Ecological Applications, 1(2), 1991, pp. 157–167

EFFECTS OF CLIMATE CHANGE ON PLANT RESPIRATION[1]

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Abstract. Plant respiration is a large, environmentally sensitive component of the ecosystem carbon balance, and net ecosystem carbon flux will change as the balance between photosynthesis and respiration changes. Partitioning respiration into the functional components of construction, maintenance, and ion uptake will aid the estimation of plant respiration for ecosystems. Maintenance respiration is the component most sensitive to changes in temperature, CO_2, protein concentration and turnover, water stress, and atmospheric pollutants. For a wide variety of plant tissues, maintenance respiration, corrected for temperature, appears to be linearly related to Kjeldahl nitrogen content of live tissue. Total and maintenance respiration may decline under CO_2 enrichment, but the mechanism, independence from changes in protein content, and acclimation are unknown. Response of respiration to temperature can be modelled as a Q_{10} relationship, if corrections for bias arising from daily and annual temperature amplitude are applied. Occurrence and control of the cyanide-resistant respiratory pathway and acclimation of respiration rates to different climates are poorly understood, but may substantially affect the reliability of model estimates of plant respiration.

Key words: climate change; CO_2; construction respiration; maintenance respiration; nitrogen; plant respiration; temperature.

INTRODUCTION

Plants respire ≈50% of the carbon available from photosynthesis (after photorespiration), with the remainder available for growth, propagation, nutrient acquisition, and litter production. Global changes in CO_2, temperature, precipitation, ozone, atmospheric pollutants, and nutrient input will affect both respiration and photosynthesis. Because respiration and photosynthesis respond differently to the environment, climate change may alter the balance between them, affecting carbon allocation within ecosystems and net carbon flux. The direction and magnitude of the net carbon flux from ecosystems, however, will likely vary both with the type of change and with the current ecosystem structure. To understand how environmental changes will affect net carbon exchange from ecosystem to atmosphere, we need to understand how photosynthesis and respiration are regulated at the scale of the ecosystem.

Partitioning plant respiration into the functional components of construction, maintenance, and ion uptake (Farrar 1985, Lambers 1985, Amthor 1986) has greatly increased our understanding of the impact of the environment on respiratory processes. Environmental change will affect each of these functional components differently, altering the relative contribution of each component to plant carbon balance. Application of these functional models of respiration to vegetation in ecosystems may help unravel the complex behavior of plant growth in response to environmental change.

I will outline a strategy for modelling plant respiration responses to climate change. First, I will review models of plant respiration. Next, I will review how environment alters the rate of respiration for each of the functional components of respiration, and suggest useful empirical relationships for modelling plant respiration and environmental change. Then, I will present estimates of plant respiration for a few forest and grassland ecosystems. Finally, I will propose a method for estimating costs of respiration for ecosystems, identify sources of error, and discuss how future climates might affect plant respiration.

FUNCTIONAL MODELS OF PLANT RESPIRATION

Ecologists and plant physiologists generally focus on the function of respiration rather than the biochemistry. However, we need a few definitions. Dark respiration (in this paper, respiration) represents the processes of glycolysis and the oxidative pentose phosphate pathway, the Krebs cycle, and electron transport to oxidative phosphorylation, with concomitant uptake of O_2 and generation of CO_2. Cyanide-resistant, salicylhydroxamic-acid-sensitive respiration is an alternate pathway for electron transport, which generates only one ATP per NADH oxidized, rather than three for cytochrome-mediated electron transport (Laties 1982). Photorespiration is the oxidation of ribulose biphosphate catalyzed by ribulose biphosphate carboxylase in the presence of oxygen. For the purposes of understanding whole-plant respiration, photorespiration al-

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ters the amount of fixed carbon available for dark respiration, and will not be treated in this paper.

To understand respiration for whole plants and ecosystems and the response of respiration to the environment, we partition respiration into functional components (Amthor 1986, 1989). McCree (1970) and Thornley (1970) first partitioned respiration into the components of construction and maintenance:

$$R = \frac{(1 - Y_G)}{Y_G} \cdot \frac{dM}{dt} + m \cdot M, \quad (1)$$

where R = integrated daily total of respiration (in grams of carbon per day), Y_G = biosynthetic efficiency (the ratio of carbon incorporated into structure to carbon used for structure plus energy used for synthesis, in grams of carbon per gram of carbon), dM/dt = absolute growth rate (in grams carbon per day), M = biomass (in grams of carbon), and m = the maintenance coefficient (grams of carbon per gram of biomass carbon per day). Maintenance respiration represents the costs of protein synthesis and replacement, membrane repair, and the maintenance of ion gradients (Penning de Vries 1975), while construction respiration is the cost for new tissue synthesis from glucose and minerals. This model is simple, represents most of the functions important for whole plants, and has been widely applied. The ecological importance of Eq. 1 is that construction costs are fixed for a unit of new tissue while maintenance of all tissue varies with environment (Amthor 1984).

Uptake of anions, particularly nitrate, can be costly, representing up to 60% of total root respiration (Veen 1980). Johnson (1983) suggested that respiration to support nitrogen uptake may explain the higher maintenance rates for roots vs. shoots commonly observed. Johnson (1983) added costs of ion uptake to the basic model (Eq. 1), assuming respiration for ion uptake was proportional to biomass constructed:

$$R = \left[\frac{(1 - Y_G)}{Y_G} + af_N\right] \cdot \frac{dM}{dt} + m \cdot M \quad (2)$$

where a = respiration per unit nitrogen uptake and f_N = fractional nitrogen content of biomass. Application of Eq. 2 is complicated by the need to know the oxidation state of the acquired nitrogen to determine a. Eqs. 1 and 2 appear to be useful for estimating plant respiration in ecosystems, because they contain important phenomenological mechanisms, but are simple models.

Reponse of Respiration to Environment

Maintenance

Maintenance is the most responsive of the functional components of respiration to environmental change, because the processes of protein synthesis and replacement, membrane repair, and maintenance of gradients of ions and metabolites vary exponentially with temperature. Changes in CO_2 concentration, moisture stress, and photochemically produced atmospheric ozone may also alter maintenance costs. Additionally, plants respond to environmental variations by shifting allocation of carbon to leaves, storage, wood, and fine roots (Waring and Schlesinger 1985). Because protein type and quantity differ in each of these tissues, their maintenance rates differ. Therefore, changes in carbon allocation to structure can alter ecosystem maintenance costs.

Temperature.—Rates of the enzymatic processes of respiration, like all chemical reactions, increase with temperature and can be described by the Arrhenius formula:

$$\frac{V_2}{V_1} = \exp\left[\frac{E_a}{R_U} \cdot \left(\frac{1}{T_1} - \frac{1}{T_2}\right)\right], \quad (3)$$

where V_1 and V_2 are reaction rates at T_1 and T_2 (in kelvins), E_a is the Arrhenius activation energy for a given reaction and R_U is the universal gas constant. This equation holds only if enzymes and enzyme–substrate–inhibitor affinities remain stable with temperature, and fits most enzymatic reactions well across physiologic temperatures (Raison 1980).

Environmental physiologists often express respiration rates in terms of Q_{10}, the change in rate with a 10°C change in temperature:

$$R = V = R_0 \exp\left(\frac{\ln Q_{10}}{10} \cdot T\right), \quad (4)$$

where R_0 is respiration at 0°. The two formulas give similar, but not identical results over 0°–50°, because:

$$E_a = \ln(Q_{10}) R(T^2 + 10T)/10. \quad (5)$$

For a wide variety of plant materials (mostly agricultural crops) Q_{10} ranges from 1.6 to 3 but centers about 2 (Amthor 1984). Q_{10} reported for woody plants appears to vary less, but may be slightly higher (2.3: Butler and Landsberg 1981, 2.0: Linder and Troeng 1981, 1.5–2.6: Lawrence and Oechel 1983, 1.8–2.8: Ryan 1990). Changes in Q_{10} with temperature indicate changes in E_a. For species not adapted to cold, Q_{10} may increase dramatically below 10° (Raison 1980). Because E_a varies differently with temperature for different enzyme systems, metabolism at low temperatures creates an imbalance between glycolysis and the Krebs cycle (Raison 1980), eventually killing the plant. However, many plants adapted to cold have high respiration rates at low temperatures (Lechowicz et al. 1980) and low Q_{10} (1.4–1.7: Earnshaw 1981). For temperate species, E_a appears constant over the physiological temperature range (Lyons and Raison 1970).

For modelling plant respiration, a value for Q_{10} of 2.0–2.3 seems reasonable (Landsberg 1986).

Protein concentration.—Maintenance respiration and tissue nitrogen content are strongly correlated (Jones et al. 1978, Merino et al. 1982, McCree 1983, Waring et al. 1985, Irving and Silsbury 1987). This relationship exists because most of the organic nitrogen in plants is in protein and ≈60% of maintenance respiration supports protein repair and replacement (Penning de Vries 1975). Maintenance respiration per unit of plant nitrogen varies with growth rate (McCree 1982), species (McCree 1983), and tissue type (Szaniawski and Kielkiewicz 1982), perhaps because protein content and protein turnover are not strictly related. However, variability in maintenance rates per unit tissue nitrogen is small when compared to the range of respiration rates expressed on a dry mass basis. Because of the strong relationship between tissue nitrogen and maintenance respiration, any change that alters tissue nitrogen (e.g., increased atmospheric deposition of nitrogen, Aber et al. 1989) has the potential to alter the rate of maintenance respiration.

The strong correlation between tissue nitrogen concentration and maintenance respiration suggests the possibility of deriving a general, empirical relationship to estimate maintenance costs for a variety of plant tissues. Fig. 1 shows that measured maintenance respiration and nitrogen content are significantly ($P < .01$) correlated for a wide variety of species and plant tissues:

$$R_m = 0.0106 \cdot N, \quad (6)$$

where R_m is maintenance respiration (moles of C per hour), and N is plant Kjeldahl nitrogen in moles of N. The relationship is linear (Fig. 1) over the range of tissue nitrogen contents normally encountered (Table 1: 1–136 millimoles of N per mole of C), or ≈0.04–6% of dry mass). The intercept is not significant ($P = .48$) and, if included, would bias rates for tissues with low nitrogen contents.

Variability of data in Fig. 1 may result from differences in methods of measuring maintenance costs. Maintenance respiration can be estimated by curve fitting (e.g., maintenance respiration is the intercept of a regression between respiration rate and growth rate when both rates are expressed on the basis of plant mass), by measuring CO_2 flux from plants kept in darkness for 48–60 h (starvation method), or by measuring nongrowing tissue (Amthor 1989). Estimates of maintenance with the starvation method are typically lower than with any of the regression methods (Penning de Vries 1975, Irving and Silsbury 1987), and this pattern is generally true for data in Fig. 1. Using the starvation method, Irving and Silsbury (1987) found that slope for a regression of maintenance respiration and plant nitrogen was 0.0069 moles of C per mole of N at 20°C, 65% of the slope in Fig. 1. Maintenance respiration estimated by regression in Irving and Silsbury's study was equivalent to that presented in Fig. 1.

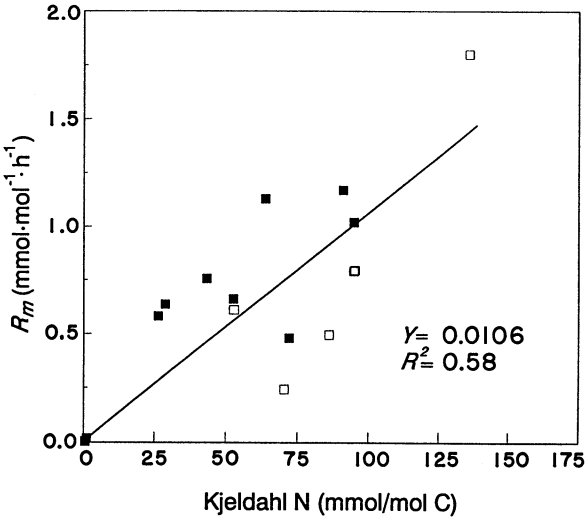

FIG. 1. Maintenance respiration (R_m) at 20°C vs. Kjeldahl N for a variety of plant material; maintenance respiration was estimated by starvation method (□) or regression or mature tissue methods (■). Respiration = 0.0106·Kjeldahl N, where respiration per hour and Kjeldahl N are expressed as millimoles of C or N per mole of carbon in the plant tissue; n = 16, $R^2 = 0.58$ [calculated as $1 - \sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2 / \sum_{i=1}^{n} (Y_i - \bar{Y})^2$, Kvalseth 1985], $S_{y.x} = 0.29$, $P < .01$. See Table 1 for explanation of the data and its sources.

Turnover rates for common enzymes can vary dramatically and also cause variability in the relationship between maintenance respiration and tissue nitrogen. For example, turnover of nitrate reductase is ≈4 d^{-1} while ribulose biphosphate carboxylase turns over at 0.12–0.55 d^{-1} (Penning de Vries 1975). Specific respiration rates can be greater in roots than leaves (Szaniawski and Kielkiewicz 1982), and enzyme turnover rates may explain these differences. In nitrogen-saturated ecosystems, a large fraction of N may be in vacuoles as nitrate or as free amino acids (Zedler et al. 1986, van Dijk and Roelofs 1988). For these systems, tissue nitrogen may overpredict maintenance respiration.

The variability in the relationship between maintenance respiration and Kjeldahl N shown in Fig. 1, is much less than the variability in tissue maintenance rates reported by Penning de Vries (1975), Amthor (1984, 1986, 1989), and Table 1. Therefore, I believe that plant maintenance respiration could be estimated for ecosystems using a relationship with tissue nitrogen content. A respiration–nitrogen relationship would be particularly useful for estimating maintenance costs in forest ecosystems, where much of the biomass has low enzyme concentrations. Forests also contain much standing dead tissue (heartwood), and inclusion of the nitrogen in these tissues might bias estimates of main-

TABLE 1. Maintenance respiration of carbon per unit biomass carbon (R_m) and Kjeldahl nitrogen for a variety of plant material. Respiration rates are corrected to 20°C, using Q_{10} reported for study, or 2.0 if none was given. Dry mass was converted to moles of carbon using values reported or conversions of 0.39 g C per gram dry mass for agricultural crops and 0.50 g C per gram dry mass for boles and chaparral species.

Species	Material	N* (mmol/ mol C)	R_m (mmol· $mol^{-1}\cdot h^{-1}$)	Method†	Source
Sorghum (*Sorghum bicolor*)	plant	70.3	0.242	1	McCree (1974)
Sorghum	plant	72.1	0.479	2	McCree (1983)
White clover (*Trifolium repens*)	plant	86.2	0.494	1	McCree (1974)
White clover (high growth)	plant	95.0	1.020	2	McCree (1982)
White clover (low growth)	plant	95.0	0.790	2	McCree (1982)
Lepechinia calycina	leaf	63.7	1.130	2	Merino et al. (1982)
L. calycina	leaf	43.4	0.756	2	Merino et al. (1982)
Diplacus aurantiacus	leaf	52.6	0.660	2	Merino et al. (1982)
D. aurantiacus	leaf	28.9	0.635	2	Merino et al. (1982)
Heteromeles arbutifolia	leaf	26.4	0.581	2	Merino et al. (1982)
Perennial rye (*Lolium perenne*)	plant	52.8	0.610	1	Jones et al. (1978)
Lodgepole pine (*Pinus contorta*)	bole	0.7‡	0.003	3	Ryan (1990)
Silver fir (*Abies amabilis*)	bole	1.2§	0.018	3	Sprugel (1990)
Sunflower (*Helianthus annuus*)	plant	91.2	1.170	2	Szaniawski and Kielkiewicz (1982)
Cucumber (*Cucumis sativa*)	plant	136.0	1.800	1	Szaniawski (1985)
Bean (*Vicia faba*)	leaf	95.3	0.795	1	Irving and Silsbury (1988)

* All studies measured Kjeldahl N, but several reported only protein concentration; reported protein-to-Kjeldahl-N conversions (5.8 or 6.25) were used to obtain Kjeldahl-N values.

† Method: 1 = CO_2 flux measured after 48–60 h in dark; 2 = calculated by regression from data obtained while plants were in light; 3 = CO_2 flux from nongrowing tissue.

‡ Nitrogen content of sapwood from Pearson et al. (1987) for trees on a similar site.

§ Nitrogen content of sapwood from Meier et al. (1985) for trees on the same site.

tenance respiration. However, nitrogen concentration in heartwood is very low (e.g., 0.022% of dry mass in lodgepole pine, Pearson et al. 1987), and bias caused by including heartwood nitrogen will likely be low. For example, in a 233-yr-old lodgepole pine forest, heartwood had a carbon content of 2780 g/m² (31% of the C in total biomass), but a nitrogen content of only 1.2 g/m², 8% of the total N in biomass (M. G. Ryan, *personal observation*).

Atmospheric CO_2.—Long-term exposure to [CO_2] > 350 μL/L can either decrease respiration (Silsbury and Stevens 1984, Gifford et al. 1985 [wheat], Reuveni and Gale 1985, Bunce 1990) or increase respiration (Gifford 1977, Azcon-Bieto and Osmond 1983, Gifford et al. 1985 [sunflower], Poorter et al. 1988, Nijs et al. 1989). Decreased plant respiration may account for increased net carbon flux into tundra ecosystems fertilized with CO_2 at 510 and 680 μL/L (Hilbert et al. 1987), although the effect declined in year 2 and was nearly absent in year 3 of chronic fertilization (Oechel and Reichers 1986). Interpreting results from these studies is difficult because construction and maintenance respiration are rarely distinguished, and respiration is related to dry mass or surface area rather than tissue nitrogen content. When construction and maintenance were identified, a decrease in maintenance accounted for 80% of the decrease in total respiration (Reuveni and Gale 1985).

Changes in tissue composition may explain changes in respiration associated with long-term elevated [CO_2]. Plants grown under elevated [CO_2] often have higher C:N (Norby et al. 1986, W. Williams et al. 1986), and tissue nitrogen content and maintenance respiration are strongly correlated. Elevated [CO_2] can increase the concentration of nonstructural carbohydrates, and respiration rates can increase as nonstructural carbohydrates increase (Amthor 1989). Additionally, cyanide-resistant respiration may increase in plants that have high concentrations of nonstructural carbohydrates (Lambers 1985).

Elevated [CO_2] during respiration measurements also can decrease respiration rate (Reuveni and Gale 1985, Bunce 1990). The mechanism for this effect is unknown, but intercellular [CO_2] can increase rapidly as [CO_2] in the air increases. High intercellular [CO_2] may affect respiratory enzymes, intercellular pH, ethylene biosynthesis, or dark CO_2 fixation, all of which could lower CO_2 flux from the plant (J. S. Amthor, *in press*).

Because tissue nitrogen and maintenance respiration are so strongly linked, and because decreases in tissue nitrogen are commonly observed in elevated-CO_2 studies, I suspect that many reports of lowered respiration rates stem from lowered tissue nitrogen contents. However, we lack an understanding of respiration reductions when [CO_2] is increased during measurement, and we lack information about the occurrence and control of the cyanide-resistant pathway at elevated [CO_2]. These gaps in our knowledge hamper the development of adequate models of the response of plant respiration to CO_2.

Water stress.—Water stress reduces photosynthesis, growth, and total plant respiration (Bradford and Hsiao 1982, Hanson and Hitz 1982). Because the processes of growth (cell expansion and cell wall synthesis) are apparently more sensitive to decreasing plant water potential, maintenance appears to have priority for labile carbon. Therefore, most of the reductions in total respiration with water stress likely derive from a decrease in construction (Hanson and Hitz 1982). When stress is applied slowly, metabolic activity slows, reducing the rate of maintenance respiration (Amthor and McCree 1990). For example, Wilson et al. (1980) found decreases in growth, total construction respiration, and maintenance respiration (but no change in growth efficiency [Y_G]) when nighttime leaf water potentials were slowly reduced to −1.1 MPa. In contrast, when plants are shocked, maintenance respiration can increase to support repair (Amthor and McCree 1990). For example, maintenance respiration increased (Moldau and Rahi 1983) as leaf water potentials decreased rapidly. Because no simple models relating maintenance respiration to water stress exist, and because water stress appears to mainly affect construction respiration, the effects of water stress on maintenance respiration may be ignored for ecosystem modelling.

Pollutants.—Exposure to ozone, sulphur dioxide, or fluoride generally increases plant respiration, but inhibition can also occur (Darrall 1989). Lack of a consistent response may stem from differences in pretreatment growing conditions (Darrall 1989) or a failure to separate components of respiration. When Amthor and Cumming (1988) and Amthor (1988) partitioned respiration for ozone-treated plants into growth and maintenance components, specific maintenance costs increased while construction respiration remained constant. Chronic, low levels of ozone (ambient, 58 nL/L) increased specific maintenance respiration 7.3% over filtered-air controls, while twice-ambient levels (114 nL/L) increased specific maintenance respiration 25% over the ambient treatment (Amthor 1988). Repair costs or increased use of the cyanide-resistant pathway may increase maintenance costs, while decreases in carbon substrate from reduced photosynthesis may decrease total respiration (Amthor 1988). Clearly, pollutants can affect respiration, but generalizations about responses of different species, pollutants, and growing conditions cannot yet be made.

Construction

The energy cost of constructing organic compounds includes both the carbon incorporated into the structure and the metabolic energy expended to assemble the compound. These costs vary substantially among compounds. For example, 1 g lignin requires 2.5 g glucose, while 1 g cellulose requires only 1.2 g glucose (K. Williams et al. 1987). The inverse of the average construction cost of all compounds in a plant is the biosynthetic efficiency or Y_G. Construction respiration is equal to the total carbon cost minus carbon incorporated into structure.

Penning de Vries et al. (1974) pioneered the theoretical analysis of anabolic biochemical pathways to obtain quantitative estimates of construction costs. In practice, elemental analyses and empirical relationships are used to determine the carbon equivalents in structure and a value for conversion efficiency of ≈0.88 (grams glucose into structure)/(grams glucose substrate), calculated from pathway analysis (McDermitt and Loomis 1981) is assumed. Empirical methods for determining construction costs include: elemental analysis (McDermitt and Loomis 1981), heat of combustion and ash and organic nitrogen (K. Williams et al. 1987), or carbon content and ash content (Vertregt and Penning de Vries 1987). The method of K. Williams et al. (1987) is simple to apply, and has the advantage of including the energy to reduce nitrogen:

$$C = \left[(0.069869 \cdot \Delta H_c - 0.065)(1 - A) + \frac{kN}{14.0067} \times \frac{180.15}{24}\right]\frac{1}{E_G}, \quad (7)$$

where C is construction cost in grams glucose per gram dry mass, ΔH_c = ash-free heat of combustion in kilojoules per gram, A = ash fraction, k = oxidation state of nitrogenous substrate (−3 for ammonium, +5 for nitrate), N = Kjeldahl-organic-nitrogen fraction, and E_G = conversion efficiency. K. Williams et al. (1987) used an E_G of 0.89. Estimates of construction cost in units of carbon (carbon skeletons plus CO_2 evolved) ranged from 1.23 to 1.40 mol/mol for chaparral leaves (K. Williams et al. 1987). Using biochemical pathway analysis, Chung and Barnes (1977) estimate loblolly pine construction costs (carbon) as 1.26 mol/mol for needles and 1.15 mol/mol for stems, assuming plant dry matter contains 50% C.

Using Eq. 7, the cost of synthesis of organic nitrogen compounds changes with the oxidation state of the nitrogenous substrate. For example, construction respiration calculated for the chaparral leaves of K. Williams et al. (1987) will be up to 40% higher, if nitrate rather than ammonium is used as the nitrogen source. Recent evidence suggests that much nitrate can be reduced inside leaves (Smirnoff et al. 1984, Smirnoff and Stewart 1985) from reductant generated directly in photosynthesis (Abrol et al. 1983, Wallsgrove et al. 1983). Where this occurs, marginal construction costs attributed to nitrogen are minor. This mechanism may be important for C_3 species under light-saturated conditions, where midday stomatal closure is common, and where species have high concentrations of nitrate reductase (Smirnoff and Stewart 1985). Gymnosperms show lower nitrate reductase activities in leaves than other woody plants, and may reduce nitrate in roots using respiration (Smirnoff and Stewart 1985).

Environment can affect construction costs. Reduc-

tions in growth from increased water stress (Bradford and Hsiao 1982, Hanson and Hitz 1982) and pollutants (Darrall 1989) will reduce total construction respiration. Additionally, air pollution can decrease leaf energy content (Singh and Mishra 1988) and elevated [CO_2] can decrease lignin and nitrogen contents (Norby et al. 1986), reducing construction costs. Because construction costs of protein are somewhat higher than those of carbohydrates (K. Williams et al. 1987), construction costs will increase if nitrogen deposition increases, particularly if nitrogen is reduced in roots. Plants also respond to a changing environment by shifting allocation patterns. Because the composition of tissues varies, construction costs will vary in response to allocation patterns (Stahl and McCree 1988). Current empirical equations appear to be adequate to model construction respiration.

Ion uptake

Nutrient uptake requires energy both to construct and maintain fine roots and the direct cost to move ions into the root. In the functional model (Eq. 2), uptake costs are the direct costs of ion transport, i.e., the energy required to overcome electropotential gradients across membranes, to work against diffusion gradients, to maintain charge balance, and to expel excess ions. Direct costs for ion transport can be estimated using mechanistic or thermodynamic models (Clarkson 1985), but estimates from the different models vary. Additionally, diffusion and electrochemical gradients within the cell can transport cations without energy cost unless the external solution is extremely dilute. However, experimentally measured costs of anion transport can be substantial (Veen 1980).

Few experimental estimates of transport costs exist. Hansen and Jensen (1977) noticed that root maintenance was greater than shoot maintenance, and speculated that costs of ion transport in the roots supplied the difference. Veen (1980) partitioned maize root respiration into construction, maintenance, and ion-uptake components, and found that the carbon requirements for ion uptake was 1.02 moles per mole of N, which is 13–60% of total root respiration. Slightly lower rates (10–38% of total respiration) were found for sedge by van der Werf et al. (1988). For both studies, anion (NO_3^-) transport costs increased with flux, so that the ion transport cost was greater during rapid growth. An alternative explanation of high maintenance respiration rates in roots is increased activity of the cyanide-resistant pathway (Lambers 1980, van der Werf et al. 1988). If the cyanide-resistant pathway is engaged, less reductant is supplied for each glucose molecule oxidized, increasing apparent respiration rates for maintenance or ion uptake.

Because estimates of ion-uptake costs are few, it is difficult to generalize. While the major carbon cost of acquiring nutrients may be in constructing and maintaining fine roots (Clarkson 1985), transport costs for a fixed amount of root may be substantial and are poorly understood. Transport costs for ecosystems may vary with nitrogen source, soil nitrogen concentration, and overall nutrient balance, all of which may be affected by changing climate and atmospheric deposition.

Magnitude of Respiratory Costs

Whole-plant respiration is ≈50% of gross photosynthesis (less photorespiration) for many species (Farrar 1985, Amthor 1989); hence, total respiration is often roughly equal to net production. Using this approximation and a carbon requirement value for construction respiration of 0.25 g per gram constructed, then respiration for maintenance and ion uptake will be ≈75% of total respiration. Direct estimates of gross production and autotrophic respiration for forest and grassland ecosystems are rare. However, these few studies show that autotrophic respiration is generally >50% of gross production (Table 2), especially where biomass is large relative to production. The mixed deciduous forest at Oak Ridge (Harris et al. 1975) had the largest cost of maintenance relative to gross production (66%). In forests, stem maintenance is a small fraction (12%) of net primary production for young conifers (Ågren et al. 1980), while for mature conifers stem maintenance may be much higher (Waring and Schlesinger 1985, Ryan 1988).

Estimating Ecosystem Maintenance Costs

Simulation models can usefully integrate our existing knowledge about plant respiration, but the basis for the models must be sound. Because of the wide utility of functional models of respiration (Amthor 1989), their use, coupled with empirical relationships to derive rate constants, should generate reasonable estimates of plant respiration for current conditions. The same approach can be used to estimate respiration in a changing environment, but the assumptions required are more problematic. Because respiration rates increase exponentially with temperature and diurnal temperature variability can be great, special procedures are needed to develop respiration estimates where temperature fluctuates. Finally, acclimation or adaptation can greatly affect the validity of our estimates.

Methodology

Use of the functional model of respiration (Eqs. 1 and 2) has greatly increased knowledge of plant respiration (Amthor 1989), and these equations seem well suited for incorporation into phenomenological models of plant growth. Coupling these models with Eqs. 6 and 7 to estimate rate constants m (maintenance) and $(1-Y_G)/Y_G$ (construction) will capture variability associated with protein content, carbon content of constructed tissue, and oxidation state of incorporated nitrogen. In the absence of other information, a rate of

TABLE 2. Estimates of total (R_A), construction (R_c), and maintenance (R_m) plant respiration (measured as carbon) for forest and grassland ecosystems. NPP = net primary production. R_c was estimated assuming carbon costs of construction respiration of 0.25 g/(g constructed); dry biomass was assumed to be 50% carbon.

Ecosystem	Biomass carbon (kg/m^2)	NPP (kg·m^{-2}·yr^{-1})	R_A (kg·m^{-2}·yr^{-1})	R_c (kg·m^{-2}·yr^{-1})	R_m (kg·m^{-2}·yr^{-1})	R_A/(NPP + R_A)	R_m/R_A	Study
Forest								
Mixed deciduous	8.76	0.73	1.44	0.18	1.26	0.66	0.88	Harris et al. (1975)
Oak–pine	7.06	0.60	0.68	0.15	0.53	0.53	0.78	Woodwell and Botkin (1970)
Grassland								
Osage site, Oklahoma	0.53–1.02	0.37	0.58	0.09	0.49	0.61	0.84	Risser et al. (1981)
Blue grama (*Bouteloua gracilis* (Kunth) Steudel)		0.07	0.08	0.02	0.06	0.53	0.75	Detling (1979)

1.02 moles of carbon per mole of N) (Veen 1980) will estimate the respiration for ion uptake.

Temperature will strongly affect m, and the nonlinear relationship between respiration and temperature can bias respiration estimates if daily and seasonal temperature amplitudes are ignored. Using temperature means in Eq. 4 without considering amplitude will underestimate daily total respiration by 3% for a daily temperature amplitude [(maximum − minimum)/2)] of 5°C and 12% for a daily temperature amplitude of 10° (Ågren and Axelsson 1980). Annual mean temperature underestimates respiration by 15% when annual temperature amplitude is 10°, daily temperature amplitude 5°, and $Q_{10} = 2$. However, if a sine function approximates the daily temperature cycle, correcting respiration estimates for bias is simple (Ågren and Axelsson 1980):

$$R_d = \tau R_0 \exp(\beta T_d) \cdot I_0(\beta A_1), \quad (8)$$

where R_d = daily total respiration, R_0 is respiration at 0°, β is $\ln(Q_{10})/10$, T_d is average daily temperature, A_1 is daily temperature amplitude, τ scales R_0 to a daily rate, and, for $x < 2$

$$I_0(x) \approx 1 + 0.25x^2 + 0.016x^4 + 0.0004x^6. \quad (9)$$

R_0 can be calculated by dividing a respiration rate at a given temperature (T) by exp (βT). Using the same approach, total respiration for a year is:

$$R_t = \tau R_0 \exp(\beta T_a) \cdot I_0(\beta A_1) \cdot I_0(\beta A_2), \quad (10)$$

where R_t = total annual respiration, T_a is average annual temperature, A_2 is annual temperature amplitude, and τ scales R_0 to an annual rate.

Soil temperature lags behind air temperature, and the amplitude decreases with soil depth. Respiration for roots (or for heterotrophic processes) estimated using mean air temperature will also be biased. However, soil temperature can be estimated from air temperature, using daily and annual temperature amplitudes, and soil thermal diffusivity, the ratio of thermal conductivity to volumetric specific heat (Campbell 1977).

To illustrate the errors arising from an assumption that roots and microbes in the soil respire at air temperature, consider a model of respiration using Eq. 4 and Campbell's (1977) model of temperature propagation in soil, with biomass distributed uniformly over a depth of 0–100 cm. For a day, respiration will be:

$$R_s = \int_0^{100} \int_{t=0}^{24} \exp(\beta T_S[z, t]) dt dz, \quad (11)$$

where R_s is daily total respiration from 0 to 100 cm, and $T_s[z, t]$ is soil temperature at depth z and time t for the day, calculated (Campbell 1977) from the thermal diffusivity of the soil and average annual and daily temperature amplitudes.

A numerical solution of the integral over an annual cycle with $Q_{10} = 2$, $A_1 = 10°$, $A_2 = 5°$, and a thermal diffusivity of 0.5 mm/s is given in Fig. 2 and compared with an estimate derived from air temperature. Daily or monthly air and soil respiration estimates differ by as much as 22%, and, perhaps more importantly, are offset seasonally. The large bias caused by using air temperature instead of soil temperature will affect performance of mechanistic models, particularly in grasslands where most of the biomass occurs belowground.

Advantages of functional models

Estimating respiration with the functional model and empirical relationships offers substantial advantages over other methods. Because maintenance rates are more sensitive to environment than construction respiration rates, separating construction and maintenance should improve estimates of respiration in a changing environment. For example, functional models will estimate a lower response to increased temperature than models that estimate respiration simply

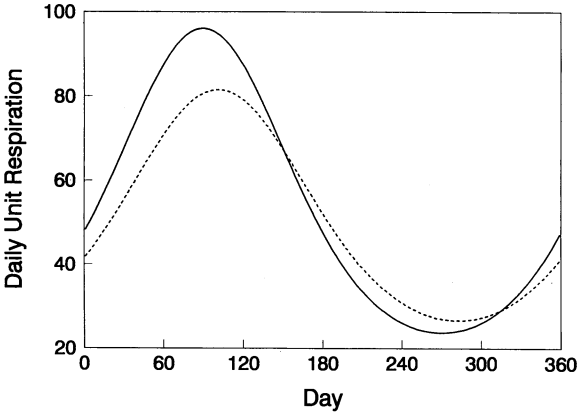

FIG. 2. Annual cycle of daily unit respiration estimated using temperature at soil surface (——) or temperature integrated over 0–100 cm soil depth (– – –). See text for parameter values (*Estimating ecosystem maintenance costs: Methodology*).

from biomass (e.g., $R = bW$, where b increases exponentially with temperature). The difference occurs because b includes respiration for construction and ion uptake, and is therefore much greater than m. Tissue nitrogen concentration appears to be a much better predictor of maintenance respiration (Fig. 1, Table 1) than biomass (or surface area in forests, Jarvis and Leverenz 1983, Landsberg 1986). Additionally, whole-plant nitrogen contents could be used to estimate maintenance respiration, instead of assembling estimates for separate tissues. Eq. 6 could also provide a value for comparison for respiration estimated using short-term measurements on leaves, stems, and roots.

Disadvantages of functional models

Disadvantages in applying the functional model arise because simple, general models of the effects of pollutants and [CO_2], acclimation and adaptation, and the engagement and control of the cyanide-resistant pathway are not available, and hence, not included in the model. Additionally, use of the functional model presumes the existence of other models to estimate photosynthesis, dry matter production, and allocation.

Acclimation of respiration rates may be an important component of plant response to climate change. Respiration rates of plants grown in warm temperatures are often lower than those of plants grown in a cooler environment (Amthor 1989), particularly when respiration is measured at warm temperatures. For example, when respiration rates were measured at 28°C, subterranean clover grown at 24° had nearly half the respiration rate of plants grown at 12° (Fukai and Silsbury 1977). If plant maintenance rates acclimate to a slowly changing average temperature, the functional model will overestimate respiratory costs. Empirical models of temperature response may also fail for arctic or tropical ecosystems, if temperatures exceed those for which the current vegetation is adapted. The fact that maintenance respiration rates can change with season (Holthausen and Caldwell 1980) and growth rate (McCree 1982) suggests capacity for acclimation.

Oechel and Reichers (1986) reported evidence that ecosystem respiration for an arctic tundra ecosystem may acclimate (return to normal) after three seasons of CO_2 fertilization. These data are difficult to interpret, because biomass and nitrogen concentrations were not reported. However, changes in net ecosystem fluxes were likely caused by changes in plant respiration, because soil respiration in this study did not respond to increased CO_2 (Oberbauer et al. 1986). Because acclimation appears to be so important in determining the long-term response of ecosystems to change, we need to better understand this process.

The cyanide-resistant pathway occurs widely in crop plants and generates heat in the genus *Arum* (Lambers 1985). However, its functional significance for non-thermogenic plants is unknown. The cyanide-resistant pathway may provide carbon skeletons for biosynthesis when energy is abundant or oxidize carbon in excess of that required for growth and maintenance (Lambers 1985). Engagement of this pathway may explain respiration assigned to ion uptake (Lambers 1980, van der Werf et al. 1988). Decreases in respiration at elevated CO_2 may result from a decrease in activity of the cyanide-resistant pathway (Gifford et al. 1985), but increased activity also occurs and can reduce growth (Musgrave et al. 1986). Clearly, the cyanide-resistant pathway may be important in the response of plant respiration to climate change, but the information to construct general models is lacking.

EFFECTS OF CLIMATE CHANGE ON PLANT RESPIRATION

Most changes postulated for global warming (increased temperature, increased CO_2, altered precipitation, increased pollutants) will cause direct or indirect changes in maintenance costs. Increasing temperature and tropospheric ozone concentrations will likely increase maintenance costs as shown, but the magnitude of the increase cannot be predicted. Indirect impacts are more subtle and difficult to estimate. For example, if an increase in CO_2 increases litter C:N ratios, nitrogen availability will be lower and allocation will shift more carbon to fine roots, increasing uptake and maintenance costs. Alternatively, increasing N availability through atmospheric deposition may decrease uptake costs, lower total root maintenance costs (because of less root biomass), but increase the unit maintenance rate for all tissues.

The effect of any change in rates of maintenance, construction, or ion uptake will depend on the balance between net photosynthate and total respiratory costs. Increased CO_2, temperature, and enzyme levels will increase photosynthesis, perhaps initially more than they change the costs of maintenance respiration. Imbalances between photosynthesis and respiration will

likely occur first in mature forest ecosystems. Because the balance between photosynthetic and respiring tissue in forests decreases with ecosystem development (Waring and Schlesinger 1985), any increase in respiratory costs will affect older trees most. With increased temperature and CO_2, forest ecosystems may grow faster, mature earlier, and die younger. Forests, particularly the coniferous monocultures with their low species diversity and simple stand structure, may have poor ability to acclimate to temperature changes.

ACKNOWLEDGMENTS

I thank Jerry Melillo for the opportunity to initiate this project, Sarah Davis for programming the temperature model, and Julie Pallant for assembling literature on maintenance rates. Jeffery Amthor supplied valuable references and a constructive review, and John Carter, Linda Joyce, Ed Rastetter, Jim Raich, Richard Waring, and Merrill Kaufmann gave valuable comments on an earlier draft. Funds from NSF grant BSR-87-18426 to John Hobbie supported this work.

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