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Terrestrial Higher Plant Respiration and Net Primary Production[1]

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The survival of green plants is based on their ability to maintain a positive balance between gain of energy through photosynthesis and loss due to respiration, death of tissues and grazing.

F. E. Eckardt (1975), "Photosynthesis and Productivity in Different Environments"

Neither the rate nor the extent of production need bear a close relation to photosynthetic rate, or be determined by it. . . . The processes that follow photosynthesis, such as respiration and translocation, or other limitations on the capacity of plants to grow and utilize photosynthate, can be major determinants of productivity.

L. T. Evans (1975), "Photosynthesis and Productivity in Different Environments"

I. Plant Respiration in Relation to Terrestrial Ecosystem Net Primary Production

A large fraction of the C assimilated in higher plant photosynthesis is released back to the atmosphere as CO_2 during subsequent plant respiration. Thus, plant respiration is a large negative component of the C budget of plants and ecosystems. It contributes to the control of ecosystem net primary production (NPP) because NPP is gross primary production (GPP) minus plant respiration (hereafter simply *respiration*). The relationship between ecosystem NPP and GPP is therefore dictated by respiration.

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In spite of the fact that respiration leads to a large loss of C from plants, its true importance is related to the functions it performs. That is to say, respiration is more than a loss of CO_2. The CO_2 released is a necessary by-product of biochemical reactions that support nearly all the growth, transport, and maintenance processes occurring in plants (except those intimately associated with photosynthesis). Most importantly, plant growth and health are impossible without respiration, so at least much of the CO_2 released in respiration is essential (Beevers, 1961, 1970). In short, respiration is the metabolic bridge from photosynthesis to growth; it consumes photosynthate to generate usable forms of energy that then drive plant growth and maintenance processes. It also supplies many of the C-skeleton building blocks needed for biosynthesis.

When considering respiration in the context of NPP, we find it appropriate to relate amounts of CO_2 released in respiration to amounts assimilated in gross photosynthesis (i.e., GPP). We prefer the use of a ratio. This ratio is the amount of CO_2 released in respiration divided by the amount assimilated in photosynthesis. This is denoted R_a/P_g, where R_a and P_g are plant respiration and photosynthesis integrated over time periods ranging from "growing seasons" to years. Annual totals are most meaningful with respect to NPP. This ratio reflects the C costs of respiratory processes relative to C gains in photosynthesis. The question arises: "How conservative is the ratio R_a/P_g within and among terrestrial plants and ecosystems?"

II. Regulation of Respiration Rate

Because respiration is a large part of a plant's C budget, it is relevant to ask "What controls respiration rate?" because those controls may be important regulators of NPP. Biochemically, respiration is presumably regulated in large part by needs for—and uses and turnover of—its products (Beevers, 1961, 1970; Dry *et al.*, 1987). Notable among those products are (1) a range of C-skeleton intermediates generated all along the respiratory pathways, (2) ATP, and (3) the reductants NADH and NADPH. It is thought that respiratory products accumulate when they are not used by other processes, and in so doing they retard respiration through negative feedback mechanisms. Also, without the use (i.e., turnover) of ATP, NADH, and NADPH, the required respiratory substrates ADP, NAD^+, and $NADP^+$ are unavailable for further respiration. When respiratory products are used rapidly, however, negative feedbacks on respiration are released and associated respiratory substrates are regenerated, with the result that respiration rate increases. Widespread circumstantial evidence in favor of this scheme of respiratory control is found in the strong positive relationship between respiration rate

and growth rate; young, rapidly growing organs have fast respiration compared to mature and more slowly growing organs, presumably because rapidly growing organs use respiratory products rapidly. And, biochemical uncouplers—which break the links between respiration rate and the use or turnover of respiratory products—generally stimulate respiration rate. The uncoupled respiration rate is a measure of respiratory *capacity*, which is set by the amount of respiratory machinery (enzymes, transporters) present. Active meristematic tissue may respire at the rate limited by respiratory capacity, whereas in more mature tissue, the uncoupled rate of respiration may be double the normal rate (Beevers, 1961). Interspecific variation in response to uncouplers may occur, however. For example, *Alocasia odora* leaf respiration increased 60–80% in the presence of an uncoupler, but *Spinacia oleracea* leaf respiration was unaffected (Noguchi and Terashima, 1997). In this case, nighttime *S. oleracea* leaf respiration was apparently regulated by carbohydrate availability (Noguchi and Terashima, 1997), carbohydrates being a main respiratory substrate.

These biochemical controls of respiration presumably occur at all levels of plant organization, from the single mitochondrion or parcel of cytoplasm to the global biosphere. Hence, the regulation of respiration is inherently scale independent and the same metabolic principles used to predict and explain respiration over the short term in cells, organs, and single plants can be used to make predictions of (and understand) respiration at larger spatial and longer temporal scales. It is, therefore, in theory possible to calculate global respiration from knowledge of the global extent of the processes consuming respiratory products. Because the rates of processes consuming respiratory products at the large spatial and long temporal scales are imprecisely known, however, present estimates of annual global terrestrial higher plant respiration are crude (and see Sprugel *et al.*, 1995). Moreover, ecosystem respiration (R_e) includes metabolism by heterotrophs, which may not be so easily generalizable.

We emphasize that direct evidence that respiration is fully coupled to useful processes in nature is lacking. We suppose that evolution favors tightly regulated respiration, but it is possible that some degree of "idling respiration" (*sensu* Beevers, 1970) is also generally present—and perhaps indirectly serves essential functions. Thus, we expect that respiration is generally coupled to the processes that use respiratory products, but we must allow for the possibility that "inefficiencies" could also be a normal aspect of respiration. To the extent that respiration is controlled by the rate of processes using respiratory products, temperature will affect respiration to the same degree that it affects the processes using respiratory products. Importantly, various stresses might reduce the coupling of respiration to "normal" growth and maintenance processes.

III. The Fundamental (Semi)Mechanistic Model of Plant Respiration

Early numerical models of respiration were empirical. They related respiration rate to easily measured plant properties such as dry mass or surface area. Although useful for summarizing data, they often lacked explanatory and predictive power. Also, relationships between respiration rate and surface area or dry mass fail to account for much of the observed variability in respiration rate (Ryan, 1990; Ryan *et al.*, 1994a; Sprugel *et al.*, 1995).

A significant step forward was to set respiration rate at the uncoupled rate in meristematic tissue, and to slow it with tissue aging (de Wit *et al.*, 1970). It had long been known that respiration rate per unit dry mass declines with increasing age in organs and whole plants; the research of Kidd *et al.* (1921) was especially significant (see also, e.g., Inamdar *et al.*, 1925; Price, 1960).

Limitations of these models in explaining and predicting respiration rate were realized 30 years ago by R. S. Loomis. He suggested to C. T. de Wit that one could, in theory, sum up all the nonphotosynthetic biochemical reactions shown in wall charts of metabolic pathways in proportion to their occurrence and rate in plants. The total CO_2 released per unit of dry mass per unit of time calculated in this way would be a mechanistic estimate of respiration rate. Although Loomis was skeptical that such a project could be carried out successfully, de Wit encouraged F. W. T. Penning de Vries to give it a try (Amthor, 2000). Penning de Vries met with considerable success. The fruits of his labors included an elegant mechanistic model of the respiratory costs (i.e., CO_2 released) of growth of tissues of a specified composition from specified substrates (see, e.g., de Wit *et al.*, 1970, 1978; Penning de Vries, 1972, 1974, 1975b; Penning de Vries *et al.*, 1974, 1983, 1989; Penning de Vries and van Laar, 1975). He also produced a refined, semimechanistic model of plant maintenance costs or maintenance respiration (Penning de Vries 1975a; Penning de Vries *et al.*, 1983). While this model development was occurring, novel approaches to measurement and analysis were used to obtain experimental estimates of growth and maintenance respiration in plants (e.g., McCree 1970; Thornley, 1970; Hesketh *et al.*, 1971).

We suggest that the simplest (clearest) way simultaneously to understand, quantify, and predict the amount of respiration—and its relationships to GPP and NPP—is to describe it with a semimechanistic model, based on the preceding work, as follows:

$$R_a = r_B B + r_I I + r_N N_a + r_T T + r_M S,$$

where B is the rate of biosynthesis of new tissue; r_B is the respiratory cost of (i.e., CO_2 released during) biosynthesis; I is the rate of active ion uptake by roots; r_I is the respiratory cost of active ion uptake; N_a is the rate of N assimilation (excluding N assimilated directly by photosynthetic metabolism);

r_N is the respiratory cost of nonphotosynthetic N assimilation; T is the rate of translocation of carbohydrates, amino acids, and other compounds; r_T is the respiratory cost of translocation (mainly phloem loading?); S is the amount of structural tissue (total mass less temporary nonstructural storage compounds); and r_M is the cost of maintaining existing structure. We believe this accounts for most of the quantitatively important aspects of respiration. The coefficients r_B, r_I, r_N, and r_T are ratios, but r_M is a rate, because B, I, N_a, and T are rates, whereas S is a state. Estimation of the coefficients r from biochemical principles was an outcome of Penning de Vries's work. Overviews of values of the coefficients are given in Thornley and Johnson (1990) and Amthor (1994a). The following may be true in general for whole plants: $r_M S = r_B B > r_N N_a \approx r_T T > r_I I$.

A simplified model is also often used. It divides respiration into the two components, growth and maintenance, as follows (Thornley, 1970):

$$R_a = g B + m S,$$

where g is the growth respiration coefficient, which includes costs of biosynthesis, ion uptake, N assimilation, and the translocation of substrates used in growth; and m is the maintenance respiration coefficient, which includes costs of maintenance and the translocation of substrates used in maintenance. Over an annual cycle, the total of B is essentially the same as NPP. The term gB is growth respiration rate (R_g) and the term mS is maintenance respiration rate (R_m). We note that NPP must be less than GPP/(1 + g) because some maintenance respiration always occurs.

A. Growth Respiration

Growth is the conversion of temporary pools of substrates such as carbohydrates and amides into new structures (including enzymes) and "permanent" storage such as starch in seeds. Growth includes monomer synthesis, polymerization of monomers into polymers such as cellulose and proteins, organization of polymers into organelles and cells, and "tool maintenance" or the turnover of molecules catalyzing growth (Penning de Vries *et al.*, 1974). (Development of the secondary and tertiary structure of polymers and the organization of polymers into organelles and cells apparently uses little energy.) Nutrient uptake and assimilation, and translocation of substances used in growth, are also growth processes in the two-component scheme of respiration. Growth respiration R_g is the CO_2 generated by growth processes, but some of that CO_2 arises outside the respiratory pathways per se (Penning de Vries *et al.*, 1974, 1989). The respiratory pathways per se that contribute to R_g are the same as the respiratory pathways contributing to R_m.

In addition to detailed reaction-by-reaction analyses based on Penning de Vries *et al.* (1974, 1983, 1989), shortcut methods of estimating g (and r_B)

from plant elemental composition and/or energy content are available (McDermitt and Loomis, 1981; Vertregt and Penning de Vries, 1987; Williams *et al.*, 1987). Comparisons of various methods of estimating g (and r_B) are in Williams *et al.* (1987), Lafitte and Loomis (1988), and Wullschleger *et al.* (1997).

A key concept is that R_g is proportional to NPP—or growth—through the ratio g. Values of g depend on the compositions of substrates used for growth and the tissue grown. Values are relatively small for high-carbohydrate tissue, and large for high-fat, high-lignin, and high-protein tissue (Amthor, 2000). At the whole-plant and ecosystem scales, typical values of g may be 0.25–0.35 mol CO_2 mol^{-1} C. Any factor that stimulates NPP without greatly altering plant chemical composition will probably stimulate R_g proportionally. Thus, rapid growth requires rapid growth respiration! Knowledge of the ratio R_g/NPP ($= g$) is central to understanding respiration–NPP connections. To the extent that g is a constant, R_g will be affected by temperature (and other environmental factors) in the same way that NPP is (de Wit *et al.*, 1970). If an environmental change reduces NPP by 30%, for example, we expect that R_g will also be reduced about 30%.

According to the model, respiration per unit dry mass and R_g/R_a increase with specific growth rate (Fig. 3-1). The release of metabolic heat also increases with growth rate, and from the perspective of plant metabolic energy balance, the ratio metabolic heat release/CO_2 release is indicative of specific growth rate for a constant g and m (Fig. 3-1).

B. Maintenance Respiration

Maintenance respiration includes the energy and C used for turnover of labile cellular constituents, active intracellular transport to counteract membrane leaks and ion imbalances, and repair and acclimation processes that result from a stressful or variable environment (see Penning de Vries, 1975a). It is difficult to measure higher plant R_m, and a wide range of estimates have been derived (Amthor, 1989; Ryan, 1990; Sprugel, 1990; Ryan *et al.*, 1996). In particular, the coefficient m can be very small in woody tissue. Moreover, a distinction should be made between metabolically inactive heartwood and more active sapwood in trees (Ryan, 1990; Sprugel, 1990; Ryan *et al.*, 1994a).

Because maintenance presumably involves mainly protein turnover and other processes that are likely to be related to protein content, R_m may be better related to plant N content (N) than to structural dry mass. This leads to the following modified model (Barnes and Hole, 1978):

$$R_a = gB + m_N N,$$

where m_N is maintenance respiration rate per unit N, and $m_N N = mS = R_m$. Variation in m_N can be smaller than variation in m (Jones *et al.*, 1978; Ryan,

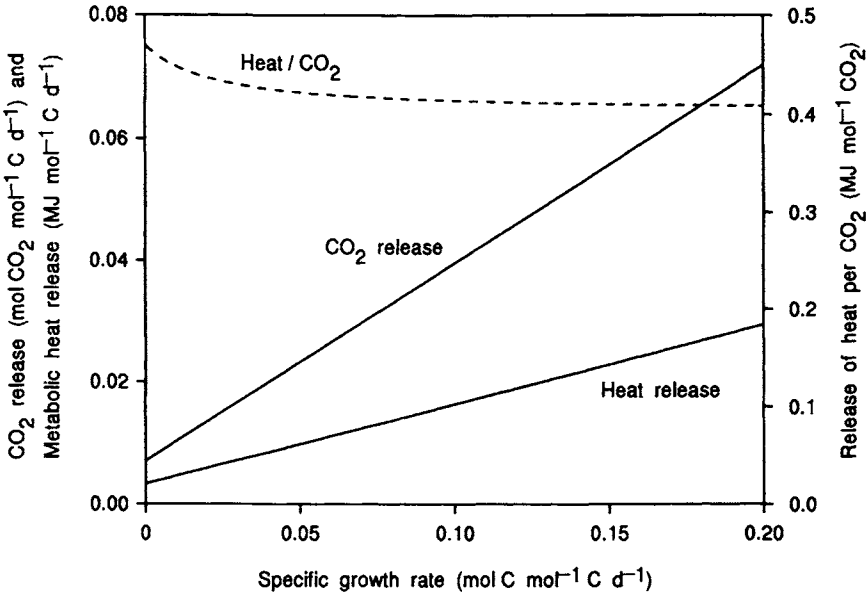

Figure 3-1 Relationships between specific growth rate and release of CO_2 and metabolic heat in plant metabolism (solid lines, left axis) and the ratio heat release/CO_2 release (dashed line, right axis). The case shown is for tissue with a (1) maintenance respiration coefficient m of 0.007 mol CO_2 mol^{-1} C d^{-1}, (2) growth respiration coefficient g of 0.325 mol CO_2 mol^{-1} C, (3) energy content of the substrates of growth of 470 kJ mol^{-1} C, and (4) energy content of new structural matter of 492 kJ mol^{-1} C. That is, 470 kJ is released as heat per mol CO_2 released in maintenance processes, whereas ~402 kJ is released as heat per mol CO_2 released in growth processes. In this example, growth conserves energy relative to C. [We note that Figs. 4.A2 and 4.A3 in Amthor (1994c) are in error with respect to metabolic heat release per CO_2 release as a function of specific growth rate; due to a typographical error in the computer program generating those figures, the heat release rate slows too much per unit increase in specific growth rate.]

1991, 1995; Collier and Grodzinski, 1996; Ryan *et al.*, 1996), indicating that indeed N may be a better predictor of R_m than is S. Although estimates of m_N vary, many are in the range 2–5 μmol CO_2 mol^{-1} N s^{-1} in the temperature range 10–20°C (Table 3-1). In some instances, it may be that only a part of R_m is related to tissue N content (Li and Jones, 1992). In any case, it seems that R_m is related not only to plant size, but also plant composition. There is a corollary: increased standing stock increases whole-ecosystem plant R_m to the extent that plant N per unit ground area increases.

The value of R_m increases about exponentially with temperature in the shortterm, but the fraction of annual daytime net canopy CO_2 assimilation used for stem maintenance increased linearly, over the range 5–13%, with site temperature in four conifer ecosystems (Ryan *et al.*, 1995).

Table 3-1 Selected Estimates of the Maintenance Respiration Coefficient m_N in Higher Plants[a]

Species	Plant part	Growth conditions	Temperature (°C)	m_N (μmol CO_2 mol^{-1} N s^{-1})	Notes	Ref.[b]
General	Leaf	Chamber	15–30	0.5–0.9	Theoretical	Penning de Vries (1975a)
Abies amabilis	Stem	Field	20	4.2		Ryan (1991)
Abies balsamea	Stem	Field	15	7–14		Lavigne *et al.* (1996)
Abies lasiocarpa	Leaf	Field	10	1.5		Ryan (1995)
Alnus crispa	Leaf	Field	10	3.0		Ryan (1995)
Betula papyrifera	Leaf	Field	10	3.1		Ryan (1995)
Cucumis sativus	Shoot	Chamber	26	3.3		Szaniawski (1985)
	Root	Chamber	26	21		Szaniawski (1985)
Diplacus aurantiacus	Leaf	Field	20	3.5–6.6		Merino *et al.* (1982)
Glycine max	Leaf	Greenhouse	23	22	Ambient CO_2	Thomas and Griffin (1994)
Gossypium hirsutum	Leaf	Chamber	29	14	Ambient CO_2	Thomas *et al.* (1993)
Helianthus annuus	Shoot	Chamber	20	2.1		Szaniawski and Kielkiewicz (1982)
	Root	Chamber	20	4.7		Szaniawski and Kielkiewicz (1982)
Heteromeles arbutifolia	Leaf	Field	20	6.6		Merino *et al.* (1982)
Larix laricina	Leaf	Field	10	2.2		Ryan (1995)
Lepechinia calycina	Leaf	Field	20	5.5		Merino *et al.* (1982)
Liriodendron tulipifera	Leaf	Field chamber	Ambient	21	Ambient CO_2	Wullschleger *et al.* (1992)
Lolium perenne	Shoot	Field	15	1.8–3.7		Jones *et al.* (1978)
Medicago sativa	Plant	Chamber	18–26	2.3	Nitrate grown, no osmotic stress	Shone and Gale (1983)
Oryza sativa	Shoot	Chamber	31	1.6		Baker *et al.* (1992)
Pennisetum clandestinum	Leaf lamina	Chamber	20	2.3		Murtagh *et al.* (1987)
Picea engelmannii	Leaf	Field	10	2.0		Ryan (1995)
Picea mariana	Leaf	Field	10	2.1		Ryan (1995)
	Stem	Field	15	2.8–2.9[c]		Lavigne and Ryan (1997)
Pinus banksiana	Leaf	Field	10	2.0		Ryan (1995)
	Stem	Field	15	2.3–3.5[c]	Young	Lavigne and Ryan (1997)
	Stem	Field	15	1.7–2.2[c]	Old	Lavigne and Ryan (1997)
Pinus contortia	Stem	Field	20	1.2		Ryan (1991)
	Leaf	Field	10	2.8		Ryan (1995)
Pinus ponderosa	Stem	Field	10–25	3.9		Carey *et al.* (1996)

Pinus radiata	Leaf	Field	15	1.7		Ryan *et al.* (1996)
	Fine root	Field	15	11		Ryan *et al.* (1996)
Populus balsamifera	Leaf	Field	10	2.9		Ryan (1995)
Populus tremuloides	Leaf	Field	10	2.1–2.4		Ryan (1995)
	Stem	Field	15	0.6–0.7[c]		Lavigne and Ryan (1997)
Quercus alba	Stem	Field chamber	Ambient	0.4	Ambient CO_2	Wullschleger *et al.* (1995, 1997)
Quercus rubra	Leaf	Field chamber	Ambient	6.1	Spring/seedlings, ambient O_3	Wullschleger *et al.* (1996)
	Leaf	Field chamber	Ambient	4.4	Fall/seedlings, ambient O_3	Wullschleger *et al.* (1996)
	Leaf	Field chamber	Ambient	2.9	Spring/mature trees, ambient O_3	Wullschleger *et al.* (1996)
	Leaf	Field chamber	Ambient	4.6	Fall/mature trees, ambient O_3	Wullschleger *et al.* (1996)
Salix plantifolia	Leaf	Field	10	2.1		Ryan (1995)
Secale cereale	Leaf	Field	20	3.5[c]		McCullough and Hunt (1993)
	Stem	Field	20	4.3[c]		McCullough and Hunt (1993)
Shepherdia canadensis	Leaf	Field	10	2.2		Ryan (1995)
Solanum tuberosum	Root	Hydroponic	18	3.1		Bouma *et al.* (1996)
Sorghum bicolor	Plant	Chamber	30	3.3		McCree (1983)
	Plant	Chamber	30	2.7	At anthesis	Stahl and McCree (1988)
Trifolium repens	Plant	Chamber	25	3.8–4.4		McCree (1982)
× *Triticosecale*	Leaf lamina	Field	20	5.7[c]		McCullough and Hunt (1993)
	Stem	Field	20	2.6[c]		McCullough and Hunt (1993)
Triticum aestivum	Leaf lamina	Field	20	6.4–12		Winzeler *et al.* (1988)
	Leaf lamina	Field	20	7.4[c]		McCullough and Hunt (1993)
	Stem	Field	20	6.1[c]		McCullough and Hunt (1993)
Vicia faba	Leaf	Chamber	20	2.4		Irving and Silsbury (1988)

[a]Different methods and assumptions are used in different studies. We think the values given may be representative of many plants, but emphasize that there is considerable uncertainty in estimates of m_N.

[b]Many of these references do not include a direct estimate of m_N; we calculated it from data given therein. For O_2 uptake measurements, a respiratory quotient of unity was assumed (i.e., mol O_2 uptake = mol CO_2 release).

[c]In some cases, R_m may be unrelated to N content of leaves and stems both within and among species (e.g., Byrd *et al.*, 1992; McCullough and Hunt, 1993), including woody stems (Lavigne and Ryan, 1997). Also, fruit R_m may be poorly related to fruit N content (e.g., Hole and Barnes, 1980) because of marked changes in "physiological activity" of N with fruit development.

C. Relative Magnitudes of Growth and Maintenance Respiration

In crops, seasonal R_m / R_a may be ~50% (Amthor, 1989). In temperate grasslands, annual R_m may account for 75–84% of R_a, and in temperate forests, it may be 78–88% of annual R_a (Ryan, 1991). When considering individual organs, estimates of R_m / R_a in a 20-year-old *Pinus radiata* plantation are 95% in foliage, 96% in branches, 52% in stem plus bark, 62% in coarse roots, and 76% in fine roots (Ryan *et al.*, 1996, for "control" trees). Other estimates of the fraction of tree stem respiration that is due to maintenance include 40–65% in cool-temperate evergreen forests (Ryan, 1990), 54 and 82% in a tropical rainforest (Ryan *et al.*, 1994a), 86–88% in cool-temperate pines (Lavigne, 1996), 56–65% in a temperate deciduous forest (Edwards and Hanson, 1996), and 49–74% in boreal forests (Ryan *et al.*, 1998). Thus, R_m is at least as important as R_g is to a plant's annual C balance.

IV. Respiration following and during Photosynthesis

In the immediate term, light (or perhaps photosynthesis) may inhibit leaf respiration (we are not concerned in this chapter with *photo*respiration, a component of photosynthesis). Moderate light level may slow respiration 15–80% (e.g., Sharp *et al.*, 1984; Brooks and Farquhar, 1985; Kirschbaum and Farquhar, 1987; Villar *et al.*, 1995; Atkin *et al.*, 1997). On the other hand, photosynthesis apparently requires concomitant respiration, at least respiratory electron transport processes (reviewed by Krömer, 1995). Knowledge of any effects of light on leaf respiration is needed to estimate daily (24 h) leaf respiration amount because leaf respiration is measured in the dark. Presently, it is impossible to state *a priori* the quantitative effects of light on leaf respiration in any particular situation. Nonetheless, when constructing daily respiratory budgets, it is imperative to state what assumptions are made about leaf respiration in the light.

In the medium term, respiration is often most rapid following a period of rapid photosynthesis. According to Weintraub (1944), these observations date to at least the 1876 and 1881 publications of J. Borodin, the 1893 publication of F. Aereboe, and the 1905 publication of G. L. C. Matthaei. Since then, these observations are common (e.g., Sale, 1974).

Why should this be the case? When photosynthesis is rapid, translocation of photosynthate will tend to be rapid, and this may entail extra respiratory metabolism for phloem loading in leaves as well as active processes associated with transport and compartmentation of recent photosynthate in sinks. Increased levels of nonstructural carbohydrates may in turn contribute to more rapid growth processes (and R_g) throughout a plant (see references in Amthor, 1997). And, perhaps idling respiration responds positively to el-

evated levels of carbohydrates resulting from rapid photosynthesis. After all, carbohydrates are a key substrate of respiration.

In the long term, photosynthesis supplies the substrates of respiration and growth, and annual R_a plus growth is limited by annual P_g. Growth and respiration are required for the construction and maintenance of photosynthetic organs, however, so photosynthesis is impossible without previous respiration. Thus, photosynthesis and respiration are codependent across a range of time scales.

V. Respiration in Leaves, Stems, and Roots

Even though typical leaf respiration rates are slow compared with photosynthetic capacity, leaf respiration can be a significant fraction of the respiratory budget and therefore plant C balance. For example, leaves may account for 40–60% of tropical forest R_a (reviewed in Allen and Lemon, 1976). In three tropical forest stands, Yoda (1983) estimated that leaf respiration was 51–56% of R_a, with stems and branches contributing 32–38% of R_a, and roots the remaining 9–15%. In a warm-temperate evergreen oak forest, leaf respiration was estimated at 50–60% of R_a (Yoda, 1978). In a temperate deciduous forest, leaf respiration (including forest floor herbs) was put at 28% of R_a, with roots contributing 26% of R_a, and branch–bole–stump respiration responsible for the other 46% (Edwards *et al.*, 1981). Annual respiration by 20-year-old *Pinus radiata* trees was reported to be 28–39% from foliage, 11–12% from branches, 24–31% from stems, 7–11% from coarse roots, and 10–20% from fine roots (Ryan *et al.*, 1996, for all treatments). In nonwoody biomes such as grasslands, we expect that leaf respiration is a large fraction of R_a, although root–crown respiration can equal shoot respiration in grasslands (based on estimates of Andrews *et al.*, 1974).

The great unknown with respect to both R_a and NPP involves roots. The partitioning of respiration between roots and shoots depends in part on the root/shoot ratio and the N content of root and shoot, the amount of growth in roots and shoots, and the extent of other processes using respiratory products such as translocation, nutrient uptake from the soil, and nutrient assimilation in roots versus shoots. Quantifying these processes *in situ* is problematic. Difficulties with access to roots and measurements of their activities are obvious. Nonetheless, insights have been gained. For example, fine root respiration rate per unit dry mass can exceed that of other tissues, and may be well coupled to N content (e.g., Ryan *et al.*, 1996). On the other hand, coarse root respiration per unit dry mass is often slow. The maintenance coefficient m is thus very different for fine and coarse roots, and coefficients derived from measurements of fine roots should not be used to estimate

coarse root R_m. Soil temperature may affect forest fine root turnover rate, or longevity, and this may be the result of temperature effects on root R_m (Hendrick and Pregitzer, 1993). Thus, soil temperature might regulate the relationship between root production rate and root standing stock through its influence on root R_m.

A perennial problem in constructing respiratory budgets is deciding what to do about mycorrhizal respiration. Are mycorrhizae part of the "effective" roots, or simply soil heterotrophs? It is perhaps most appropriate to consider root and mycorrhizal respiration together, because the activities of mycorrhizae are presumably linked to root activity (and vice versa?). In root exudates, carbon that is respired by microorganisms associated with roots might also be considered part of overall "root" respiration, but such definitions are tricky.

VI. Respiration in Comparison to Photosynthesis at the Ecosystem Scale

Unfortunately, it is impossible to directly measure whole-plant or plant-community respiration during the course of a 24-h day (or season or year) because of simultaneous daytime photosynthetic CO_2 uptake. Also, separation of *in situ* root respiration from the CO_2 released by other soil organisms is difficult (Hanson *et al.*, 2000). This means that all estimates of daily, seasonal, and annual R_a are equivocal to some degree. In spite of these difficulties, potentially useful estimates of R_a and the ratio R_a/P_g—in nature—exist (Table 3-2). These estimates are, however, just that: estimates. They all include errors in measurements and assumptions. They are primarily useful as educated guesses placing respiration into a semiquantitative framework for evaluating the efficiency with which plants use photosynthate in growth and storage. Presentation of even two digits in Table 3-2 may imply greater precision than there is in reality. In fact, estimates of R_a are sometimes made without underlying measurements of CO_2 (or O_2) exchange. For example, *Fagus sylvatica* root respiration estimates by Möller *et al.* (1954) were simply set to 20% of stem plus branch respiration estimates, whereas whole-tree respiration estimates by Grier and Logan (1977) were made without any respiration measurements at the study site! Nonetheless, educated guesses summarized in Table 3-2 place considerable significance on R_a in the C balance of terrestrial ecosystems and encourage improved understanding of its regulation.

Temperate forests are relatively well studied, and our view is that the most reliable studies give R_a/P_g in the range ~0.50–0.60 in those forests. Boreal forest R_a/P_g may be larger (Table 3-2). The ratio may also be larger in trop-

Table 3-2 Estimates of the Fundamental Ratio R_a/P_g for Terrestrial Ecosystems[a]

Ecosystem	R_a/P_g	Ref.
Crop		
Alfalfa	0.35–0.49	Thomas and Hill (1949)
Maize, rice, and wheat	~0.3–0.6	Amthor (1989)
Grassland		
Shortgrass prairie	0.34	Andrew *et al.*, (1974)
	0.51	Detling (1979)
Tall grass prairie		
No grazing	0.61	Risser *et al.*, (1981)
Seasonal grazing	0.65	Risser *et al.*, (1981)
Year-round grazing	0.62	Risser *et al.*, (1981)
Forest		
Tropical moist		
Ivory Coast	0.75	Müller and Nielsen (1965)
Puerto Rico	0.88	Derived from Odum (1970)
Southern Thailand	0.66	Kira (1975)
Temperate		
Warm evergreen	0.72	Kira (1975)
Warm evergreen "oak"	0.66	Kira and Yabuki (1978)
Abies sachalinensis	0.53	Kira (1975)
Castanopis cuspidata	0.575	Kira (1975)
Chamaecyparis obtusa plantation	0.62	Hagihara and Hozumi (1991)
Cryptomeria japonico plantation	0.71	Kira (1975), mean of five estimate
Fagus crenata		
Secondary forest	0.44	Kira (1975)
Plantation	0.56	Kira (1975)
Fagus sylvatica		
8 years old	0.46	Möller *et al.* (1954)
25 years old	0.39	Möller *et al.* (1954)
46 years old	0.43	Möller *et al.* (1954)
85 years old	0.47	Möller *et al.* (1954)
Fraxinus excelsior plantation	0.37	Kira (1975)
Liriodendron tulipifera	0.66	Harris *et al.* (1975)
Picea abies plantation	0.32	Kira (1975)
Pinus densiflora plantation	0.71	Kira (1975)
Pinus ponderosa	0.55	Law *et al.* (1999)
Pinus taeda plantation	0.58	Kinerson (1975)
Pinus spp.	0.39–0.71[b]	Ryan *et al.* (1944b)
Pseudotsuga–Tsuga	0.93	Grier and Logan (1977)
Quercus–Acer	0.44–0.55	Amthor (2000)
Quercus–Acer	0.54	M. L. Goulden (personal communication, 1997)
Quercus–Pinus	0.55	Whittaker and Woodwell (1969)
Quercus spp.	0.61	Satchell (1973), as cited by Edwards *et al.* (1981)
Quercus–Carpinus	0.38	Medwecka-Kornas *et al.* (1974), as cited by Edwards *et al.* (1981)

(*continues*)

Table 3-2 (*Continued*)

Ecosystem	R_a/P_g	Ref.
Forest (*continued*)		
Subalpine		
Coniferous	0.72	Kitazawa (1977), as cited by Edwards *et al.* (1981)
Abies	0.675	Kira (1975)
Abies veitchii	0.61	Kira (1975), mean of three estimates
Boreal		
Picea mariana	0.69	M. L. Goulden (personal communication, 1997)
Picea mariana	0.72–0.77	Ryan *et al.* (1998)
Pinus banksiana	0.68	Baldocchi *et al.* (1997)
Pinus banksiana	0.69–0.74	Ryan *et al.* (1998)
Populus tremuloides	0.55[c]	Black *et al.* (1996)
Populus tremuloides	0.64–0.67	Ryan *et al.* (1998)
Temperate coastal salt marsh		
Spartina	0.77	Teal (1962)
Spartina–Distichlis	0.69	Woodwell *et al.* (1979)
Arctic tundra	0.50	Reichle (1975)

[a]Both R_a and P_g must have the same units, e.g., mol C m^{-2} [ground] $year^{-1}$. As implied by the sample units just given, estimates of R_a and P_g should be for an entire year, except for crops, where they apply to the "growing season." Nonetheless, some of the values in this table represent data from periods less than a full year. To our knowledge, these estimates of R_a/P_g are based on the assumption that leaf respiration occurs at about the same rate in the light as in the dark, at a given temperature. Data from controlled-environment chambers are included in this summary.

[b]Range of values for seven young (16–40 years olds) *Pinus* stands. Ryan *et al.* (1994b) gave daily (24-h) stem, branch, and root respiration, but foliage respiration was for nights only. The measure of photosynthesis presented was daytime canopy net CO_2 assimilation. Here, to obtain R_a, we doubled the nighttime foliage respiration amounts. To obtain P_g, we added nighttime foliage respiration amount to daytime canopy net CO_2 assimilation. Both our transformations are based on the assumption that daytime foliage respiration was similar to nighttime foliage respiration.

[c]Assuming belowground NPP is 35% of NPP.

ical forests, though "modern" measurements there are limited. Many estimates for crops indicate a relatively low R_a/P_g, often in the range 0.35–0.50 (see Amthor, 1989). We believe that crop R_a/P_g is generally small, and we attribute this to the selection of plants that efficiently convert photosynthate into storage compounds in seeds and tubers. Other ecosystems are poorly represented, but ratios in the range 0.50–0.70 are typical. In a speculative vein, we note that R_m may be positively related to R_g and growth rate (Amthor, 1989; Lavigne and Ryan, 1997), which might contribute to a relatively conservative ratio R_a/NPP and therefore a conservative R_a/P_g.

An obvious requirement for accurately assessing R_a/P_g is accurate measurement of R_a (and P_g). Nighttime eddy covariance measurements of

ecosystem CO_2 exchange provide estimates of R_e when daytime values of R_e can be derived from the nighttime measurements (Goulden *et al.*, 1996). If, in addition, CO_2 efflux from ecosystem heterotrophs (R_h) can be estimated, R_a would be given by difference (i.e., $R_a = R_e - R_h$). Unfortunately, nighttime measurements of R_e by eddy covariance contain uncertainty. In eight forest stands, eddy covariance estimates of R_e were compared to estimates of R_e derived from chamber measurements of soil surface, bole, and leaf respiration (Goulden *et al.*, 1996; Lavigne *et al.*, 1998; Law *et al.*, 1998). Although the estimates of R_e made by the two methods were correlated, it seems that the eddy covariance approach often underestimated R_e by 15–40% in those forests. This implies that direct measurements of R_e using the eddy covariance technique are presently unreliable, at least in those forests. And, nighttime eddy covariance measurements are variable (noisy). There are also, however, uncertainties in estimates of R_e derived from chamber measurements. In addition, eddy-covariance-measurement "footprints" in forests are relatively large and dynamic (Baldocchi, 1997), and may not be adequately sampled with a small number of chamber locations. In any case, R_a cannot presently be determined from R_e in forests because of difficulties in determining both R_e and R_h.

The R_a/P_g values in Table 3-2 may be contrasted with typical leaf-level estimates of respiration and photosynthetic capacity, which typically indicate that high-light photosynthesis assimilates CO_2 at rates 40–100 times faster than CO_2 is released in nighttime leaf respiration (e.g., Pearcy and Sims, 1994). Thus, comparisons between leaf respiration rate and photosynthetic capacity greatly underestimate the significance of respiration to a plant's C balance. Obviously, it is 24-h (or seasonal or annual) totals of plant-community respiration and photosynthesis that are the quantities relevant to NPP (Edwards *et al.*, 1981).

VII. Optimum Leaf Area Index: Does It Exist?

It is sometimes stated that an optimum leaf area index (L) for NPP exists (e.g., Larcher, 1995, p. 149). This notion comes from a simple conceptual model that assumes (1) P_g per unit ground area increases asymptotically with increasing L and (2) R_a increases about linearly with increasing L. The result is that NPP increases, passes through a maximum, and then decreases with increasing L. The L giving maximum NPP is called the "optimum" L. An underlying idea is that shaded leaves at the canopy bottom are "parasitic."

Photosynthesis is indeed expected to approach a maximum with increasing L as light interception becomes complete. The precise form of this relationship depends on things such as the angles of leaves, sun elevation, and

the ratio of direct beam to diffuse radiation (see Chapter 2, this volume). But, canopy and whole-plant respiration is not expected to increase *linearly* with L. Instead, respiration by shaded leaves within a canopy acclimates to low light so incremental increases in L do not result in proportional increases in leaf respiration. Part of the acclimation to shade is a reduction in N per unit leaf area, arising because shade leaves are generally thin (Ellsworth and Reich, 1993; Pearcy and Sims, 1994), and this can contribute to lower R_m per leaf area. The smaller N per unit leaf area and thinner leaves in the shade also reduce leaf growth respiration per unit leaf area in the shade. Moreover, slow photosynthesis in shade leaves—due to low light—limits the amount of translocation from shade leaves, and this would limit translocation respiration proportionally. All the metabolic controls on respiration in sun versus shade leaves are as yet, however, incompletely understood (Noguchi *et al.*, 1996). Our view is that respiration generally proceeds as rapidly as is required to meet metabolic demands—limited perhaps by substrate availability—and shade leaves have limited metabolic demands. The overall result is commonly observed: leaf respiration per unit leaf area and per unit leaf mass declines with depth in a canopy (e.g., Nishioka *et al.*, 1978; Yoda, 1983).

Asymptotic increases in photosynthesis and respiration with increasing L result in an asymptotic increase in NPP with L. This is most easily studied in crops, for which L can be experimentally controlled and precisely measured (e.g., Fig. 3-2). In other ecosystems, L–NPP relationships are not so easily studied. Nonetheless, some insight can be gained into the possibility of an optimum L in other ecosystems with available observations. For example, no obvious optimum L for aboveground NPP (ANPP) exists in forests, according to a pooling of data (Fig. 3-3). The considerable scatter in Fig. 3-3 is expected given the diversity in forest types, climates, and other factors included in the data set. In any case, it is clear that ANPP does not generally decline with increase in L at high L. For example, with $L > 12$, all ANPP estimates are large (Fig. 3-3). Broadleaf forests in Fig. 3-3 (●) generally have L in the range 4–8, with no obvious relationship to ANPP. We also examined the relationship between leaf area duration (LAD) and ANPP using data represented in Fig. 3-3, but there was no indication of an "optimum" LAD for ANPP (not shown). An obvious difficulty in assessing NPP–L relationships from a literature survey is the significant uncertainty in many estimates of L.

Whether an optimum L could exist is an open question. Available data indicate that canopies do not grow enough leaves to surpass an optimum L. They also indicate that any optimum L would greatly exceed the L needed for nearly complete solar radiation capture by a canopy. In short, the notion of an optimum L for NPP has little, if any, application to nature. That is, respiration is not a slave to L; rather, respiration responds to the environment

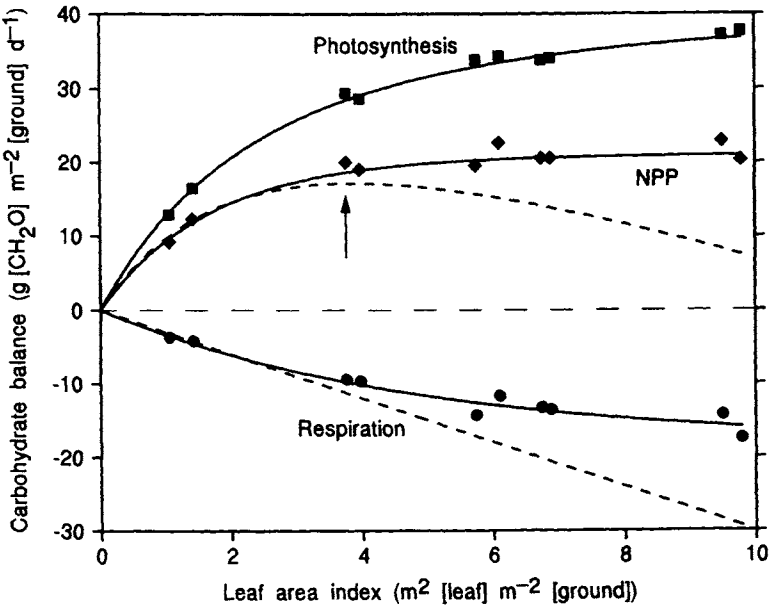

Figure 3-2 Daily plant respiration, NPP, and photosynthesis in a rice crop in the field as a function of leaf area index (L) for variety Peta, 4 weeks before flowering (Cock and Yoshida, 1973). Photosynthesis is given by the sum of measured respiration and NPP (in units of mass of carbohydrate). ■, Photosynthesis; ●, respiration; ◆, NPP. Solid lines are drawn to approximate the data. Also shown is an unverified, but often suggested, linear increase in respiration with increasing L and the resulting NPP (both shown with dashed lines). The arrow marks the optimum L for the case of the fictional linear R_a–L relationship. The dashed lines may be compared to, e.g., the simplistic model results shown in Zelitch (1971, Figs. 9.8–9.10).

(including within-canopy light gradients) and the metabolic needs of the canopy and whole plant.

VIII. Big Trees and Declining Forest Net Primary Production

Forest NPP may decline with increasing tree age (see Ryan *et al.*, 1997). A common but unverified assumption is that the biomass accumulated in old, large trees leads directly to large amounts of respiration, in particular R_m. This presumably increases R_a/P_g because canopy closure occurs early in stand development with little prospect for increasing GPP with further age increases (Ryan and Waring, 1992). This assumption is similar to that underlying the optimum-L notion, and indicts respiration as a drain on NPP. Additional considerations, however, indicate that rapid respiration is un-

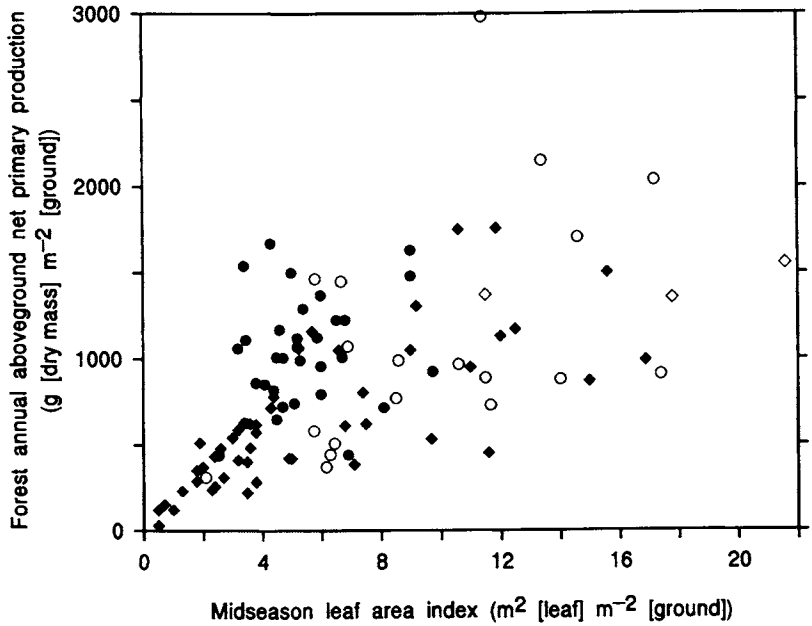

Figure 3-3 Aboveground NPP as a function of maximum or summer leaf area index (L) as reported for 83 forests and tree plantations in the International Biological Programme woodlands data set (DeAngelis *et al.*, 1981), 15 diverse conifer stands in Oregon (Gholz, 1982; Runyon *et al.*, 1994), and four boreal pine stands (Vogel, 1997). Some of the conifer values of L are for total leaf surface area, and some are for half-total surface area. ●, Broadleaf forests; ○, broadleaf plantations; ♦, conifer forests; ◇, conifer plantations.

likely to be the (main) cause of relatively low NPP in old stands, in spite of large biomass (Ryan and Waring, 1992; Ryan *et al.*, 1994b, 1997; Yoder *et al.*, 1994; Ryan and Yoder, 1997). Note also that once canopy closure occurs during early stand development (for closed-canopy forests), whole-forest leaf and fine-root masses may remain more or less constant over time. So, therefore, should their R_m. And, to the extent that NPP declines with age, we expect that R_g declines.

If it is not fast respiration, then what causes low NPP in old stands? Declining GPP with stand age increase, along with a relatively conservative ratio R_a/P_g, would result in declining NPP (Möller *et al.*, 1954). Reduced photosynthetic activity in old, large trees could be caused by low vascular-system hydraulic conductance, which in turn causes reduced stomatal conductance and CO_2 uptake (see Yoder *et al.*, 1994; Ryan *et al.*, 1997). Slow photosynthesis in old trees might also be caused, in part, by limited N availability to leaves, or other factors (see, e.g., Landsberg and Gower, 1997).

IX. Respiratory Responses to Environmental Change: The Future

Several regional and global environmental-change factors might affect R_a and the ratio R_a/P_g in terrestrial ecosystems. Global warming is a present concern, and we assume that warming affects respiration to the extent that it affects processes using respiratory products. Growth respiration is expected to respond to temperature in parallel with the temperature response of NPP, and R_m is presumably affected by temperature to the degree that maintenance processes are affected. Short-term responses of respiration to temperature are positive and strong, but long-term responses may be more moderate. Two processes seem important [see Precht *et al.* (1973) and references in Amthor (1994b)]: (1) acclimation to temporary, e.g., weekly and seasonal, changes in temperature and (2) adaptation to the prevailing climate. Acclimation and adaptation of R_a to future warming (if any) may be incomplete, but our expectation is that they will diminish effects of long-term warming on respiration. If there is a change in R_a/P_g with warming, it might be a slight increase, and driven by an increase in the ratio R_m/R_a. The extent of any increase in R_a/P_g or R_m/R_a with warming may depend on ecosystem type and present climate. In winter-deciduous ecosystems, warming may increase growing season length, which may also influence R_a/P_g and R_m/R_a.

The threat of global warming comes from ongoing atmospheric changes, most notably increasing CO_2. Increasing CO_2 itself is likely to affect most plant processes, including respiration (reviewed in Amthor, 1997). Our general expectations with respect to respiration are (1) R_g will increase about in proportion to increasing NPP; (2) the growth coefficient g could be affected by changes in plant composition, most notably a slight decrease associated with reduced N (or protein) concentration; (3) R_m might increase with increase in plant size, except that the ratio N/S may decline, resulting in a decline in the maintenance coefficient m but perhaps not m_N; and (4) to the extent that g or m values are lower in the future due to plant compositional changes, the ratio R_a/P_g may decline slightly. In addition to these indirect effects of CO_2 on respiration (*sensu* Amthor, 1991), there are several reports of a direct (short-term) inhibition of leaf and root respiration by CO_2 in the dark (e.g., Amthor *et al.*, 1992; reviewed in Amthor, 1997). There are no reports that CO_2 directly inhibits woody-stem respiration. There are also many reports of a lack of an effect of nighttime CO_2 on leaf respiration (Amthor, 1997), and our research with eight species using six methods to measure gas exchange, including measurements in the field, indicates that leaf respiration (CO_2 efflux and O_2 uptake) is unaffected by CO_2 in the dark (G. W. Koch and J. S. Amthor, unpublished data, 1992–1997). And, another report indicates that root respiration in the tree species

Citrus volkameriana is largely insensitive to CO_2 (Bouma *et al.*, 1997), albeit this contrasts previous reports for roots of the tree species *Pseudotsuga menziesii* and *Pinus* sp. (see Amthor, 1997). On balance, we think that direct effects of CO_2 on future respiration will be at most small. Nonetheless, a direct effect of increasing CO_2 on leaf and root respiration is an open issue.

Other environmental changes might also affect respiration. For example, increasing N deposition in temperate ecosystems might stimulate GPP, NPP, and R_a (Melillo *et al.*, 1996), but perhaps not R_a/P_g. Also, increases in regional tropospheric O_3 levels might inhibit photosynthesis and subsequent growth and respiration. Increased O_3 pollution might also increase the ratios R_m/R_a and R_a/P_g (Amthor, 1994b).

X. Summary

Plant respiration is the metabolic link between GPP and NPP. It is also a large component of a plant's C budget; perhaps typically 50–70% of C assimilated in GPP is released back to the atmosphere as CO_2 during subsequent plant respiration. Because great uncertainty remains concerning *in situ* measurements of R_a (and P_g), it is hard to quantify more precisely the role of R_a in C cycles of various ecosystems. We judge the available data to be too imprecise to assess properly whether R_a/P_g is at the present time conservative within or among ecosystems. Moreover, environmental change such as warming and increasing CO_2 concentration may affect R_a and P_g differently, so the ratio R_a/P_g may change in the future. In any case, future studies of the relationship between R_a and NPP or GPP will be more enlightening than simple measurements of respiration rate.

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