (*Abies amabilis* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) chronosequence.

Description of method

Annual gross primary production (GPP) is the total of all C fixed by vegetation in ecosystems. Conventionally, carbon fixed but lost through photorespiration is excluded from GPP. For forest ecosystems with closed canopies, the sum of aboveground foliage and wood production plus associated construction respiration, aboveground foliage and sapwood maintenance respiration, and total belowground C allocation (production plus construction and maintenance respiration) approximates GPP. Most ecosystem studies gather information on aboveground production and litterfall; nitrogen (N) concentration in various tissues is also commonly available (O'Neill and DeAngelis 1981, Vogt et al. 1986). Often lacking are estimates of belowground production and construction and maintenance respiration.

Here I show how annual gross carbon budgets for forest stands can be constructed from gross biomass production, and empirical relationships with readily available data to estimate total belowground C allocation (Raich and Nadelhoffer 1989) and maintenance respiration (Ryan 1991). The proposed method is not intended to replace direct measurements or conventional modeling estimates of GPP, but to provide either a check on traditional estimates or a rough approximation when information on respiration or belowground allocation is lacking.

Foliage production and associated construction respiration

Estimates of aboveground foliage production (F_p , $\text{g C m}^{-2} \text{ year}^{-1}$) are generally available from canopy production data, or can be obtained from total annual litterfall (L_f , $\text{g C m}^{-2} \text{ year}^{-1}$) provided that stand leaf area has reached equilibrium. Construction respiration used to build wood and foliage can be estimated from empirical relationships based on heat of combustion, ash, and organic N content of the tissue (Williams et al. 1987), or on tissue C and ash content (Vertregt and Penning de Vries 1987). Where information to apply these relationships is lacking, a reasonable estimate of construction respiration can be made by assuming that it consumes carbon equal to one quarter of that incorporated into new tissue (Ryan 1991). Thus, carbon utilized in leaf production, including construction respiration (F_{p+c} , g C m^{-2}

year⁻¹) is given by:

$$F_{p+c} = 1.25 F_p, \quad (1)$$

$$\text{or } 1.25 L_f.$$

Aboveground wood production and associated respiration

Estimates of aboveground wood production, i.e., biomass that is not foliage, (W_p , g C m⁻² year⁻¹) are readily available. When construction respiration cannot otherwise be determined, I estimate it as for foliage. Thus carbon utilized in aboveground wood production, including construction respiration (W_{p+c} , g C m⁻² year⁻¹), is given by:

$$W_{p+c} = 1.25 W_p, \quad (2)$$

Foliage maintenance respiration

Maintenance respiration and tissue N content are strongly correlated (Jones et al. 1978, McCree 1983, Waring et al. 1985, Irving and Silsby 1987, Ryan 1991). This relationship exists because most of the N in plants is in protein and roughly 60% of maintenance respiration supports protein repair and replacement (Penning de Vries 1975). Tissue N content is also a good, general index of metabolic activity (Field 1983, Field and Mooney 1986). Ryan (1991) found that maintenance respiration was linearly related to tissue N content for tissues ranging from 0.04% to 6% N (dry weight). This relationship can be used to estimate annual maintenance respiration for evergreen foliage (F_m , g C m⁻² year⁻¹) from tissue N content, mean annual temperature, and daily and seasonal temperature amplitude:

$$F_m = N_{\text{tot}} 27 \exp(0.07 T_a), \quad (3a)$$

where N_{tot} (g N m⁻²) is total N in canopy calculated from canopy biomass and canopy N concentration, and T_a (°C) is average annual temperature.

For a deciduous canopy, duration of leaf area display (D , days) is also required and average growing season temperature (T_s , °C) is used:

$$F_m = N_{\text{tot}} D 0.059 \exp(0.07 T_s). \quad (3b)$$

For these equations, I assumed temperature amplitude was 5 °C for a day and 15 °C for the year. See Appendix for a complete derivation.

Aboveground sapwood maintenance respiration

A large fraction of woody biomass (heartwood) does not respire, and the proportion of biomass in sapwood is necessary for good estimates of maintenance respiration of woody tissues. If sapwood volume is not available, published information can be used to estimate sapwood volume of conifers (Ryan 1989) and oaks (Rogers and Hinckley 1979). A relationship similar to that used to estimate annual maintenance

respiration for evergreen foliage can be used to estimate annual maintenance respiration for sapwood (S_m , $\text{g C m}^{-2} \text{ year}^{-1}$) from tissue N content, mean annual temperature, and daily and seasonal temperature amplitude:

$$S_m = N_s 27 \exp(0.07 T_a), \quad (4)$$

where N_s (g N m^{-2}) is total N in sapwood calculated from sapwood biomass and sapwood N concentration.

Total belowground C allocation

Total belowground C allocation (production, construction, and maintenance respiration, $(B_{p+c+m}$, $\text{g C m}^{-2} \text{ year}^{-1}$) is strongly correlated with annual litterfall for litterfall of 70–500 $\text{g C m}^{-2} \text{ year}^{-1}$ (Raich and Nadelhoffer 1989):

$$B_{p+c+m} = 130 + 1.92 L_f. \quad (5)$$

Equation 5 was developed by assuming (1) that soil respiration equals autotrophic respiration plus heterotrophic decomposition of aboveground and belowground inputs, (2) soil respiration minus aboveground litter inputs approximates decomposition of belowground inputs plus belowground autotrophic respiration, (3) inputs of C by precipitation or wind transport and losses of C through leaching and erosion are minor, and (4) soil C storage is near steady state. Where measurements of annual soil CO_2 flux and annual aboveground litterfall exist, total belowground C allocation may be calculated directly by difference, if all the assumptions are met.

Validation

Because of the difficulty of separating heterotrophic from autotrophic respiration at the ecosystem level, no direct estimates of GPP exist. To evaluate C budgets estimated by the procedure described above and to illustrate their application, I compared annual C budgets developed with the relationships given in Equations 1–5 to the annual total of net daytime C fixation estimated with the Forest-BGC model (Running 1984, Running and Coughlan 1988). Comparisons with Forest-BGC estimates were made for young and old Pacific silver fir and lodgepole pine stands.

The Pacific silver fir stands were even aged (23 and 180 years), growing at the Findley Lake research area about 65 km southeast of Seattle, WA. The stands have previously been used to study productivity, belowground allocation (Grier et al. 1981), nutrient cycling (Vogt et al. 1983, Meier et al. 1985), foliage respiration (Brooks 1987), and stem respiration (Sprugel 1989, 1990). The lodgepole pine stands, which were even-aged (40 and 245 years old), and growing at the Fraser Experimental Forest near Winter Park, CO (39°54' N, 105°52' W), were used previously to study woody tissue respiration (Ryan 1988, 1990).

Forest-BGC requires daily values for maximum and minimum temperatures, relative humidity, total irradiance, and precipitation. For the Pacific silver fir site,

weather data from a nearby National Oceanic and Atmospheric Administration (NOAA) weather station (Stampede Pass, WA) for the years 1977 and 1978 were used to estimate respiration and GPP. Weather at Stampede Pass closely matches that at Findley Lake (C.C. Grier, personal communication). The NOAA station did not record relative humidity and insolation, which were estimated from minimum temperature, site geometry, and temperature amplitude by use of the MTCLIM interpolation program (Running et al. 1987).

For the lodgepole pine site, weather data for the period 1981–85 at a station 1600 m distant and 50 m lower in elevation were used to estimate respiration and net daytime C fixation, with two adjustments: (1) minimum temperatures were adjusted to offset the effect of cold air drainage at the weather station (Kaufmann 1984), and (2) irradiance was estimated with MTCLIM.

For the Pacific silver fir site, aboveground wood production, canopy production, litterfall, aboveground woody biomass, and canopy biomass are given in Grier et al. (1981). Sapwood and foliar N content are given in Meier et al. (1985) and were used in Equations 3a and 4 to estimate maintenance respiration. Branches were assumed to be 100% sapwood and the fraction of stem sapwood to total stem wood for a similar species (subalpine fir, Ryan 1989) was used to estimate sapwood volume. Stem wood was assumed to be 65% sapwood for the 23-year-old stand and 25% sapwood for the 180-year-old stand. Because Forest-BGC estimates net C fixed during the day, to make annual budgets comparable, I divided foliage maintenance by two to estimate night respiration. Forest-BGC was run for 1977 and 1978; estimates are averages for the two years. Production values were measured in 1978 (Grier et al. 1981).

For the lodgepole pine site, aboveground wood production, woody biomass, canopy biomass, and sapwood volume were given in Ryan (1988) and Ryan and Waring (unpublished results). Maintenance respiration for aboveground woody biomass was estimated using Equation 4, actual sapwood volume, and N content for sapwood from lodgepole pine trees on a similar site (Pearson et al. 1987). For foliage, mean N content for the canopy was 0.87% of dry weight (Schoettle 1989), and canopy maintenance was estimated from canopy biomass, N content, and Equation 3. I divided canopy maintenance by two to estimate night respiration, to make annual budgets comparable with Forest-BGC estimates of gross production. Canopy growth was estimated from the fraction of 1-year-old needles in the canopy (12%, Schoettle 1989). Litterfall required to estimate belowground C allocation was also estimated from the fraction of 1-year-old needles scaled to total litterfall using values for similar lodgepole pine stands (Fahey 1983).

Carbon budgets and Forest-BGC estimates are averages over 1981–85, the period during which stem radial growth was measured. The model was run separately for each of the 5 years, using actual leaf biomass and leaf N in 1986, actual soil water capacity, and actual snowpack for a nearby Soil Conservation Service snowcourse as initial conditions.

For the Pacific silver fir site, the estimates of fine-root production made by Grier et al. (1981) were compared with total belowground C allocation estimated with

Equation 5, and estimated by difference from soil CO_2 flux (Vogt et al. 1980) and litterfall. Additionally, construction and maintenance respiration for woody tissues in the 23-year-old stand estimated by Sprugel (1989) were compared with estimates derived from Equations 2 and 4. For the lodgepole pine site, estimates of maintenance respiration for sapwood reported by Ryan (1988) and Ryan and Waring (unpublished observations) were compared with estimates from sapwood N content.

Results and discussion

Total annual C flux into vegetation, estimated using Equations 1–5, was 941 and $1204 \text{ g C m}^{-2} \text{ year}^{-1}$ in the 23-year-old and 180-year-old Pacific silver fir stands, respectively (Figure 1). Forest-BGC estimates were roughly equivalent to the estimated total annual C flux for both stands. In the 23-year-old stand, wood production consumed the highest proportion of annual C fixed, whereas in the 180-year-old stand, maintenance respiration for foliage accounted for the highest proportion of annual C flux. Maintenance respiration for aboveground wood was almost 4 times greater in the 180-year-old stand.

Coupling simple estimates of total annual C flux with model estimates of net canopy C fixation illustrates the utility of these tools for identifying problem areas in annual C budgets. Estimates of total belowground C allocation in the 180-year-old stand varied from $340 \text{ g C m}^{-2} \text{ year}^{-1}$ (Equation 5) to $915 \text{ g C m}^{-2} \text{ year}^{-1}$

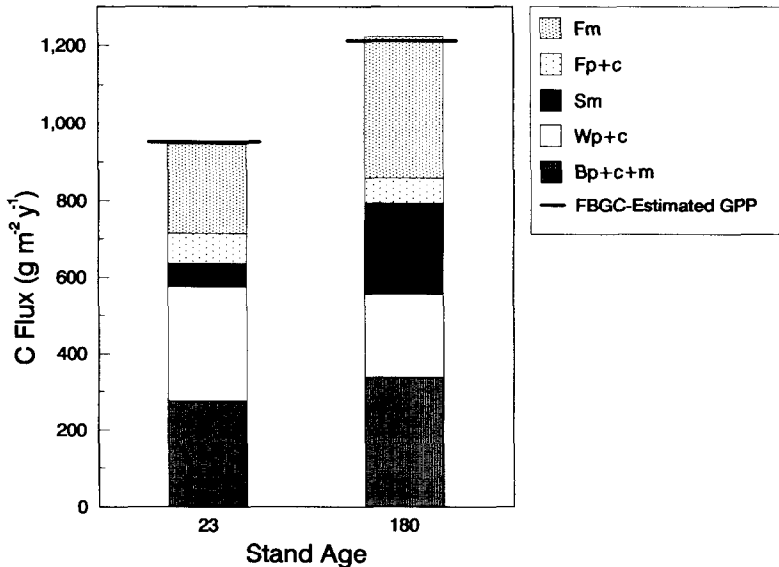


Figure 1. Annual carbon flux estimates using Equations 1–5 and net canopy fixation estimated from Forest-BGC for a Pacific silver fir chronosequence. Symbols: F_m = foliage maintenance respiration, F_{p+c} = foliage production and associated construction respiration, S_m = sapwood maintenance respiration, W_{p+c} = aboveground wood production and associated construction respiration, and B_{p+c+m} = total belowground C allocation.

(belowground production from Grier et al. (1981), plus Equation 4 for maintenance respiration of fine roots). Estimates of belowground dry-matter production by Grier et al. (1981) were about $600 \text{ g C m}^{-2} \text{ year}^{-1}$, substantially greater than estimates of total belowground C allocation estimated from litter with the Raich-Nadelhoffer equation (Figure 2). For the 180-year-old stand, annual soil CO_2 flux is $616 \text{ g C m}^{-2} \text{ year}^{-1}$ (calculated from Figure 5 in Vogt et al. 1980) and litterfall is $111 \text{ g C m}^{-2} \text{ year}^{-1}$ (Grier et al. 1981). Total belowground C allocation calculated directly by difference is $507 \text{ g C m}^{-2} \text{ year}^{-1}$. If respiration is roughly equivalent to production (Ryan 1991), the belowground dry-matter production would be $254 \text{ g C m}^{-2} \text{ year}^{-1}$. Clearly, additional work will be needed to resolve estimates of belowground allocation in these stands.

For the 23-year-old stand, Equations 2 and 4 estimate construction and maintenance respiration for aboveground woody tissues as $120 \text{ g C m}^{-2} \text{ year}^{-1}$. For the same stand 7 years later, Sprugel (1989) estimated aboveground woody-tissue construction and maintenance respiration to be $245 \text{ g C m}^{-2} \text{ year}^{-1}$. Higher growth rates and stem biomass in the 30-year-old stand may explain some of the discrepancy between the two estimates. Also, high rates for branch respiration in this species (Sprugel 1990) and large branch biomass are likely responsible for the larger fluxes

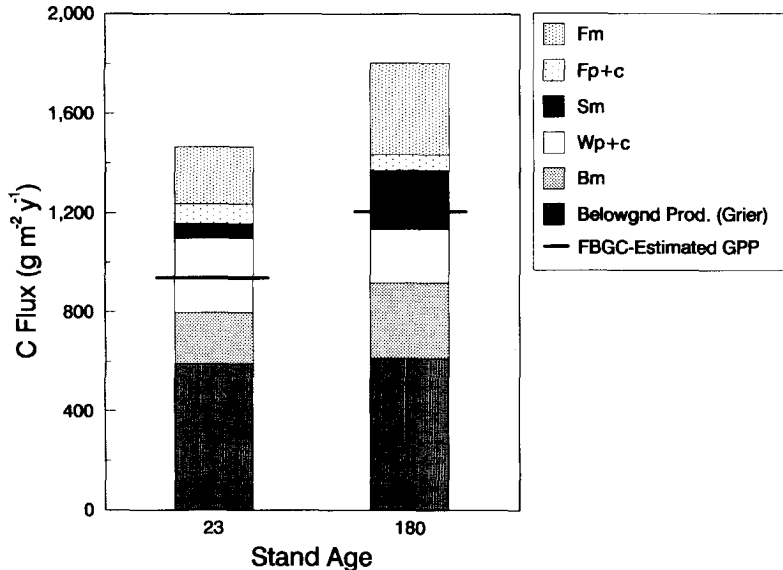


Figure 2. Annual carbon flux estimates using Equations 1–4 for aboveground foliage and wood production and construction respiration; aboveground wood, belowground root, and canopy maintenance respiration; and belowground production estimated by Grier et al. (1981) for a Pacific silver fir chronosequence. Total annual C flux is compared with net canopy fixation estimated from Forest-BGC. Symbols: F_m = foliage maintenance respiration, F_{p+c} = foliage production and associated construction respiration, S_m = aboveground wood production and associated construction respiration, W_{p+c} = aboveground wood production and associated construction respiration, and B_m = fine root maintenance respiration.

reported by Sprugel (1989).

For the lodgepole pine site, total annual carbon flux into vegetation was 957 and 632 $\text{g C m}^{-2} \text{ year}^{-1}$ for the 40-year-old and 245-year-old stands, respectively. Estimated annual C flux was 95% of the Forest-BGC estimate in the young stand and 69% of the Forest-BGC estimate in the older stand (Figure 3). Total belowground allocation was the largest annual C flux in both stands, and maintenance respiration for aboveground wood was only slightly higher in the older stand. Maintenance respiration for sapwood estimated with Equation 4 was 20–30 $\text{g C m}^{-2} \text{ year}^{-1}$ greater than estimates derived from direct measurements (Ryan and Waring, unpublished results).

The low estimate of total annual C flux compared with the Forest-BGC model estimate in the older stand suggests that using canopy demographics to estimate canopy production and litterfall in the older stand may underestimate true values. Additionally, the approach used does not account for bark or understory production, and the plot size used may underestimate losses to mortality. Results for the lodgepole pine stand appear to indicate that good estimates of production and litterfall are required to get good estimates of GPP using Equations 1–5.

An alternative explanation for the discrepancy between estimates of carbon flux in the older stand is that the Forest-BGC overestimates stomatal conductance and photosynthesis for older trees. Leaf water potential is known to affect stomatal conductance (Schulze and Hall 1984) in conifers. Any reduction in water potential

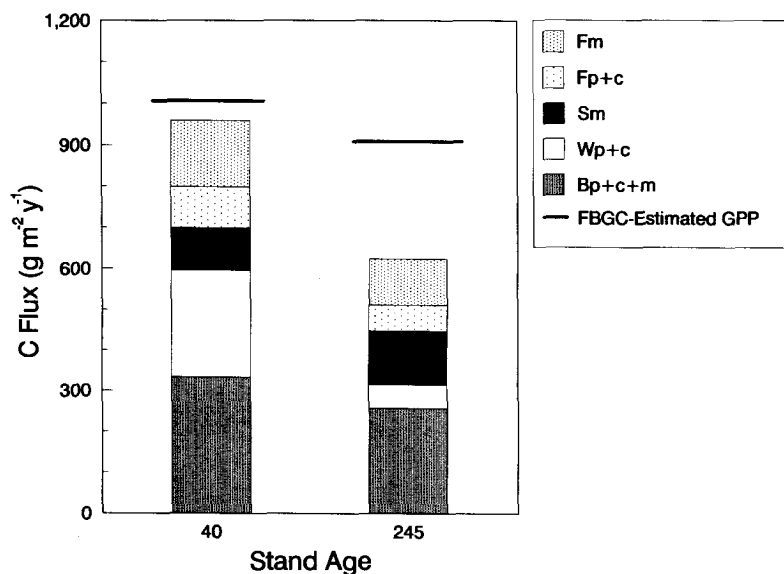


Figure 3. Annual carbon flux estimates using Equations 1–5 and net canopy fixation estimated from Forest-BGC for a lodgepole pine chronosequence. Symbols: F_m = foliage maintenance respiration, F_{p+c} = foliage production and associated construction respiration, S_m = aboveground wood production and associated construction respiration, W_{p+c} = aboveground wood production and associated construction respiration, and B_{p+c+m} = total belowground C allocation.

could lead to reduced stomatal conductance and carbon fixation (Schulze and Hall 1984), because for a given irradiance and enzyme level, carbon fixation is controlled by stomatal conductance. Foliage in the tops of tall, old trees may experience higher water potential gradients (and consequently more negative leaf water potentials) because of increasing resistance from longer branches and longer stems. For example, Mattson-Djos (1981) found that 16-m tall Scots pine have stomatal conductances about 50% of those in 2-m tall saplings. Additionally, Kline et al. (1976) found that total transpiration per unit of sapwood conducting area in a 75-m tall Douglas-fir was 30% less than that of trees 18–25 m tall. This reasoning suggests that Forest-BGC overestimates C fixation in the older stand. Preliminary measurements of stomatal conductance and predawn and midday leaf water potential in these lodgepole pine stands support this hypothesis (Ryan, Schoettle, and Kaufmann, unpublished observations). Furthermore, it has been observed that stomatal conductance and photosynthesis were about 25% lower in old (30-m tall) ponderosa pine than in adjacent young (10-m tall) trees (Yoder and Waring, unpublished observations).

In summary, the proposed method appears to offer a simple, powerful tool for constructing estimates of total annual C flux. The method can generate estimates for comparison with direct measurements or where no flux measurements exist. The critical relationships (estimating total belowground allocation from litterfall and maintenance respiration from tissue N) would benefit from local testing, and the method itself should be tested broadly.

Acknowledgments

I thank Steve Running and Ray Hunt for supplying Forest-BGC and MTCLIM. Partial funding for this research was provided by NSF grant BSR-87-18426 to John Hobbie.

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Appendix

Derivation of equation for maintenance respiration

Maintenance respiration for a wide variety of plant tissue is linearly related to tissue N concentration (Ryan 1991):

$$R_m = 0.0106 N, \quad (\text{A1})$$

where R_m (mol C h^{-1}) is maintenance respiration at 20 °C, and N is plant Kjeldahl-nitrogen in mol N.

The simplest equation relating respiration to temperature is:

$$R_m = R_0 \exp\left(\frac{\ln Q_{10}}{10} T\right), \quad (\text{A2})$$

where R_0 is respiration at 0 °C, and Q_{10} is the change in respiration rate with a 10 °C change in temperature. For the nitrogen relationship, R_0 is 0.0027 (0.0106/4), assuming a Q_{10} of 2.

Temperature will strongly affect R_m , and the nonlinear relationship between respiration and temperature can bias respiration estimates if daily and seasonal temperature amplitudes are ignored. However, if a sine function approximates daily and seasonal temperature cycles, correcting annual respiration estimates for bias is simple (Ågren and Axelsson 1980):

$$R_t = \tau R_0 \exp(\beta T_a) I_0(\beta A_1) I_0(\beta A_2), \quad (\text{A3})$$

where R_t = total annual respiration, τ scales R_0 to an annual rate, β is $\ln(Q_{10})/10$, T_a is average annual temperature, A_1 and A_2 are average daily and annual temperature

amplitudes, and for $x < 2$

$$I_0(x) \approx 1 + 0.25 x^2 + 0.016 x^4 + 0.0004 x^6 . \quad (\text{A4})$$

Combining Equations A1–A4, assuming Q_{10} is 2, assuming temperature amplitudes are 5 °C for a day and 15 °C for the year, and converting moles to grams gives:

$$R_t = 27 \exp (0.07 T_a) \quad (\text{g C year}^{-1} \text{ g N}^{-1}). \quad (\text{A5})$$

For a partial year, assuming daily and seasonal amplitudes are 5 °C, respiration:

$$= 0.059 \exp (0.07 T_s) D \quad (\text{g C year}^{-1} \text{ g N}^{-1}), \quad (\text{A6})$$

where T_s is average temperature and D is number of days when foliage is present.