4 Higher Plant Respiration and Its Relationships to Photosynthesis

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The heat produced by a respiring cell is an inescapable component of cellular metabolism, the cost which Nature has to pay for creating biological order out of physical chaos in the environment of plants and animals.  
J.L. Monteith (1972)

4.1 Introduction

Respiration is the complement of photosynthesis in higher plants.\(^1\) The primary function of photosynthesis is to assimilate \(\text{CO}_2\) and radiant energy in the formation of carbohydrates. A significant portion of those carbohydrates become the main substrates of respiration (James 1953; Krotkov 1960; ap Rees 1980), but often after some period of storage or distance of transport. The function of respiration is to convert photoassimilate into substances usable by growth, maintenance, transport, and nutrient assimilation processes (Beevers 1961). Respiration does this by breaking down sugars into smaller molecules (carbon skeleton intermediates), phosphorylating ADP and other nucleosides, and reducing nucleotides – respiration does not only generate ATP. Some of the carbon skeleton intermediates become the precursors of growth and are diverted away from respiratory metabolism and used in biosynthetic reactions, whereas the ATP and NAD(P)H formed during respiration are used in all heterotrophic energy-requiring processes (Fig. 4.1).

During respiration and growth, \(\text{CO}_2\) is released as a byproduct. Indeed, it is commonly surmised (Kira 1975; Amthor 1989; Ryan 1991) that up to half, or even more, of the carbon assimilated in photosynthesis (less respiratory decarboxylations) is eventually released during plant respiration, albeit “accurate and relevant estimates of [the ratio of respiration to photosynthesis] are rare because plant physiologists have seldom tried to measure the respiration rate of whole plants” (Monteith 1972). Heat is another important byproduct of respiration and growth, with perhaps half of the energy contained in photosynthate released as heat during plant heterotrophic metabolism. The fraction of carbon and energy in photoassimilate that is “lost” during subsequent metabolism depends on the pathways of respiration and mitochondrial ADP:O, relative rates of growth and main-

\(^1\)The focus herein is on terrestrial higher plants. Moreover, except where specifically noted, the discussion is limited to C\(_3\) plants, which comprise 95% of known plant species. Gardeström and Edwards (1985) and Dry et al. (1987) have discussed various aspects of mitochondria and respiration in C\(_4\) and CAM plants. Geider (1992) has reviewed respiration in phytoplankton.
Fig. 4.1. Simplified scheme of the roles of photosynthesis and respiration in the carbon and energy economy of a plant. Here, photosynthesis means the balance of photosynthetic carboxylations and photorespiratory decarboxylations (carboxylations will exceed decarboxylations in the light under normal conditions). Short-term storage refers to starch in chloroplasts, sucrose in vacuoles, and the like. Carbohydrates include compounds such as cytosolic hexoses that are immediately available to metabolic processes such as respiration. Growth includes the processes of nutrient uptake and assimilation, transport of photosynthetic products from sources to sinks, and biosynthesis of new structure (cell wall, plasmalemma, and protoplasm) and long-term storage such as starch and protein in seeds and tubers. Maintenance refers to active processes associated with the turnover (breakdown and replacement) of existing structure and intracellular metabolite transport to counteract leakage through membranes. Processes other than respiration and photorespiration can release CO₂, but their quantitative contribution to the carbon balance of a plant is usually small and is not shown.

ten processes, and efficiencies of energy use in maintenance and of carbon and energy retention in growth (see Appendix). The latter is, in part, a function of tissue composition (Penning de Vries et al. 1974; McDermitt and Loomis 1981; Williams et al. 1987; Lafitte and Loomis 1988).

Fig. 4.2. Carbon metabolism phase of higher plant respiration. All the redundant and some of the ATP formed during respiration are associated with the carbon metabolism phase. Glucose and fructose may arise from compounds other than sucrose and starch. Glycolysis and the oxidative pentose phosphate network occur in the cytosol, and at least in part in plastids, and are linked by the common metabolites G-6-P, F-6-P, and Gly-3-P. Pyruvate is probably the main carbon substrate of the TCA cycle, but malate can also serve as a substrate, for example, via the malate shunt. Much of glycolysis may be catalyzed by a multienzyme complex (Srere 1987) associated with the outer mitochondrial membrane. Similarly, the TCA cycle may be largely confined to a multienzyme complex associated with the matrix side of the inner mitochondrial membrane, perhaps at complex I sites. Under physiological conditions, pyruvate and malate cross the inner mitochondrial membrane via carriers. According to Douce (1985), a plant cell is likely to contain hundreds to thousands of mitochondria, and these can occupy about 7% of the cytoplasmic volume. Abbreviations: CoA coenzyme A; DiHOAcP dihydroxyacetone-P; 1,3-DiPGA 1,3-diphosphoglycerate; E-4-P erythrose 4-P; F-1,6-P; fructose 1,6-P₂; F-6-P fructose 6-P; GL-6-P glucono-δ-lactone 6-P; G-1-P glucose 1-P; G-6-P glucose 6-P; Gly-3-P glyceraldehyde 3-P; α-KG α-ketoglutarate; OAA oxaloacetate; PEP phosphoenolpyruvate; 6-PG 6-phosphogluconate; 2-PGA 2-phosphoglycerate; 3-PGA 3-phosphoglycerate; P₇ orthophosphate (inorganic); PP pyrophosphate (inorganic); R-5-P ribose 5-P; Ru-5-P ribulose 5-P; Su-7-P sedoheptulose 7-P; UDP-G UDP-glucose; Xu-5-P xylulose 5-P.
4.2 Pathways and Controls of Respiration

Respiration is composed of glycolysis, the oxidative pentose phosphate network, the TCA cycle, mitochondrial electron transport, oxidative phosphorylation, and related reactions. (Photorespiration is distinguished from respiration, although the two may interact in photosynthesizing cells.) In general, the pathways (Figs. 4.2 and 4.3) and control of respiration are similar among higher plants and other organisms, indicating the conservation of the
prevalent features of respiration during evolution (Chapman and Ragan 1980). The reactions and structures of respiration evolved under a wide range of environmental and biological conditions, often building upon metabolism and structures already in place. Glycolysis is "the most universal of metabolic pathways" (Prosser 1986) and developed early in the evolution of life. Parts of the TCA cycle (anaerobic, reductive, perhaps lacking α-ketoglutarate dehydrogenase) and the oxidative pentose phosphate network arose later. The photosynthetic carbon reduction cycle probably followed this, but due to the extensive oxidation of iron and other metals, it was some time before O$_2$ released by photosynthetic light reactions accumulated in the atmosphere (Cloud 1976). Under the aerobic conditions that eventually existed, α-ketoglutarate dehydrogenase may have appeared, perhaps from pyruvate dehydrogenase, and the TCA cycle was complete and functioning oxidatively (Gest 1987). Later, electron transport to O$_2$ and oxidative phosphorylation greatly increased the yield of usable energy from a unit of
substrate such as glucose. It is possible, even probable, that mitochondria (and chloroplasts) originated from free-living aerobic eubacteria that invaded a primitive eukaryote, leading to a permanent symbiotic relationship (Lehninger 1965; Margulis 1970; Douce 1985; Sitte and Eschbach 1992).

4.2.1 Unique Properties of Plant Respiration and Mitochondrial Metabolism

While respiratory biochemistry is similar among eukaryotes, higher plant respiration differs from that of many other organisms in notable ways (see, e.g., Ikuma 1972; Palmer 1979; ap Rees 1985; Douce and Neuburger 1989). For example: (A) in plants, sucrose is a major product of photosynthesis and a primary form of carbon translocated between organs, and it is often appropriate to take sucrose (rather than, say, glucose) as the starting point of respiration. (B) In addition to the nonreversible conversion of fructose 6-P to fructose 1,6-P₂ by phosphofructokinase, many plants contain PP₁-requiring fructose 6-P 1-phosphotransferase that catalyzes the same reaction, but reversibly and using PP₁ (forming P₃) rather than ATP (forming ADP). (C) Plant succinate-CoA ligase phosphorylates ADP rather than GDP (but see Weitzman 1987). (D) The rate of mitochondrial O₂ uptake per unit protein can be faster in plants than in animals. (E) Rotenone-resistant electron transport (bypass of complex I) is possible in many plants. (F) Rapid cyanide-resistant O₂ uptake is possible in plants. (G) Plant mitochondria can oxidize cytosolic NADH and NADPH (a separate dehydrogenase exists for

Fig. 4.3. Higher plant mitochondrial respiratory chain (drawn sizes and shapes are arbitrary). Complexes I, II, III, and IV are not known to differ greatly in plants and other organisms. Cytochrome c (Cyt c) is a peripheral protein linking complexes III and IV. The matrix-facing NADH dehydrogenase (NADH DH) other than complex I is insensitive to rotenone and is not known to exist in animals. That rotenone-resistant NADH dehydrogenase may actually be a second UQ binding site on complex I (within the membrane) that is not coupled to proton pumping (Soole et al. 1990, 1992). The alternative pathway refers to electron transport from ubiquinol (reduced ubiquinone) to O₂ via the alternative oxidase (Alt ox). Succinate and fumarate are intermediates of the TCA cycle. The NADH and NADPH dehydrogenases facing the intermembrane space are found in plants and fungi but not mammals although mammals can oxidize cytosolic reducing equivalents indirectly via metabolite shuttles. Compared to the dehydrogenases facing the intermembrane space, succinate (Complex II) may have preferential access to the alternative oxidase, perhaps due to some spatial "association," or more simply, a shorter diffusion-path length between the two (Day et al. 1991). Oxidative phosphorylation is presumably driven by the movement of protons from the intermembrane space to the mitochondrial matrix via F₁ · F₀ ATPases passing through the inner membrane (Nicholls and Ferguson 1992). The outer membrane pores are large enough to be freely permeable to ATP and NAD(P)H. The plant mitochondrial outer membrane is discussed by Mannella (1985) and the inner membrane by Douce (1985). Proposed "respiratory" electron transport in chloroplasts in the dark apparently does not pump protons (e.g., Singh et al. 1992) — a major function of mitochondrial electron transport — so it is not similar to this figure
each nucleotide). (H) Rapid transport of oxaloacetate (OAA) across the inner membrane of plant mitochondria can occur under physiological conditions. (I) NAD$^+$ can be actively accumulated from an external medium by plant mitochondria, apparently via a specific NAD$^+$ transporter. (J) Plant mitochondria readily oxidize malate in the presence of OAA and absence of pyruvate. (K) Plant mitochondria contain some unique cytochromes and the composition of common cytochromes can differ among plants and other organisms. (L) In leaf mitochondria, glycine decarboxylase may account for as much as half of the matrix protein and rapid glycine decarboxylation, a component of photorespiration, is possible. (M) Fatty acid oxidation is generally slow in plant mitochondria. (N) Plants contain the largest, most complex mitochondrial genome. Many of these “unique” properties confer a large degree of metabolic flexibility to plants.

4.2.2 Control of Respiration Rate

Respiration rate can be regulated by the amount of respiratory machinery (enzymes and transporters), the amount of respiratory substrate (carbohydrates and O$_2$), the rate of ATP and NAD(P)H use [ADP and NAD(P)$^+$ regeneration], or the rate of respiratory intermediate use. There has also been considerable interest in the control of respiration by calcium in plants (Wellburn and Owen 1991) and mammals (Brown 1992). In rapidly growing plant cells, the amounts of respiratory machinery or carbohydrate may limit respiration because the demands for respiratory products (carbon skeletons, ATP, and reductant) are high and those products are used as rapidly as they are produced. Moreover, the amount of respiratory machinery in very young cells may be small, being in a state of construction itself, and the supply of carbohydrate may be limited by incompletely developed phloem near growing cells. In mature or slowly growing plant cells, short-term (seconds to hours) control of respiration rate is probably brought about by the rate of use of respiratory products, and in particular ATP,$^2$ rather than a lack of metabolic machinery or carbohydrates (French and Beevers 1953; Beevers 1961, 1970; Copeland and Turner 1987; Dry et al. 1987; Farrar and

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$^2$Control of respiration rate by ADP availability (use of ATP) can exist with respect to glycolysis, the TCA cycle, and oxidative phosphorylation. Generally, the term respiratory control is used to refer to a feedback inhibition of respiratory chain (Fig. 4.3) activity due to a large proton motive force ($\Delta p$) arising when ADP levels are low and oxidative phosphorylation is slow. Respiratory control has been studied with the use of uncoupling agents, which not only disengage the link between respiratory chain activity and $\Delta p$ and therefore oxidative phosphorylation, but also limit pyruvate and P$_i$ uptake by mitochondria because that transport is driven by $\Delta p$ (see Figs. 4.2 and 4.3). This may underlie the observation that uncouplers stimulate glycolysis to a greater extent than they do the TCA cycle (Wiskich and Dry 1985) and indicates that the capacity of respiration is underestimated under the influence of uncouplers.
JHH Williams 1991). That is, in all but the youngest cells, respiration may be pulled along at a rate appropriate to the rate of growth, transport, nutrient uptake and assimilation, and maintenance processes, and this is generally below the rate limitation set by the amount of carbohydrates and respiratory enzymes. Because respiratory products are used by nearly all heterotrophic processes, and because the respiratory network is flexible and contains many branch points (see Figs. 4.2 and 4.3), "it seems inevitable that control will be found to be extremely complex and to be shared among a variety of reactions and a range of regulators" (ap Rees 1988).

Even when respiration is coupled to other processes via the use of its products, it does not follow that those other processes obligatorily use respiratory products with maximum efficiency. Although it is difficult to imagine extensive inefficiencies in higher plants following their long evolution, there is no compelling evidence that plant metabolism is optimal, nor need there be any, for "contrary to a widely held belief, the anatomical and physiological features of...extant life forms are not necessarily optimal solutions from the synchronic point of view, which takes into account only the present situation.... [But instead,] it appears that evolution used, not what was theoretically optimal, but whatever happened to be available to it and could be appropriated to serve a needed function" (Delbrück 1986) (see also Maynard Smith 1978). Moreover, "consumption of ATP by simple hydrolysis in which there is no outcome useful to the plant probably occurs in all cells at a finite rate and would yield a minimal background of idling respiration" (Beevers 1970). Also, in most plant communities, no more than a few percent of the energy in solar radiation absorbed by leaves is contained in the plant mass resulting from growth (Larcher 1983). Nevertheless, the efficiency of higher plant heterotrophic metabolism is, by many measures, impressive.

4.2.3 Energy Conservation During Plant Respiration

As many as 30 to 36 ADP can be phosphorylated per hexose oxidized completely during plant respiration (see Figs. 4.2 and 4.3; Nicholls and Ferguson 1992; Amthor 1993a). When ATP use is rapid but carbon skeleton use is slow, the mitochondrial ADP:O can be expected to be high (perhaps near 3) and the ratio of carbon diverted away from the respiratory network to that released as CO₂ will be small. That is to say, carbohydrate metabolism in respiration may yield mostly CO₂, heat, and ATP in mature cells rather than carbon skeletons. Under different circumstances, e.g., in rapidly growing tissue, NADH produced during carbon skeleton use in growth may exceed that required for ADP phosphorylation (for ATP use) via the respiratory chain and oxidative phosphorylation (Penning de Vries et al. 1974). In such a case, the circumvention of respiratory control by ADP availability may be required. The rotenone-resistant complex I bypass (item
Fig. 4.4. Proposed place of carbohydrates and respiratory products in regulating photosynthesis (net of photorespiratory decarboxylations), respiration, and growth. In the short term, carbohydrate accumulation in leaves can lead to feedback inhibition of photosynthesis. In the long term, sugars may limit photosynthetic capacity via the repression of photosynthetic genes. Conversely, carbohydrates may elicit an increase in both respiratory capacity and the rate of growth and related heterotrophic metabolism. The products of respiration must be used in order for respiration to continue so that, e.g., growth, can pull respiration along at a rate appropriate to the need for respiratory products. The control of respiration is unlikely to be “absolute” in vivo and some “unneeded” respiration is likely to occur. Notably, stress may uncouple photosynthesis, respiration, growth, and carbohydrate level (see Amthor 1993b).

E above; see Fig. 4.3) and cyanide-resistant bypass of complexes III and IV (item F above; see Fig. 4.3) facilitate such a bypass of respiratory control (Bryce et al. 1990). The complex I bypass is engaged when matrix NADH levels are high (Soole et al. 1990). The cyanide-resistant, alternative pathway is common among higher plants, but is also found in some animals, fungi, bacteria, and algae (Henry and Nyns 1975). It is engaged when the ubiquinone (UQ) pool is highly reduced (Dry et al. 1989). Also, as Δp increases, the conductance of the inner membrane to passive proton transport or “leaks” increases. Thus, a large Δp aids the oxidation of NAD(P)H under ADP limited conditions via passive dissipation of the proton gradient due to a large driving force (Δp) and a large conductance. Moreover, the NADP⁺- linked 3-phosphoglycereraldehyde dehydrogenase reaction in glycolysis (Kelly and Gibbs 1973; Duff et al. 1989) bypasses ADP phosphorylation. When “excess” ATP is formed, futile cycling or an adenylate kinase system coupled to fatty acid processing (Fricaud et al. 1992) can regenerate ADP.

On the whole, it remains worthwhile to consider respiration as being coupled to the rate of use of its products even though there are opportunities for uncoupling and these may well come into play during the normal course
of metabolism. In support of this generalization, it is commonly observed that the rate of plant respiration displays a stoichiometric relationship with the rates of, e.g., growth, translocation, nutrient uptake, and nitrogen assimilation (Farrar 1985; Amthor 1993b).

4.2.4 Respiration Rate and Carbohydrate Level

A strong positive correlation often exists between plant or tissue carbohydrate content and respiration rate, suggesting that carbohydrate level and respiration rate are related (Williams and Farrar 1990; Farrar and JHH Williams 1991; Amthor 1993b). Respiration can be under short-term (minutes to hours) control by ADP availability, however, even though it is correlated with carbohydrate level over the longer term (Journet et al. 1986; Brouquisse et al. 1991; Douce et al. 1991). Notably, the addition of sugars to a tissue increases respiration in the short term when that tissue has been starved or excised from a supply of endogenous sugars, but not usually otherwise (ap Rees 1988; Rebeille 1988; Williams and Farrar 1990). Moreover, the relationship between carbohydrate level and respiration rate is often strongest in growing tissues, and may be absent in mature organs, i.e., growth respiration appears to be controlled by carbohydrate level but maintenance respiration does not (Amthor 1989).

It has been inferred that carbohydrates induce processes consuming respiratory products so that over the long term (hours to days) respiration is positively related to carbohydrate level, but through respiratory control mechanisms (Bingham and Farrar 1988; Farrar and JHH Williams 1991; Farrar and ML Williams 1991). For example, an increase in (specific) sugars may stimulate root nitrate uptake and assimilation (Hänisch ten Cate and Breteler 1981; Aslam and Huffaker 1984) and perhaps enhance cell division and differentiation (Williams and Farrar 1990; Farrar and JHH Williams 1991). Each of these increase the demand for carbon skeletons and energy. Protein levels may be regulated by carbohydrate concentration (Baysdorfer and van der Woude 1988; Wenzler et al. 1989) with a decrease in cellular carbohydrate level leading to a loss of respiratory machinery (Journet et al. 1986) and an increase in sugars resulting in increased respiratory capacity (Avelange et al. 1990; Farrar and JHH Williams 1991). Conversely, sugars can lead to short-term inhibition of photosynthesis (Foyer 1988) and repress photosynthetic genes (Sheen 1990; see also Krapp et al. 1991; Schäfer et al. 1992). The motif is that carbohydrates – even specific sugars – can act as “messages” as well as substrates of growth and respiration (Williams and Farrar 1990). The messages, which are products of photosynthesis and common forms of carbon translocated from sources to sinks, would coordinate carbon and energy fluxes through photosynthesis and on to growth and respiration (Fig. 4.4).
4.3 Respiration in Photosynthesizing Leaves

Respiration, photosynthesis, and photorespiration occur simultaneously in photosynthesizing cells. The most immediate spatial and temporal interactions between respiration and photosynthesis therefore occur in photosynthesizing cells where respiration and photorespiration are concurrently releasing CO$_2$ in mitochondria; chloroplast metabolism as well as respiration can be contributing ATP and reductant to the cytosol; and carbon skeletons are produced in respiration, photosynthesis, and photorespiration.

In leaves subject to moderate to high light and normal temperature and CO$_2$ concentration, photosynthetic CO$_2$ assimilation may proceed 10 to 20 times faster than CO$_2$ release in respiration in the dark at the same temperature. Nonetheless, the extent of respiration in leaves during the day has been of considerable interest from the earliest studies of plant respiration and photosynthesis, and opinions concerning the effects of light or photosynthesis on respiration have varied extensively, even up to the present. Because a principal function of respiration is to supply reductant and usable energy for active processes, often via the cytosol, and because photosynthesis can supply the cytosol with both reductant and ATP (Fig. 4.5), some respiration might be superfluous in the light. Thus, the needs for respiration can differ in light and dark, and respiration may slow in the light compared

![Diagram of photosynthetic carbon reduction cycle](image)

**Fig. 4.5.** Transport of photosynthetically generated ATP and reductant from a chloroplast to the cytosol via the DiHOAcP/3-PGA shuttle. The ATP and NADPH in the chloroplast are formed from ADP and NADP$^+$ during the light reactions of photosynthesis. Not all the intermediates of the photosynthetic carbon reduction cycle are shown. The cytosolic conversions of 3-PGald to 3-PGA are also (alternative) components of glycolysis, and are the “site” of a direct interaction between photosynthesis and respiration in the light. The NADP$^+$-linked 3-PGald dehydrogenase reaction, which can be induced by low P$_i$ (Duff et al. 1989), might affect activity of the oxidative pentose phosphate network via the NADP$^+$/NADPH (Copeland and Turner 1987). Abbreviations: DiHOAcP dihydroxyacetone-P; 3-PGA 3-phosphoglycerate; 1,3-bisPGA 1,3-bisphosphoglycerate; 3-PGald 3-phosphoglyceraldehyde; RuP$_2$ ribulose 1,5-bisphosphate
to the rate in the dark at the same temperature, although total mitochondrial CO₂ release could increase due to photorespiration. Although enzymes of glycolysis and the oxidative pentose phosphate network exist in chloroplasts (ap Rees 1985), it is reasonable to assume that those pathways are inhibited or reversed during photosynthesis.

A high cytosolic ATP:ADP can inhibit oxidative phosphorylation (Dry and Wiskich 1982), and although the ratio may increase in the light under physiological conditions (Gardeström and Wigge 1988), it may not be high enough to be inhibitory. The availability of free (unbound) ADP to respiratory reactions in the light and dark has not, apparently, been well characterized and is probably important, and dynamic, in vivo. Photosynthesis may produce mostly NADPH in the cytosol, compared to ATP and NADH; Krömer and Heldt (1991b) cite evidence that NADPH may exceed NADH by 250 times in the cytosol of photosynthesizing *Spinacia oleracea* cells. This suggests an inhibition of the cytosolic oxidative pentose phosphate network, but not necessarily glycolysis or the TCA cycle unless the NADPH is oxidized by the respiratory chain (see Fig. 4.3).

Because CO₂ is assimilated in photosynthesis while being released in respiration, and O₂ is generated by photosynthesis while being consumed in respiration, simple gas exchange techniques cannot be used to estimate rates of respiration in leaves in the light. The use of labeled CO₂ or O₂ will not fully overcome this difficulty for several reasons. The photosynthetic assimilation of respired CO₂ – mitochondria and chloroplasts are generally in close association in leaves – is of particular importance. A similar situation has existed for the direct measurement of photorespiration, resulting in a range of “unreliable” estimates of its rate (Sharkey 1988). Fortunately for the study of photorespiration, the kinetics of a single enzyme (Rubisco) determines the ratio of RuP₂ carboxylation to RuP₂ oxygenation, and it is possible to calculate the ratio of photosynthesis to photorespiration if chloroplast CO₂ concentration is known (Sharkey 1988). Diversion of photorespiratory glycine to processes other than serine synthesis, which results in photorespiratory decarboxylation (Fig. 4.6), will alter the ratio of photosynthetic carboxylation to photorespiratory decarboxylation for a given chloroplast CO₂ concentration, but nonetheless, accurate estimates of the concurrent CO₂ fluxes associated with photosynthesis and photorespiration are possible because of the central role of Rubisco in those processes. When the chloroplast CO₂ concentration is equal to the CO₂ compensation point in the absence of respiration (Γₚ; Farquhar et al. 1980), respiration rate in photosynthesizing leaves can be estimated from gas exchange rate (see, e.g., Kirschbaum and Farquhar 1987). The value of Γₚ is a function of the CO₂/O₂ specificity of Rubisco (see Laing et al. 1974; Farquhar et al. 1980; Jordan and Ogren 1984). If respiration rate is affected by CO₂ concentration (e.g., Amthor et al. 1992), effects of CO₂ on respiration must be accounted for to estimate respiration rate at CO₂ levels different from Γₚ.
The Kok effect, an apparent abrupt decrease in the quantum yield of photosynthesis as radiation increases in the vicinity of the light compensation point (Kok 1948), is evidence of an inhibition of respiration by light. In careful experiments, Sharp et al. (1984) and Kirschbaum and Farquhar (1987) observed Kok effects, whereas Björkman and Demming (1987) did not. Björkman and Demming (1987), however, used high CO₂ concentrations which may have inhibited respiration (Amthor et al. 1992) and overridden effects of light on respiration. Based on measurements of leaf CO₂ exchange and a mechanistic model of RuP₂ carboxylation/oxygenation, Brooks and Farquhar (1985) concluded that respiration was slowed by light to a considerable degree. The bulk of the effect of light on respiration occurred as light increased from darkness to 10 to 50 μmol photons m⁻² s⁻¹.

After reviewing the literature, Graham (1980) concluded that cytosolic glycolysis can, apparently, operate in the light, and that “the provision of essential carbon skeletons required in synthetic reactions is the raison d’être for the continued operation of ‘dark’ respiration in the light”. Graham and Chapman (1979) stated that in the light the TCA cycle “can operate at a rate comparable with that in the dark,” and that owing to its function as a source of carbon skeletons for growth, the TCA cycle might be little affected.
by light in growing tissue, but perhaps slowed by light in mature tissue. McCashin et al. (1988) presented evidence that TCA cycle activity was slowed only 20% (but see Gemel and Randall 1992) by light in growing *Triticum aestivum* leaves, but they used nonphysiological, i.e., nonphotorespiratory, conditions. Evidence that the TCA cycle (but not necessarily mitochondrial electron transport and oxidative phosphorylation) is slowed in the light comes from the partial inactivation of mitochondrial pyruvate dehydrogenase complex (mtPDC) by light. The light inactivation is apparently transduced through some product of photosynthesis or photorespiration resulting in the phosphorylation of the mtPDC (Gemel and Randall 1992).

Graham (1980) surmised that “inhibition of oxidative phosphorylation in the light seems probable.” Conversely, the results of Krömer et al. (1988) and Krömer and Heidt (1991a) indicate that oxidative phosphorylation is actually required for rapid photosynthesis (measured as O₂ evolution). They suggested that mitochondria contribute needed ATP to the cytosol in photosynthesizing cells and can oxidize excess photosynthetic redox equivalents (see also Ebbighausen et al. 1985). Oxidative phosphorylation may be most important to photosynthesis in leaves not capable of rapidly producing starch – respiratory ATP is apparently required to support rapid cytosolic sucrose-P synthesis (Hanson 1992) and the consequent release of P₁ for further use in photosynthetic carbon metabolism (Sharkey 1985), whereas rapid starch synthesis (and P₁ release) can occur without concurrent respiration. Active mitochondrial electron transport might limit photoinhibition of photosynthesis through the lessening of over-reduction of the photosynthetic apparatus (Saradadevi and Raghavendra 1992). Also, respiratory chain activity (which will be slowed if oxidative phosphorylation is inhibited as in the experiments of Krömer and his colleagues) may be needed for continued operation of photorespiration via the turnover of mitochondrial NADH required by glycine decarboxylase.

Clearly, photosynthetic metabolism can alter the demands for respiratory products. Indeed, mutual interactions between photosynthesis and respiration in the light are likely. Quantitative effects of light on respiration remain largely unknown, however. A diversity of estimates of effects of photosynthesis on respiration are not necessarily contradictions, for they might result from differing needs for respiration in the light in different studies; photosynthesis will not inhibit respiration by some constant fraction irrespective of environmental, physiological, and ontogenetic factors. Regarding the significance of effects of photosynthesis on respiration, it was suggested (Amthor 1989) that respiration by mature leaves is not overly important to the whole-plant carbon balance, especially in crops during seed growth (see, e.g., Gaastra 1963). In forests, however, where net primary production may be a smaller fraction of gross primary production (Kira 1975), leaf respiration may account for a majority of whole-plant respiration (Allen and Lemon 1976; Hagihara and Hozumi 1991), and effects of light on respiration are more important to productivity. To the extent that photo-
synthetic reductant and ATP are generated in excess of that used in CO₂ assimilation, and that they serve to "replace" the need for some respiratory metabolism, the resulting reduction in respiration is a benefit to the carbon and energy balance of a plant. But, a reduction in respiration without replacement sources of ATP, reductant, and carbon skeletons is likely to be a detriment to the plant as growth and maintenance processes will be deprived of substrates.

4.4 Photorespiration and Mitochondrial Metabolism

Mitochondrial glycine decarboxylation and the linked NAD⁺ reduction is central to photorespiratory carbon metabolism (Tolbert 1980) with CO₂ release by photorespiration probably exceeding that of respiration under moderate to high light and ambient CO₂. Reduction of mitochondrial NAD⁺ (forming NADH + H⁺) by glycine decarboxylase could deprive NAD-linked TCA cycle dehydrogenases of that cosubstrate and limit TCA cycle activity. Moreover, a supply (regeneration) of NAD⁺ is required for photorespiration as well as TCA cycle activity. If carbon flux through the photorespiratory cycle does not match and rate of RuP₂ oxygenation, which is a function of chloroplast CO₂ and O₂ partial pressures and the temperature-dependent substrate specificity of Rubisco (Jordan and Ogren 1984), photosynthesis is slowed (Dry et al. 1987). The fate of mitochondrial NADH during daytime is therefore important to rates of respiration, photorespiration, and photosynthesis.

4.4.1 Oxidation of Photorespiratory NADH by the Respiratory Chain

Matrix NADH formed by glycine decarboxylase (Fig. 4.6) can be oxidized by the mitochondrial respiratory chain and coupled to as many as three sites of proton translation (Douce 1985; Fig. 4.3), but that oxidation might compete with TCA cycle-generated NADH and succinate for access to the UQ pool. Photorespiratory NAD⁺ reduction might elicit rotenone-resistant complex I bypass activity because of high matrix NADH levels and also enhance alternative pathway engagement due to increased reduction of the UQ pool. Dry et al. (1987), however, consider the latter to be relatively unimportant to normal daytime activity of the respiratory chain.

Glycine may have preferential access to some mitochondrial NAD⁺, or the resulting NADH may have preferential access to the respiratory chain, compared to NAD⁺-linked TCA cycle enzymes and the NADH formed by them. Glycine decarboxylation will not saturate the respiratory chain however, for when a second substrate such as malate is added to mitochondria supplied with glycine, O₂ uptake can increase markedly (Dry et al. 1987;
Wiskich et al. 1990). Thus, the TCA cycle can continue to operate during glycine decarboxylation, although perhaps at a reduced rate.

Cytosolic ATP:ADP declines if photorespiration is slowed, indicating that photorespiration contributes to ATP production (Gardeström 1987; Gardeström and Wigge 1988). This implicates the mitochondrial respiratory chain as one mechanism of photorespiratory NADH oxidation. Photorespiratory NADH production may exceed the capacity of the respiratory chain to oxidize it, however, in which case other means of oxidizing NADH, such as substrate shuttles, are also required (Dry et al. 1987).

4.4.2 Oxidation of Photorespiratory NADH via Substrate Shuttles

If carbon is conserved in photorespiration – i.e., 3/4 of it – so that glycerate is formed from hydroxypruvate in peroxisomes and then transported to chloroplasts, an amount of NADH equal to the amount formed in mitochondria by glycine decarboxylase is required in peroxisomes. Carbon conservation need not, however, be complete (Grodzinski 1992) as serine and related compounds may be exported from leaves and this can increase with low CO₂ (high photorespiration). Nonetheless, NADH is required in peroxisomes when glycerate is being formed and it might then be beneficial to transfer redox equivalents from mitochondria to peroxisomes. The oxidation of NADH by malate dehydrogenase (MDH; OAA → malate) coupled to a malate/OAA shuttle is one mechanism for this transfer (Fig. 4.6). Dry et al. (1987) concluded that such a shuttle is “likely to operate in vivo as an adjunct to the NADH reoxidation capacity of the mitochondrial respiratory chain.” NADH oxidation by MDH requires a supply of OAA whereas OAA is also required for activity of the TCA cycle and is formed in the TCA cycle from malate. Plant mitochondria can import OAA via a translocator with a high affinity for cytosolic OAA (Ebbighausen et al. 1985) and are able to export malate (Douce 1985).

Oxidation of NADH by MDH and activity of a malate/OAA shuttle might seem impossible if the TCA cycle is engaged because MDH would be catalyzing OAA → malate and malate → OAA reactions simultaneously. One population of mitochondria supporting photorespiration and another the TCA cycle would allow this, but experimental data do not support this notion (Wiskich et al. 1990). Another possibility, and one supported by experimental evidence (Dry and Wiskich 1985; Wiskich et al. 1990), is that within individual mitochondria, glycine decarboxylase and malate and OAA transporters are spatially separated from TCA cycle enzymes. This separation might be facilitated by enzyme or enzyme complex “attachment” to specific locations on the matrix side of the inner mitochondrial membrane.

To the extent that photorespiratory NADH is oxidized by the respiratory chain and glycerate is formed from glycolate, NADH required in peroxisomes must come from nonmitochondrial sources. These sources can include the
chloroplast dihydroxyacetone-P/3-phosphoglycerate shuttle (Fig. 4.5), glycolysis, or a chloroplast malate/OAA shuttle. An α-ketoglutarate/glutamate–malate/aspartate shuttle between mitochondria and peroxisomes is apparently not important in leaves (Krömer and Heldt 1991b).

4.5 Daytime Photosynthesis and Nighttime Respiration

Respiration in a mature leaf at night can be positively related to the previous daytime net photosynthesis of that leaf (Ludwig et al. 1975; Azcón-Bieto and Osmond 1983). Similarly, fruit (Satterlee and Koller 1984) or shoot and whole-plant (Amthor 1933b) nighttime respiration may be positively related to the amount of photosynthesis during the previous daytime. High sugar levels resulting from rapid photosynthesis may increase energy use for compartmentation. Short-term storage of sucrose occurs in vacuoles (ap Rees 1988), and although Kaiser and Heber (1984) reported that sucrose transport across the tonoplast in *Hordeum vulgare* mesophyll protoplasts was not energy-dependent, Getz (1991) observed ATP-dependent sucrose transport into tonoplast vesicles from *Beta vulgaris* root tissue. High sugar levels might also accelerate futile cycling between triose-Ps and hexose-Ps (by mass action or allosteric mechanisms) which is thought to enhance the sensitivity of metabolism to demands for sugars and carbon skeletons (Dancer et al. 1990; Hatzfeld and Stitt 1990; Hatzfeld et al. 1990). Fast respiration after rapid photosynthesis is probably in part related to metabolic costs of translocation (phloem loading, unloading, and related processes; Amthor 1993a) and is conceivably linked to maintenance of enzymes and membranes used during the day for carbon and nitrogen assimilation and processing. In the long term, ample carbohydrates resulting from rapid photosynthesis might induce growth in immature organs as outlined above (see Fig. 4.4), leading to increased respiration to support processes such as biosynthesis and nitrogen assimilation.

According to Azcón-Bieto et al. (1983), respiration rate and engagement of the alternative pathway (Fig. 4.3) are enhanced when sugar levels are high. The implication is that the alternative pathway allows rapid respiration (bypassing respiratory control by ADP) and functions to oxidize “excess” sugars (e.g., Steingröver 1981). Ap Rees (1988), however, has argued that insufficient evidence exists to show that the alternative pathway aids in the disposition of excess carbohydrates. Moreover, if sugars stimulate rapid growth, “overproduction” of NAD(P)H may result (Penning de Vries et al. 1974). Engagement of the alternative pathway, and the rotenone-resistant bypass of complex I, would then facilitate the regeneration of NAD(P)+ in the face of ADP limitations and expedite biosynthetic processes rather than waste carbohydrates.
Work to date relating respiration to previous photosynthesis has been with herbs and with seedlings and small individuals of woody plants, whereas the bulk of global higher plant photosynthesis and respiration occurs in large trees. Temporal relationships between whole-tree photosynthesis and respiration may be loose because of the greater average distance of transport from sources to sinks and slower turnover time of some carbohydrate storage pools. Knowledge of those relationships, however, is scant. Also, differences between on/off and sinusoidal (natural) light treatments have not been well studied with respect to the links between photosynthesis and respiration occurring over a few hours, with most quantitative research employing on/off light treatments. Temporal patterns of leaf metabolite levels differ with sinusoidal and on/off light regimes (Fondy et al. 1989; Servaites et al. 1989a,b) and respiration could respond to those differences.

4.5.1 Light Level

One consequence of long-term high light is fast leaf respiration (Björkman 1981). This is independent of photosynthetic capacity (Sims and Pearcy 1991) and may reflect a response to daytime net photosynthesis. Actual CO₂ assimilation (use of machinery) rather than capacity for assimilation (amount of machinery) could be the link to maintenance processes and therefore leaf maintenance respiration. Respiratory acclimation to a change in prevailing light can occur within a few days and disrupts the relationship between mature leaf respiration rate and nitrogen content (Sims and Pearcy 1991), showing that a leaf maintenance coefficient based on nitrogen or protein level \( m_\text{(N)} \); see Appendix) is a function of prevailing light as well. Also, the true growth yield \( Y_{G(C)} \); see Appendix) of leaves can be inversely related to light level during growth (Williams et al. 1989).

In addition to the relationship between daytime light levels and subsequent respiration caused by different photosynthesis rates, Heichel (1970) found that leaf respiration of the C₄ species Zea mays was positively related to previous light level independent of net CO₂ assimilation. Measurements were made in CO₂-free air so CO₂ was assimilated only at the rate at which it was released in respiration and other decarboxylation processes. Heichel (1970) concluded that "light . . . was required to produce a substrate which was subsequently used in . . . respiration," but it is also plausible that non-CO₂-assimilating light-driven reactions related to, e.g., nitrogen metabolism, were supported in part by respiration and that such metabolism (including related maintenance processes) continued into the dark period. Notably, blue light can stimulate respiration by unknown mechanisms in the absence of photosynthesis and this can persist into a following dark period (Kowallik 1982). Both past and present light levels affect respiration rate.
4.5.2 CO₂ Concentration

Ludwig et al. (1975) observed that the relationship between *Lycopersicon esculentum* leaf nighttime respiration and previous daytime net photosynthesis was stronger when photosynthesis was varied by changing light level (CO₂ held constant) compared to changing CO₂ level (light held constant) with on/off light treatments. In other instances too, elevated daytime CO₂ level leads to a decline in the ratio of nighttime respiration to daytime photosynthesis (e.g., Gifford et al. 1985; Du Cloux et al. 1987; Dutton et al. 1988; Gaudillère and Mousseau 1989), but the ratio may eventually return to that of plants under ambient CO₂ (Grodzinski 1992; Morin et al. 1992). Charles-Edwards and Ludwig (1975) attributed this to high levels of “glycolate pathway products” (versus starch) with low CO₂ and that the glycolate pathway intermediates, e.g., glycine, were important substrates for CO₂ releasing reactions during the night. Photorespiratory intermediates do appear to contribute to CO₂ efflux for the first ca. 20–30 min of a dark period following a period of constant light in *Triticum aestivum* leaves (Azcón-Bieto and Osmond 1983), but the differential response of respiration to previous photosynthesis across CO₂ levels is more far-reaching.

It is not surprising that growth and respiration can respond markedly to a change in light. Diurnal and seasonal cycles of light include large amplitudes, and spatial variation in light levels within plant communities is often high. Plants are adapted to such spatial and temporal variations in light, and several photoreceptors are known to exist. Conversely, natural temporal and spatial variations in CO₂ are small. Indeed, no CO₂ sensor is known to exist in higher plants, although carbamate formation on Rubisco might serve such a function (see Lorimer 1983).

Elevated CO₂ increases the ratio of starch to sucrose, with sucrose production being linked to growth and other processes using respiratory products, but with starch accumulating in a less coordinated way (Morin et al. 1992). (Wullschleger et al. 1992a) observed decreased leaf sucrose in spite of enhanced photosynthesis due to elevated CO₂ in two field-grown tree species.) Some of the increase in carbon accumulation and decline in the ratio of nighttime respiration to daytime net photosynthesis (increase in growth efficiency, \( Y_C \); see Appendix) with elevated CO₂ is due to increased short-term storage pool size (Rowland-Bamford et al. 1990) rather than only increased efficiency of growth or respiration. A corollary is that 24-h net CO₂ exchange is not a reliable measure of growth because the size of the short-term storage pools can vary considerably from day to day depending on environmental and developmental circumstances (Moldau and Karolin 1977; McCree 1986).

Long-term elevated daytime CO₂ often results in a decrease in specific (dry mass basis) respiration rate even though photosynthesis increases (Amthor 1991; Drake and Leadley 1991). On a nitrogen or protein basis, however, effects of CO₂ history on respiration are less striking or non-
existent (Amthor 1991; Baker et al. 1992; Wullschleger et al. 1992b). Photorespiration is inversely related to CO₂, so mitochondrial NADH oxidation during the day may also be inversely related to CO₂. Decreased daytime demand for NADH oxidation with elevated CO₂ might lead to decreased mitochondrial oxidative capacity (diminution of respiratory chain components), resulting in the observed decrease in nighttime respiration rate. But, if a decrease in mitochondrial oxidative capacity due to slowed mitochondrial photorespiratory NADH oxidation does lead to a decrease in oxidative activity, respiration is not normally under tight control by product use, unless the decreased capacity is also related to a decline in, say, ATP use for respiratory chain maintenance.

In addition to negative effects of long-term daytime elevated CO₂ on specific respiration rate, nighttime shoot and leaf CO₂ efflux is negatively and instantaneously related to nighttime CO₂ level (Decker and Wien 1958; Gale 1982; Bunce 1990; Amthor et al. 1992; but see Ryle et al. 1992). The apparent inhibition of respiration by CO₂ in the dark is readily reversible (Amthor et al. 1992). Elevated nighttime CO₂ can slow mobilization of leaf starch and this, too, may be related to slowed respiration (Wullschleger et al. 1992a). Both past and present CO₂ levels affect respiration rate.

4.6 Photosynthesis and Root Respiration

Root respiration supports growth and maintenance in roots and active uptake of nutrients from the soil solution. It also supports nutrient assimilation, although a considerable fraction of nitrate assimilation may occur in shoots (Pate and Layzell 1990). Roots are frequently chosen for respiratory studies to avoid concurrent photosynthesis and photorespiration, but root respiration is difficult to study in soil because access to roots is limited and soil microbes also respire. (Soil microbes oxidize primarily dead roots, shoot litter, and root exudates so that soil respiration is linked to long-term previous photosynthesis and plant growth.) Thus, root respiration and carbon budgets are often studied in nutrient solution culture (e.g., Farrar and JHH Williams 1991) whereas little is known of in situ root respiration (but see, e.g., Mogensen 1977; Holthausen and Caldwell 1980; Wagner and Buayanovsky 1989). In solution culture, a significant portion of nutrient uptake may function to replace nutrients lost during efflux from roots whereas in soil this component of uptake may be small (Macduff and Jackson 1992). Theoretical estimates of minimal respiratory requirements for ion uptake, maintenance, and growth have been outlined frequently (e.g., Amthor 1993a).

The linkages between root and shoot growth and metabolism (Brouwer 1983) and stoichiometry between whole-plant photosynthesis and growth (Farrar 1985) dictate a linkage between photosynthesis and root respiration
to support nutrient acquisition for the whole plant and growth and maintenance of the root. In herbs, a change in photosynthesis caused by higher or lower light results in a respective increased or decrease in root respiration within a few hours (Hansen 1977; Massimino et al. 1981). Carbohydrate reserves allow some temporal delays in the linkage. At constant temperature, root respiration may be most rapid during the day (Huck et al. 1962). The relationship between photosynthesis and root respiration is paralleled by changes in nutrient uptake (Huck et al. 1962; Massimino et al. 1981; Gastal and Saugier 1989) and perhaps nitrate reduction (Hansen 1980) and root growth. Daily root respiration may be linearly related to translocation of sugar to roots (Hatrick and Bowling 1973), which is likely to depend to daytime photosynthesis. Respiration rate of nodulated *Trifolium repens* roots is sensitive to changes in shoot photosynthesis in as short a time as 10 min, which may reflect the time taken to translocate photosynthate from leaves to roots and indicates that "current photosynthate [rather than reserve carbohydrate] is the primary source of energy for N₂ fixation" in such plants (Ryle et al. 1985). On the whole, herb root and nodule respiration responds positively to shoot photosynthesis; this is not surprising. In keeping with the previous theme, translocation of sugars to roots will tend to stimulate processes using sugars and respiratory products, and root activity itself is likely to facilitate import of photosynthate. In nature, respiration in individual roots or groups of roots is likely to vary from the average rate of the whole root system due to local differences in soil conditions and root activity and ontogeny (Holthausen and Caldwell 1980).

### 4.7 Conclusions

Photosynthesis, photorespiration, and respiration most likely interact in photosynthetic cells during the day because the three processes share intermediates. Both photorespiration and respiration release CO₂ in mitochondria and probably compete for access to the respiratory chain. Photosynthesis and respiration can each supply ATP, reductant, and carbon skeletons to the cytosol. Moreover, products of the individual processes are substrates and cofactors of the other processes, e.g., CO₂ released by respiration and photorespiration is a photosynthetic substrate and sugars produced by photosynthesis are respiratory substrates. Respiration and photosynthesis can interact via source-sink relationships, too; an increase in sink activity can stimulate photosynthesis whereas a decline in sink activity may slow photosynthesis (Herald 1980) with respiration often coupled to sink activity. Respiration and photosynthesis are also related because respiration contributes to the construction of photosynthetic machinery.

There is a more or less fixed ratio of daily whole-plant carbon gain in photosynthesis (less photorespiration), carbon use in growth, and carbon
loss in respiration within a species or genotype (Farrar 1985; Farrar and JHH Williams 1991) although the precise chain of events underlying that relationship is incompletely understood. Indeed, the rate of whole-plant respiration depends in large part on previous photosynthesis and the partitioning of photosynthate to growth or storage. Thus, the physical environment is expected to influence respiration in part by controlling photosynthesis and carbon partitioning—conditions favorable for photosynthesis tend to enhance respiration. The environment can also influence respiration independent of an effect on photosynthesis (Amthor 1993b). Many environmental stresses inhibit growth to a greater extent than they reduce photosynthesis, resulting in an accumulation of nonstructural carbohydrates (Munns 1988). The reduction in growth lessens the demand for growth and maintenance respiration and the ratio between respiration and photosynthesis becomes smaller. This gives rise to an apparent increase in the efficiency of photoassimilate use \((Y_{(C)}\text{, see Appendix; McCree 1986})\). In healthy plants, the balance between capacities for carbohydrate production in photosynthesis and use in heterotrophic metabolism may be coordinated by induction and repression triggered by carbohydrate status (Fig. 4.4). In sum, photosynthesis, respiration, and growth interact across wide temporal and spatial scales. The success of a plant is dependent on a coordination of those processes across those scales. The significance of photosynthesis to plant success can scarcely be appreciated without a consideration of those interactions.

Appendix

It is traditional for plant ecophysiologists to consider respiration as composed of two or more functional components. The separation of components is based on different processes supported by respiratory products rather than different respiratory pathways. The basic relationships underlying the simple and common two-component view (e.g., WohI and James 1942; Pirt 1965; Thornley 1970, 1971) begin with the tenet that the rate of use of substrate carbon is the sum of carbon use rate for growth \((\dot{C}_G, \text{mol C s}^{-1})\) and for maintenance \((\dot{C}_M, \text{mol C s}^{-1})\)

\[
\dot{C} = \dot{C}_G + \dot{C}_M,
\]

where \(\dot{C}\) is the rate of substrate carbon use (mol C s\(^{-1}\)) and is derived from, e.g., "carbohydrates" of Fig. 4.1. All the carbon used for maintenance is respired and released as CO\(_2\). Part of the substrate used for growth, however, is added to plant structure and long-term storage so \(\dot{C}_G\) is itself the sum of two components

\[
\dot{C}_G = \dot{C}_T + \dot{C}_R,
\]

where \(\dot{C}_T\) (mol C s\(^{-1}\)) is the rate of growth (i.e., addition of carbon to structure and long-term storage) and \(\dot{C}_R\) is the rate of respiration (mol
Cs⁻¹) required to support that rate of growth. From a two-component viewpoint, growth includes translocation and nutrient uptake and assimilation in addition to cellular biosynthesis per se.

Respiration rate (R, mol CO₂ s⁻¹) is then given by

\[ R = \dot{C}_M + \dot{C}_R, \]

where \( \dot{C}_M \) is called maintenance respiration rate and \( \dot{C}_R \) is called growth respiration rate. Specific respiration rate (\( r, \) mol CO₂ g⁻¹ s⁻¹) is equal to \( R/W \), where W is plant dry mass (g).

The specific maintenance respiration rate or maintenance coefficient \( (m, \) mol CO₂ g⁻¹ s⁻¹) is equal to \( \dot{C}_M/W \), but maintenance respiration rate may be better related to plant protein content than to dry mass (Ryan 1991; but see Byrd et al. 1992 concerning leaves) in which case a protein-based maintenance coefficient \( (m_{(N)} \), mol CO₂ g⁻¹ protein s⁻¹) can be defined by

\[ m_{(N)} = \dot{C}_M/N, \]

where \( N \) is the protein content (g) of existing phytomass. The maintenance coefficient can be estimated experimentally or theoretically, but all available methods are problematic (Amthor 1989). In any case, given a value for \( m_{(N)} \), maintenance respiration rate is equal to \( m_{(N)} N \). Because maintenance processes occur continuously in all living cells, \( R \) will always be greater than zero. The above relationships can be extended by dividing metabolism into a greater number of classes of process (Amthor 1993a).

The apparent growth yield is the amount of new plant structure and long-term storage formed per unit of substrate consumed. It is also called the growth efficiency (Tanaka and Yamaguchi 1968; Yamaguchi 1978; Amthor 1989). The apparent growth yield in terms of carbon (\( Y_{(C)} \), mol C added to new structure and long-term storage per mol C in substrate used for growth and respiration, or mol C mol⁻¹ C) is

\[ Y_{(C)} = \dot{C}_T/\dot{C} = \dot{C}_T/(R + \dot{C}_T). \]

The apparent growth yield with respect to energy (\( Y_{(E)} \), J J⁻¹) is given by

\[ Y_{(E)} = \dot{E}_T/\dot{E}, \]

where \( \dot{E}_T \) (J s⁻¹) is \( \dot{C}_T \) times the energy content (J mol⁻¹ C) of the products of growth and \( \dot{E} \) (J s⁻¹) is \( \dot{C} \) times the energy content (J mol⁻¹ C) of the substrates of growth and respiration, e.g., carbohydrates.

The yield of the growth processes per se, or true growth yield (Pirt 1965), in terms of carbon (\( Y_{G(C)} \), mol C added to new structure and long-term storage per mol C used in growth processes, or mol C mol⁻¹ C) is

\[ Y_{G(C)} = \dot{C}_T/\dot{C}_G, \]

which is related to the production value (PV) of Penning de Vries et al. (1974). Again, a comparable relationship defines the true growth yield in terms of energy (\( Y_{G(E)} \), JJ⁻¹)
Fig. 4.A1. Calculated true growth yields of energy \([Y_{G(E)}]\) and carbon \([Y_{G(C)}]\) as a function of tissue protein content (the underlying principles of calculation are outlined by Penning de Vries et al. 1989). Here, growth includes biosynthesis of new structure, mineral uptake, translocation, and nitrogen assimilation. The source of nitrogen is nitrate with 25% of nitrogen assimilation taking place heterotrophically (i.e., 75% is supported directly by photosynthetic metabolism). The dry composition (mass/mass) of this hypothetical tissue is 5% fats, 7% lignins, 5% organic acids, and 8% minerals. The protein content is shown on the figure (abscissa) and the carbohydrate content is given by the remainder (i.e., 25% to 75%, from right to left).

\[
Y_{G(E)} = \frac{\dot{E}_T}{\dot{E}_G},
\]

where \(\dot{E}_G\) (J s\(^{-1}\)) is \(\dot{C}_G\) times its initial energy content, i.e., as carbohydrate. An upper limit (theoretical maximum value) of \(Y_{G(C)}\), and \(Y_{G(E)}\), can be calculated based on stoichiometries of biosynthetic and respiratory pathways. If \(Y_{G(C)}\) is determined from such a pathway analysis, a minimum rate of growth respiration can be estimated from

\[
\dot{C}_R = (1 - Y_{G(C)}) \frac{\dot{C}_T}{Y_{G(C)}}.
\]

For many plant tissues, \(Y_{G(C)}\) and \(Y_{G(E)}\) will take on values between about 0.75 and 0.80 (Fig. 4.A1). That is, no more than 0.75–0.80 of the carbon and energy in photosynthesize can be retained in new plant structure because of growth costs. Values of \(Y_{(C)}\) and \(Y_{(E)}\) are always less than the values of \(Y_{G(C)}\) and \(Y_{G(E)}\), respectively.

The ratio of heat released to CO\(_2\) released in heterotrophic metabolism (\(\beta\), kJ mol\(^{-1}\) CO\(_2\)) will be negatively related to relative growth rate if the composition of growing tissue does not change with growth rate (Fig. 4.A2). Moreover, \(r\) should increase as relative growth rate increases (Fig. 4.A2), as is commonly observed (see Amthor 1993b). Specific respiration rate is expected to be positively related to growth efficiency, whereas the ratio of energy release to CO\(_2\) release should be negatively related to growth efficiency (Fig. 4.A3).
Fig. 4.A2. Calculated specific respiration rate \(r\) and ratio of heat released to \(\text{CO}_2\) released \((\beta)\) as a function of relative growth rate (RGR) for plant structure that is 55% carbohydrates, 20% proteins, 5% fats, 5% lignins, 5% organic acids, and 10% minerals. The maintenance respiration coefficient is set to 0.15 \(\mu\text{mol CO}_2\text{g}^{-1}\text{protein s}^{-1}\) in this simulation and the growth costs are based on Penning de Vries et al. (1989), Pate and Layzell (1990), and Amthor (1993a). Nitrogen source and assimilation are as in (Fig. 4.A1). Growth respiration is divided among biosynthesis of new structure (59%), translocation (18%), nitrogen assimilation (10%), nitrogen uptake (9%), and non-nitrogen mineral uptake and transport (4%). An RGR of 0 denotes mature tissue, i.e., a state of maintenance. The specific rate of heat production is the product of \(\beta\) and \(\text{r}\), i.e., 51.6 \(\text{J g}^{-1}\text{h}^{-1}\) for \(\text{RGR} = 0\) and 82.2 \(\text{J g}^{-1}\text{h}^{-1}\) for \(\text{RGR} = 0.5 \text{d}^{-1}\) for this hypothetical plant.

Fig. 4.A3. Calculated specific respiration rate \(r\) and ratio of heat released to \(\text{CO}_2\) released \((\beta)\) for tissue described in (Fig. 4.A2) as a function of instantaneous growth efficiency or apparent growth yield \((Y_{(C)}\)). With \(\text{RGR} = \infty\), growth efficiency is about 0.76 \(\text{mol C mol}^{-1}\text{C}, \beta\) is about 123 \(\text{kJ mol}^{-1}\text{CO}_2\), and \(\text{r}\) is infinite. In this simulation, which assumes that tissue composition, \(Y_{G(E)}, Y_{G(C)}, \text{and } m_{(N)}\) remain constant across growth rates, it is an increase in \(\text{RGR}\) that increases growth efficiency and \(\text{r}\) while decreasing \(\beta\).
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*Addeà in proof*: Gly-3-P in Fig. 4.2 is the same as 3-PGald in Fig. 4.5 and 1,3-DiPGA in Fig. 4.2 is the same as 1,3-bisPGA in Fig. 4.5