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Respiration from the Organ Level to the Stand

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I. Introduction

As several reviews have emphasized, respiration is a major factor in plant, stand, or ecosystem energy budgets, estimated to consume anywhere from 30 to 70% of total carbon fixed (Sprugel and Benecke, 1991; Hagihara and Hozumi, 1991; Ryan, 1991a). Respiration has been an area of particular interest and concern recently because of the possibility that CO_2-induced global warming might lead to substantial increases in respiration in temperate and boreal ecosystems, which could decrease net primary productivity (Ryan, 1991a). This concern, coupled with a general interest in scaling of physiological processes (e.g., Ehleringer and Field, 1993), has led to a resurgence of interest in respiration and in techniques for estimating respiration of stands and ecosystems.

Before we begin our discussion of respiration, a few definitions are in order. This chapter will deal with dark respiration (henceforth simply respiration), the process by which glucose is enzymatically combined with oxygen to liberate chemical energy and CO_2. It is generally assumed that most respiration in trees is through the "normal" cytochrome-mediated pathway, but there is an alternative; cyanide-resistant or salicylhydroxamic acid-sensitive respiration is a nonphosphorylating respiration pathway that generates only 40–50% as much chemical energy per glucose oxidized (Lambers, 1980). In most ecophysiological

studies respiration is defined as CO_2 evolution, and if the results are the only thing being considered, it makes little difference which pathway is involved. However, when the respiration costs of producing plant tissue are estimated from tissue analyses (see Section V), it is implicitly assumed that any ATP required for synthesis is produced by cytochrome-mediated respiration. If alternate-path respiration is important, these calculations could be in error. Photorespiration is a by-product of photosynthesis in C_3 plants in which ribulose bisphosphate carboxylase/oxygenase (Rubisco) binds to O_2 instead of CO_2. It manifests as a reduction in the rate of photosynthesis and will not be considered further here.

Respiration is unusual among major physiological processes in that until recently (see Section V) there have been no techniques for estimating stand-level respiration that do not rely directly or indirectly on extrapolation from small-scale samples. Most physiologically based ecosystem processes can be quantified on a stand scale by measuring some whole-system property that represents the ecosystem-scale manifestation of the physiological process. Net primary productivity, for example, can be estimated by measuring litterfall, biomass increment, and grazing (with a potentially major error in estimating the belowground component). For transpiration there are more possibilities; stand- or watershed-level evapotranspiration can be estimated by using weighing lysimeters or whole-tree sap-flux gauges; through micrometeorological methods (e.g., eddy correlation, Bowen ratio, or boundary layer gradients); or by calculating the difference between precipitation inputs and streamwater outputs. For respiration, though, no such stand-level estimator has been available; until the development of eddy correlation methods for forests (see Section V), the only way to estimate stand-level respiration was to make physiological measurements on individual organs throughout the canopy and then sum or integrate to get a stand-level value.

The absence of such a large-scale proxy measurement of stand-level respiration has had several important consequences. First, because integrating and scaling up is much more laborious and time-consuming than whole-system measurements, there have simply not been very many attempts to estimate total autotrophic respiration for a stand or an ecosystem. Although there have been hundreds of estimates of whole-stand NPP for ecosystems around the world, the estimates of whole-stand respiration, or even total aboveground respiration, could be counted on the fingers of one or two hands. Moreover, the absence of a system-level estimator has made it difficult to check those estimates that have been made. For some processes it has been possible to achieve closure (Kaufmann and Landsberg, 1991) by measuring all components of a system

and checking the total against an independent measurement. With respiration, this has not been possible (but see discussion in Section V of the possible use of eddy correlation to achieve this end). As a result, considerable effort has been put into developing techniques for scaling individual measurements up to stand level. This chapter will focus on these scaling techniques and how they deal with known sources of variation in respiration.

As in all scaling efforts, the crucial problem in extrapolating from small- to large-scale respiration estimates is finding an index that is easily measured on both large and small samples and is also closely tied to respiration of some important stand component. The search for such an index is made more difficult by the fact that respiration is an active process, highly responsive to environmental and physiological factors, and also highly variable within the plant. It is crucial to understand the nature and source of this variation before attempting to extrapolate from shoot-scale measurements up to the next higher level of organization (Dawson and Bliss, 1993). For example, past studies have often measured respiration per unit foliage biomass or per unit stem surface area for a few samples and then extrapolated these estimates up to the stand level simply by multiplying by the total foliage biomass or stem surface of the stand. However, Brooks *et al.* (1991) found that at a given date and time, respiration of mature *Abies amabilis* foliage varied by a factor of 7 within the canopy of a single stand; Sprugel (1990) found that in the same stand respiration per unit stem surface area varied by up to 20-fold. Given variation of this magnitude, uncritical use of these indices, particularly if combined with unlucky choice of sampling locations, could lead to disastrously bad estimates of total stand respiration. This large variation makes an understanding of within-stand variation critical both in choosing sample locations for respiration measurements and in selecting an index for extrapolating from those locations to the whole tree or stand.

A. Construction versus Maintenance Respiration

In attempting to scale respiration estimates up to stand level, or even simply to understand the factors controlling respiration, it is frequently useful to distinguish construction and maintenance components of respiration (Johansson, 1933a; Lambers *et al.*, 1983; Sprugel and Benecke, 1991; Ryan, 1991a). This distinction is often referred to as the "functional model" of respiration (McCree, 1970; Thornley, 1970) and is expressed by the following equation:

$$R = g(\Delta W/\Delta t) + mW, \tag{1}$$

where R is total respiration (grams C/day), $\Delta W/\Delta t$ is growth rate (grams C/day), g is the respiration cost of producing a unit of tissue (grams C/gram C), W is plant weight (grams C), and m is the cost of maintaining a unit of tissue (grams C/gram C/day). Thus the first term represents construction respiration (the cost of producing new tissue) and the second represents maintenance respiration (the cost of maintaining current tissue). Numerous alternative formulations of this model, and particularly of the "growth coefficient" g, are given in Lambers *et al.* (1983).

The functional model of respiration is not universally accepted because (1) biochemically, the process of glucose oxidation is the same regardless of what the energy is used for and (2) experimentally, it is often very difficult to separate the two components. Moreover, the model does not account for storage, which can be a major component of tree energy budgets at some times of the year [but see Thornley (1977) for an improved version]. Finally, the model as expressed in Eq. (1) is not quantitatively applicable to whole trees because different tissues have different construction and maintenance costs (Chung and Barnes, 1977), and even the same tissue may have different maintenance costs at different locations in the tree (Brooks *et al.*, 1991), so g and m are not well-defined on a whole-tree basis. However, from a conceptual standpoint, the functional model does provide an excellent logical framework within which to structure respiration studies, and in many cases this advantage outweighs some practical difficulties.

Construction respiration is defined more precisely as the carbon cost of constructing new tissue, exclusive of the materials that are actually incorporated into the tissue. The cost of producing a given amount of a particular type of tissue (grams of C respired/gram of C of new tissue produced) is determined solely by the chemical composition of the tissue and the oxidation state of the minerals used to produce it, and is unaffected by the temperature at which the synthesis occurs or any other environmental or genetic factors (Penning de Vries *et al.*, 1974; Penning de Vries, 1975a). (Temperature may indirectly affect construction respiration rates by changing the rate at which new tissue is produced, but the respiration per gram of tissue should be constant.) Because construction respiration is an inevitable consequence of producing new tissue and is linearly related to the amount of new tissue produced, it is often modeled simply as an "overhead" added to the cost of the tissue (which means, of course, that to model construction respiration accurately one must first be able to model growth accurately). Methods of calculating the total construction respiration involved in producing different types of tissues based on chemical or elemental composition are outlined in Section V.

Maintenance respiration, on the other hand, is the cost of maintaining

established tissue once it has been formed (grams of C respired/gram of tissue per day). It includes the costs of protein synthesis and replacement, membrane repair, and the maintenance of ion gradients, and is very temperature sensitive (Penning de Vries, 1975b). The term "maintenance" is somewhat misleading, because it seems to imply a relatively passive process. In fact, the rate of maintenance respiration is highly variable even among leaves on the same tree (Brooks *et al.*, 1991), and is affected by many factors, including the overall level of metabolic activity and stress in the tissue. Accurate prediction of the maintenance respiration of a stand thus requires detailed understanding of its variation and the factors responsible for it.

Some of the most important classical and current questions about "respiration" become much more tractable when construction and maintenance respiration are clearly distinguished. For example, ecologists have wondered for years if net primary productivity decreases with stand age primarily because respiration uses an increasingly large fraction of total photosynthesis (Møller *et al.*, 1954; Kira and Shidei, 1967; Sprugel, 1984, 1985; Ryan and Waring, 1992). On examination it becomes clear that the only type of respiration that is likely to increase in older forests is maintenance respiration, because if net productivity goes down, construction respiration also decreases. So the question really is, does maintenance respiration increase enough with stand age to cause the observed decrease in NPP? To answer this, one needs to be able to estimate maintenance respiration directly rather than attempting to work with a blend of maintenance and construction respiration. Questions about the effect of climate change on respiration (Woodwell, 1987; Melillo *et al.*, 1990; McGuire *et al.*, 1992, 1993) are similar. No one is really very interested in how global warming will affect total respiration, because an increase in total respiration could result from increased maintenance respiration (which might lead to decreased biomass production), increased construction respiration (which would imply increased biomass production), or a combination of the two, and each would have vastly different consequences. The real question is whether maintenance respiration will increase so much that net productivity (and construction respiration) will decline as a result (Ryan, 1991a). In all of these cases distinguishing maintenance and construction respiration tends to clarify the issue and make it more amenable to logical and experimental analysis.

Numerous methods have been suggested for partitioning respiration into construction and maintenance components (e.g., Lambers *et al.*, 1983; Amthor, 1984; Sprugel and Benecke, 1991). Most of these are rather difficult to apply to trees in the field, but some are useful, and will be discussed in the following sections.

B. Temperature Effects on Respiration

It is well known that respiration is highly sensitive to temperature (Berry and Raison, 1981; Amthor, 1984, 1989; Ryan, 1991a). This sensitivity can be dealt with in several different ways. If the intent is simply to standardize measurements for comparison purposes, the simplest technique is to measure respiration at the same temperature for all samples using a temperature-controlled cuvette. However, in many studies temperature response curves are necessary, either (1) to allow the investigator to "remove" the effect of temperature from rates measured at ambient temperatures so that influences of other plant and environment variables can be ascertained, or (2) to predict respiration over a range of temperatures (as is often the case in scaling studies). In such cases there are two options. If a temperature-controlling device such as a growth chamber or a temperature-controlled cuvette is available, one can measure respiration over a predetermined range of temperatures to generate the desired response curve or surface. If measurements are to be made in the field without a temperature-controlled cuvette (or if temperature control is impractical due to the large thermal mass of the sample, as may be the case with large stems), respiration can be measured at ambient temperatures over a period of 1 or 2 days. However, temperature response curves derived from natural temperature variation must be used with caution, because respiration rates may also be altered by changes in plant water status and carbohydrate storage. Curves developed during periods of rapid developmental change (e.g., the time immediately after bud break) are even more tenuous and should be avoided.

The shape of the respiration–temperature curve has been a matter of extended and so far inconclusive debate. The usual presumption has been that respiration increases exponentially with an increase in temperature (Amthor, 1984). The response is usually expressed in terms of Q_{10}, the proportional change in respiration resulting from a 10°C increase in temperature:

$$R(t) = R_0(Q_{10})^{(T/10)}, \tag{2}$$

where R_0 is the respiration at 0°C. For most plants the Q_{10} of respiration is about 2.0 (i.e., respiration doubles when temperature increases by 10°C), but for woody plants the value may be higher (Ryan, 1991a).

Although it is convenient for modeling and has substantial empirical and theoretical support, the assumption that respiration increases exponentially with increasing temperature is probably accurate only over a fairly narrow temperature range. Over a broader temperature range, it is found that the exponential Q_{10} response applies only between about 10 and 25°C (for temperate species) (Larcher, 1983; Fitter and Hay,

1987). Below 10°C, the response to temperature is nearly linear; above 35°C, the response flattens out (and at very high temperatures becomes negative as thermal death approaches). In terms of Eq. (2), this is equivalent to saying that Q_{10} decreases at high temperatures and increases at low temperatures. Paembonan *et al.* (1991) found such a pattern in the respiration of a whole *Chamaecyparis obtusa* tree; Q_{10} varied from about 1.5 in August, when the mean temperature was 20–25°C, to 3.0–3.5 in January (mean temperature 5°C). Interpreting these data is difficult, though, because they could include seasonal as well as temperature-related changes in Q_{10}, and because the observations at various times of the year include both maintenance respiration and construction respiration (i.e., growth) in varying proportions. But other studies have also questioned the uncritical use of the Q_{10} relationship; for example, Brooks *et al.* (1991) found that over the range 5–35°C the instantaneous temperature response of *A. amabilis* foliage fitted a straight line better than an exponential curve. It may be that the use of Q_{10} values for describing temperature responses of respiration has been overemphasized, and that it would be better to focus more on comparing temperature response over a broad range of temperatures. In any case, the simplest solution is to measure the temperature response of respiration whenever it is needed to interpret the results of measurements.

In this paper, we review methods for obtaining stand-level estimates of autotrophic dark respiration in conifers. Because each type of tissue poses different problems and opportunities, we consider foliage, woody tissues, and fine roots separately. For each tissue type, we document methods for measuring respiration, examine the variability in respiration rates reported, and discuss whether existing models account for the observed variability. Then, we discuss extrapolating chamber measurements to the stand using our understanding of what controls variability. Finally, we discuss methods for obtaining independent stand-level estimates of autotrophic respiration, and system-level constraints on those rates.

II. Foliar Respiration

The confusion of construction and maintenance respiration that pervades measurements of other tissues is less of a problem in foliar respiration, because there are an abundance of measurements of respiration of mature leaves (Table I), which presumably represent maintenance respiration only. Construction respiration is less commonly measured; we know of no attempts to measure and isolate the construction costs of conifer foliage by regularly or continuously measuring CO_2 efflux from

Table I Maintenance Respiration Rates of Conifer Foliage[a]

Species	Location	Temperature (°C)	R_{PLA} (μmol/m²/sec)	R_{TLA} (μmol/m²/sec)	R_g (nmol/g/sec)	Reference
Abies amabilis	Pacific Northwest, United States	15	0.2–1.86	—	0.6–5.9	Brooks *et al.* (1991)
Abies veitchii	Japan	15	—	—	1–5	Matsumoto and Negisi (1982)
Chamaecyparis obtusa	Japan	14	0.1–1.3	—	—	Hagihara and Hozumi (1977)
Laris decidua × *leptolepis*	Germany	?	1[b]	0.45[c]	11	Matyssek and Schulze (1988)
Picea abies	Scotland	?	0.6–1.6	—	—	Barns *et al.* (1990)
Picea excelsa	Austria	15	—	—	1.9–3.2	Pisek and Winkler (1958)
Picea mariana	Canada	?	—	0.3–0.65	2.4–5.5[c]	Greenway *et al.* (1992)
Picea rubens	Southeastern United States	9.5	—	—	2.5–10.8	McLaughlin *et al.* (1991)
Picea sitchensis	Scotland	16	0.45–2.2	—	—	Leverenz and Jarvis (1979)
Pinus cembra	Austria	15	—	—	1.4–2.6	Pisek and Winkler (1958)
Pinus contorta	Scotland	13–22	0.5–1.5	—	—	Dick *et al.* (1991)
Pinus elliottii	Southeastern United States	15	0.16–0.6[b]	0.05–0.18[c]	0.5–1.6	Cropper and Gholz (1991)
Pinus radiata	New Zealand	15	0.4–1[b]	0.13–0.3	—	Benecke (1985)
Pinus sylvestris	Sweden	18	2.5	—	—	Leverenz (1988)
Pinus taeda	Southeastern United States	15	0.34[b]	0.11	1.3	R. O. Teskey, personal communication (1992)
Pseudotsuga menziesii	Pacific Northwest, United States	15	0.3–1.2	—	2–8.6	J. R. Brooks (unpublished data, 1989)

[a] Rates are for saplings or mature trees measured in the field. The rates included have been measured on mature, fully developed needles. Respiration rates are expressed on a projected leaf area basis (R_{PLA}), a total leaf area basis (R_{TLA}), and a unit weight basis (R_g).

[b] Converted from total leaf area by multiplying by 3.14 for *Pinus* spp. (R. O. Teskey, personal communication, 1992) and 2.2 for *Larix* spp.

[c] Calculated from author's specific leaf area measurements.

developing leaves. The only direct measurements of construction respiration in mature woody plants are those of Merino *et al.* (1984) for chaparral shrubs and Wullschleger *et al.* for *Quercus alba* and *Liriodendron tulipifera* (Wullschleger and Norby, 1992; Wullschleger *et al.*, 1992). (Several authors have also estimated construction costs of foliage using various chemical methods, as described in Section V.) There are also a substantial number of measurements of foliage respiration during leaf expansion that combine construction and maintenance respiration, but for scaling purposes these are of limited utility because it is impossible to partition out the components after the fact and the measurements are very sensitive to the exact stage of leaf expansion. In the following discussion, "respiration" of foliage means maintenance respiration unless specified otherwise.

A. Measurement Techniques

Infrared gas analyzers (IRGA) are the most common and most accurate way to measure CO_2 gas exchange; therefore, the techniques discussed here concern only the use of carbon dioxide exchange systems incorporating IRGAs. More details concerning gas exchange techniques in general are available in reviews by Leverenz and Hällgren (1991) and Field *et al.* (1991), and in an older classic by Šesták *et al.* (1971).

Equipment used to measure photosynthesis can generally also be used to measure respiration with only minor modification. The main difference is that, because the rate of foliage respiration is much lower than the rate of photosynthesis, systems designed for measuring photosynthesis may need to be modified to increase the accuracy of measuring CO_2. This is especially true if the study involves measuring respiration of old, shaded foliage at ambient temperatures, because on a cold day the CO_2 evolution of a cuvette-full of old needles can be very low indeed. If an open system is used, it may be helpful to lower the flow rates from that used for photosynthesis. In a closed system, it may be helpful to use a smaller cuvette to reduce the volume of the system so that the increase of CO_2 can be detected more accurately. For both open and closed systems it will be important to maximize the leaf area within the cuvette.

An obvious but critical decision for measurements of dark respiration is whether to measure respiration at night or during the day. The advantage of measuring respiration at night is that one need not control light and that within a few hours after darkness it can be assumed that foliage is completely dark acclimated (see below). The disadvantages of measuring respiration at night include physical difficulties in conducting the experiment, the fact that stomatal closure may restrict CO_2 evolution from the needles, and the fact that nighttime temperatures are generally low (especially in montane and boreal forest) and not very variable.

Under such conditions, if a temperature-controlled cuvette is not used, respiration can also be very low, resulting in small changes in CO_2 concentration that may be difficult to measure accurately. If a temperature-controlled cuvette is used when ambient temperatures are substantially lower than the standard temperature, there may be some concern about the effect of the rapid changes in temperature that occur when foliage is placed in the cuvette and the time required for complete acclimation to a new temperature level. Finally, some IRGAs (and many physiologists) do not function well below 5° C, adding mechanical difficulties to the other inconveniences of darkness.

The advantages of measuring respiration during the day include convenience and (usually) more satisfactory temperature conditions. The disadvantage is that foliage must be shaded during measurement and for a period of time prior to measuring so that the effect of recent illumination on respiration can be avoided. There is, however, substantial debate as to just how long this effect lasts. Using tomatoes, Ludwig *et al.* (1975) found that respiration rates are greatest directly after a period of illumination, and the brighter the illumination the greater the respiration response. The illumination effect lasted from 10 to 30 minutes, after which respiration reached a steady state. Brooks *et al.* (1991) also found that there were no significant differences between respiration rates measured in the field after 1 hour of shading and rates measured on the same samples in the laboratory after 12 hours of darkness. However, M. G. Ryan (unpublished, 1991) found that respiration of 1-year-old foliage of *Pinus strobus*, *Pinus ponderosa*, *Pinus resinosa*, and *Pinus elliottii* at a given temperature was 20–40% lower at night than during the day after 1 hour of shade. At a minimum, foliage should be dark acclimated for 30–60 minutes prior to measuring respiration during the day, but caution is still needed in interpreting the results of such measurements. Further research to clarify this situation would be very useful.

B. Rates

Conifers generally have lower respiration rates than broadleaf plants. Even within the conifer group, considerable variation exists both within and between species. Table I contains respiration rates of mature needles compiled from a number of studies to represent a broad range of coniferous species. Rates ranged between 0.1 and 2.5 μmol/m^2/sec and between 0.5 and 11 nmol/g/sec for temperatures ranging from 13 to 22° C. The observed variation in rates within a single species spans much of the ranges stated above. This wide variation makes comparisons on a species level very difficult, but in examining just the maximum rates reported for each species, some trends become evident. On a unit weight basis, the highest rates of respiration were observed in the deciduous

Larix, but on a per unit area basis, the rates are comparable to other species. This is due to the fact that *Larix* spp. have higher specific leaf area (based on total leaf area, 323–243 cm^2/g) than other coniferous species (Matyssek and Schulze, 1988; Gower and Richards, 1990). The lowest rates of respiration, on both a unit weight and area basis, were measured on *P. elliottii* (Cropper and Gholz, 1991).

Generally, baseline respiration rates increase with the elevation at which an individual or species originated (Billings *et al.*, 1971). In a classic study, Pisek and Winkler (1958) found that respiration was higher in *Picea excelsa* grown in the mountains compared to individuals grown in the lower elevation valley. This difference was detected even in the winter when respiration rates were much lower. Cropper and Gholz (1991) attributed the low rates of *P. elliottii* as an adaptation of the species to the warm subtropical climate of the southeastern United States. Rook (1969) found that seedlings of *Pinus radiata* had higher respiration rates when they were preconditioned under cold temperature conditions; however, respiration rates declined rapidly when seedlings were moved to warmer growing temperatures, indicating that this species acclimates rapidly to the temperature regime under which it grows. McLaughlin *et al.* (1991) observed higher respiration rates of *Picea rubens* growing at high-elevation sites compared to those at low-elevation sites. In contrast to the conclusions of Pisek and Winkler (1958), McLaughlin *et al.* (1991) concluded that nutrient deficiencies at their high-elevation sites (induced either naturally or by acid deposition) caused the increase in rates. On a per unit area basis *A. amabilis*, a high-elevation conifer growing at 1150 m, respired at twice the rate of *Pseudotsuga menziesii*, a lower elevation conifer growing at 160 m (1.86 vs. 0.76 $\mu mol/m^2/sec$ measured at 15°C on 1-year-old upper canopy sun foliage), although on a per unit weight basis, differences were much smaller (5.86 vs. 5.24 nmol/g/sec) (J. R. Brooks, unpublished data, 1989).

C. Variation within the Canopy

Foliage respiration has a distinct pattern of variation within the canopy. This pattern is similar to that of other foliage processes such as photosynthesis and transpiration. In general, foliage respiration is highest in regions near where growth is occurring (i.e., close to strong carbohydrate sinks) and where photosynthetic rates are high. These regions are usually in the upper exposed parts of the canopy (Hagihara and Hozumi, 1977; Matyssek and Schulze, 1988; Brooks *et al.*, 1991).

The degree to which respiration varies within a canopy depends on the species being examined. For example, Brooks *et al.* (1991) found that within a dense stand of *A. amabilis*, respiration rates were five times higher in the upper canopy than in the lower canopy. In a more open

canopy of *P. elliottii*, Cropper and Gholz (1991) measured upper canopy rates that were less than twice that of the lower canopy. In a young stand of *P. menziesii* that had not achieved crown closure, no significant difference between upper and lower canopy positions were observed (J. R. Brooks, unpublished data, 1989).

The primary factors determining this pattern of variation appear to be light, growth, foliage age, and nitrogen content. These factors either directly or indirectly affect the photosynthetic rate and production of carbohydrates, which can in turn increase respiration rates by increasing enzyme turnover ion transport. Therefore, these factors can affect the rate of respiration, and may be useful indices in efforts to scale the variability of respiration within conifer canopies.

1. Ambient Light The most obvious factor that decreases with depth into the canopy is light. Hagihara and Hozumi (1977) found that foliage respiration rates were well correlated with light levels, and used light levels in the canopy as an index to estimate whole-canopy foliage respiration. Brooks (1993) also found a close correlation between light availability and foliage respiration rates in *A. amabilis*. The fact that respiration varied more in an *A. amabilis* stand than in a *P. menziesii* stand is also consistent with a strong control by light, because at the base of the *A. amabilis* canopy, light was less than 1% of the light at the top of the canopy, whereas at the base of the *Pseudotsuga* canopy, light was more than 20% of light at the top.

Light can affect foliage respiration in two ways: first, a short-term ($\leq$1 hour) effect on metabolic activity and carbohydrate levels, and second, a long-term (days to years) effect on foliage morphology and photosynthetic capacity. As noted in Section II,A, the short-term effects of light on respiration have been noted repeatedly, but in most field studies sampling protocols are designed specifically to avoid the postillumination burst of respiration. Over a longer time period, respiration per unit area of foliage formed in sun is higher than that of foliage formed in the shade (Björkman, 1981; Larcher, 1983). The lower rates in shade foliage have been attributed to a lower demand for ATP and a reduced respiratory machinery, as well as a reduced leaf thickness (Björkman, 1981). Leverenz and Jarvis (1979) found that respiration was twice as high in sun foliage as in shade foliage on *Picea sitchensis*. In *P. radiata*, sun foliage respired at approximately three times the rate of shade foliage (Benecke, 1985). Although *Pinus* and *Picea* spp. do not form palisade mesophyll and thus cannot form true sun and shade foliage, they do have some ability to acclimate both morphologically and physiologically to the different light environments. *Tsuga* and *Abies* spp. do form palisade mesophyll cells and thus should have greater ability to acclimate to differences in light.

In evergreen conifers where foliage can live for numerous years, a canopy does not consist simply of sun foliage in the sun and shade foliage in the shade. Foliage that was formed in the sun is shaded as the tree continues to grow, so that a tremendous quantity of sun foliage eventually is in the shade. Although the morphological aspects of light acclimation are fixed after development is completed, mature foliage of *A. amabilis* can continue to acclimate physiologically to changes in light (Brooks, 1993). Brooks *et al.* (1991) noted that respiration decreased with depth in the canopy for any age class and that this decrease was not related to changes in foliage morphology as measured by specific leaf area. The ability to acclimate after leaf expansion is complete may be quite significant in conifers, because in some evergreen canopies (especially in shade-tolerant species) a large proportion of the canopy may undergo a dramatic light change in the years between development and senescence (Leverenz and Jarvis, 1979; Sprugel *et al.*, 1992).

2. Seasonal Growth Activity A large component of respiration is associated with the production of new tissue. As tissues expand, there is a burst of construction respiration in the developing tissue, and a strong local demand for carbohydrates that affects the maintenance respiration rate of nearby source foliage. As a result, "maintenance" respiration rates of mature foliage fluctuate seasonally and spatially with the growth of the tree (Hagihara and Hozumi, 1977; Matsumoto and Negisi, 1982; Brooks *et al.*, 1991). Teskey *et al.* (1984) observed that respiration rates of 1-year-old foliage were highest immediately following bud break and during shoot elongation for *A. amabilis*. However, not all studies have found seasonal differences in respiration rates. Cropper and Gholz (1991) observed no seasonal pattern of respiration in *P. elliottii*, but they point out that in northern Florida, *P. elliottii* is physiologically active year round. And in *P. radiata*, which also grows in a fairly equitable climate, Benecke (1985) found seasonal differences in current-year foliage only when he included the bud respiration in the sample; when the bud was excluded from the sample chamber there was no distinct seasonal pattern.

The degree of variation in respiration within the canopy may also be influenced by the seasonal pattern of growth activity. In *A. amabilis*, Brooks *et al.* (1991) found that the greatest variation in respiration within the canopy occurred during the early part of the growing season and that respiration in mature foliage was high in regions of intensive growth and low in regions of minimal growth. The respiration pattern within the canopy was far less distinct at the end of the growing season. The growth of reproductive structures also influences the pattern of foliage respiration. Dick *et al.* (1991) noted that the rate of foliage respiration for *Pinus contorta* was highest on branches that bore female cones.

They also found that foliage respiration fluctuated seasonally, but differences between branches were still detectable in autumn even though respiration rates were lower.

3. Foliage Age Foliage respiration rates change throughout the life span of a leaf. Respiration rates are at a maximum during growth and development, when construction respiration is occurring. Once a leaf matures the rate of respiration decreases dramatically. Respiration has also been noted to increase during the senescence of foliage as transport activity increases when nutrients and amino acids are rapidly exported from the leaf (Chabot and Hicks, 1982).

Conifer needle life spans range from 3 months to over 50 years (Reich *et al.*, 1994). This tremendous variation in leaf life span makes it difficult to generalize about the effects of age on any process. In *A. amabilis*, whose needles live 15 or more years, Brooks *et al.* (1991) found that even for mature needles, respiration decreased with age in the upper canopy, but in the lower canopy there was no detectable difference between age classes. They hypothesized that the decrease in respiration with age in the upper canopy was not simply a function of leaf age but was also related to the fact that as leaves age they become increasingly shaded as the tree grows around them, and are also more distant from active sinks. However, for *Abies veitchii*, Matsumoto and Negisi (1982) found a decrease in respiration with foliage age for seedlings grown in both the open and the shade. Greenway *et al.* (1992) did not observe any variation in foliage respiration with leaf age in *Picea mariana* growing on nutrient-poor sites; however, they also noted that the photosynthetic capacity of these needles did not differ until after the age of 6 or 8 years. How respiration changes with age has not been addressed in most studies involving conifers; yet, if respiration follows a trend similar to photosynthesis and leaf nitrogen content, then respiration should decrease with age in other conifer species as well as in those noted in the studies above. Hom and Oechel (1983) found both decreasing nitrogen content and photosynthetic capacity with needle age in *P. mariana*, and Linder and Troeng (1980) noted that photosynthetic capacity decreased with age in *Pinus sylvestris*. However, Nebel and Matile (1992) observed no photosynthetic decrease with age in *Pinus cembra*.

4. Nitrogen It has been suggested that nitrogen content of leaves should be a good indicator of foliage photosynthetic capacity because of the relationship between nitrogen content and the amount of reactants for the dark reaction of photosynthesis (Field and Mooney, 1986; Evans, 1989). If there is a correlation between respiration and photosynthetic capacity, then it would be expected that respiration and nitrogen content would also be correlated. Kawahara *et al.* (1976) showed a correlation

between respiration and foliar N concentration within a *Pinus densiflora* canopy, and M. G. Ryan and R. M. Hubbard (unpublished, 1993) found correlations between respiration and N content in canopies of unfertilized *Tsuga heterophylla*, *P. ponderosa*, *P. resinosa*, and *P. elliottii*. Brooks (1993) found a correlation between respiration and N content in an *A. amabilis* canopy, although the correlation was considerably weaker than correlation between respiration and light ($R^2 = 0.28$ for N vs. $R^2 = 0.45$ for light; temperature is included in both correlations). Results of fertilization studies, however, tend to cloud this picture. Cropper and Gholz (1991) found no differences in respiration between fertilized and unfertilized trees of *P. elliottii*. R. O. Teskey (personal communication, 1992) also observed no differences in foliar respiration in *Pinus taeda* trees even though there were differences in foliar nitrogen content. These plants may have been experiencing luxury levels of nitrogen, in which case increases in N content would not affect the photosynthetic capacity or the respiration rate, although the nitrogen content of the fertilized plants was approximately 1.3%, which is not exceptionally high for conifers.

The lack of correlation between respiration and N content in fertilized trees may reflect the fact that in a N-rich environment, N in plant tissues may be present as amino acids rather than protein (van Dijk and Roelofs, 1988). In this case, foliar N estimated from total Kjeldahl nitrogen will be a poor estimator of foliar protein content. Because the relationship between foliar N and maintenance respiration depends on the N being in protein, if N is in amino acids or storage proteins, foliar N will likely not be a good predictor of maintenance respiration. For this reason, the relationship between respiration rates and N may not be valid for fertilized conifers. Similar problems have been noted for the relationship between photosynthesis and foliar N content (e.g., Reich and Schoettle, 1988). Further research on this question would be exceedingly useful.

D. Techniques for Extrapolating to Stand-Level and/or Long-Term Estimates

Scaling foliage respiration from measurements on a twig to an estimate of stand respiration requires knowledge of both the variation of respiration and the distribution of foliage within the canopy. As discussed previously, foliage respiration rates vary significantly both temporally and spatially. Ideally one would like to find an index closely related to respiration rates whose spatial distribution could be easily mapped, but few studies to date have taken this approach. A notable exception is Hagihara and Hozumi (1977), who related foliar respiration in *Chamaecyparis obtusa* to light levels and then used Beer's law of light extinction to estimate total canopy respiration. Most other studies, however, have used relatively complex methods of quantifying foliage

distributions within canopies, and these cannot easily be transferred to other systems (Norman and Jarvis, 1974; Rook and Corson, 1978; Ågren *et al.*, 1980; Brooks, 1987; Hashimoto, 1990; Wang and Jarvis, 1990; Cropper and Gholz, 1990; Mori and Hagihara, 1991).

An additional factor that must be considered when examining the distribution of respiration within canopies is the within-canopy variation in temperature, because temperature has such a strong influence on the rate of respiration. Temperature varies both temporally and spatially within canopies (Fritschen *et al.*, 1973; Brooks *et al.*, 1991), with higher leaf temperatures in the upper exposed parts of the canopy and decreases in temperature with depth in the canopy. Brooks (1987) found that a fivefold difference in modeled respiration rates between the top and bottom of the canopy was increased to a sevenfold difference when temperature differences within the canopy were included in the calculations. This may represent an extreme case, because many conifer canopies are better coupled to the atmosphere than the dense *A. amabilis* canopy (McNaughton and Jarvis, 1991), but it does show that in at least some canopies temperature variation can play a significant role.

III. Woody-Tissue Respiration (Stems, Branches, and Coarse Roots)

Respiration of woody tissues (stems, branches, and coarse roots) has been measured much less often than respiration of foliage, but of those measurements that have been made, a relatively high proportion have been aimed at stand-level estimates (e.g., Hagihara and Hozumi, 1981; Linder and Troeng, 1981; Benecke, 1985; Sprugel, 1989; Ryan and Waring, 1992). Several methods have been used for scaling, but recent work (Ryan, 1990; Sprugel, 1989, 1990; Sprugel and Benecke, 1991; Ryan and Waring, 1992) has led to the development of relatively straightforward and general techniques that appear to hold great promise for the future.

A. Measurement Techniques

Techniques for measuring respiration of woody tissues have recently been reviewed in detail by Sprugel and Benecke (1991) and will be discussed only briefly here. Historically, two methods have received the most use. In the first, excised branch, stem, or root sections are removed from the tree and brought back to the laboratory for measurement of CO_2 evolution (or occasionally O_2 uptake) (Müller, 1924; see additional references in Sprugel and Benecke, 1991). This method requires little in the way of sophisticated equipment and permits the use of a large

sample size, but it is difficult to be confident that respiration of an excised stem is not affected in some way by the harvesting process (e.g., through wounding or changes in water status, internal CO_2 concentration, carbohydrate content, or hormonal supplies). It is also impossible to make repeat measurements on the same sample to follow respiration trends through the year, and adequate sampling involves considerable destruction of trees in or near the study area.

The main alternative to excision methods has been *in situ* methods in which sections of living stems, branches or roots are enclosed in permanent cuvettes and CO_2 evolution through the bark is monitored continuously over prolonged periods of time (Johannson, 1933a; for others, see Sprugel and Benecke, 1991). This technique is much less intrusive than excision techniques, but it generally requires expensive and complex equipment to maintain airflow through the cuvettes, measure changes in CO_2 concentration, and record the data for future analysis. The main problem with this technique is that the extensive hardware requirements usually result in a very small sample size (one or two sections is typical), which makes it difficult or impossible to determine which characteristics of the sampled branch or stem are most important in determining respiration rates and thus to extrapolate to other parts of the tree.

A third technique that has been gaining in popularity involves the use of a moderate number of removable cuvettes that can be clamped onto a stem, branch, or root section while a measurement is being made, then removed until the next sampling date (Sprugel, 1990; Ryan, 1990; Sprugel and Benecke, 1991). This technique shares with the continuous monitoring technique the advantage that measurements are made *in situ* on living trees, but because CO_2 is not continually monitored, hardware requirements are much smaller, and a significantly larger sample size is possible. These larger sample sizes, coupled with the ability to make repeat measurements on the same site, have been crucial in recent efforts to separate construction and maintenance respiration in woody tissues.

A continuing problem with all measurements of woody-tissue respiration is the concern that CO_2 produced by respiration in the sapwood may be carried away by the transpiration stream instead of being released through the bark, so that measured CO_2 evolution would underestimate the actual respiration of the sample section (Boysen Jensen, 1933; Negisi, 1972, 1975, 1978, 1979; Martin, 1992; Martin *et al.*, 1994). Negisi (1975) reported that CO_2 evolution from a *P. densiflora* stem was reduced about 50% at midday compared with what would have been expected based on temperature alone. It is also possible that CO_2 produced by root or sapwood respiration might be carried upward into the stem or branches and released there, in which case measured CO_2 evolution higher in the tree would overestimate actual sapwood respiration.

However, no examples of excess CO_2 release during periods of high sap flow have been reported, with the possible exception of high rates of CO_2 release from *A. amabilis* branches in the spring that significantly exceeded what would have been expected from the sapwood volume and growth rate (Sprugel, 1990). After 60 years of controversy (cf. Boysen Jensen, 1933; Johannson, 1933b), the problem of CO_2 movement in the translocation stream remains a central concern in all measurements of woody-tissue respiration (Sprugel and Benecke, 1991).

An additional issue in measuring woody-tissue respiration is refixation of respiratory CO_2 by bark photosynthesis. Bark photosynthesis is reviewed in detail by Sprugel and Benecke (1991); here it suffices to say that for thin-barked trees, bark photosynthesis can refix a very substantial fraction of the CO_2 produced in stem respiration. Most studies of refixation have focused on angiosperms such as *Populus tremuloides* [where refixation rates of up to 90% have been reported (Schaedle, 1975)], but data in Sprugel and Benecke (1991) suggest that bark refixation reduced apparent respiration of a *P. radiata* branch by 35–40% over 24 hours. The possibility of significant refixation must thus be taken into account in any study of woody tissue respiration. If the intent is simply to measure respiration per se, then opaque cuvettes should be used to eliminate bark photosynthesis. If, on the other hand, the intention is to determine the contribution of the stem and branches to the tree's carbon budget, then it may be desirable to use clear cuvettes for at least some measurements and to minimize the shading by analysis equipment. (This, however, adds several additional complications, including the problem of heating of the enclosed stem if airflow rates are low and the difficulty of scaling bark photosynthesis over the entire surface of the tree).

B. Rates

There have been a substantial number of studies of woody-tissue respiration in conifers, including *Abies amabilis* (Sprugel, 1989, 1990), *Abies balsamea* (Lavigne, 1987, 1988), *Abies sachalinensis* (Yoda *et al.*, 1965), *Chamaecyparis obtusa* (Hagihara and Hozumi, 1981; Negisi, 1982), *Cryptomeria japonica* (Yoda *et al.*, 1965), *Larix decidua*, *Larix leptolepis*, and *Larix sibirica* (= *Larix russica*) (Johannson, 1933a), *Larix decidua* × *leptolepis* (Matyssek, 1985; Matyssek and Schulze, 1988), *Picea abies* (Johannson, 1933a), *Picea glehni* (Yoda *et al.*, 1965), *Picea engelmannii* (Ryan, 1990), *Picea jezoensis* (Yoda *et al.*, 1965), *Pinus cembra* (Havranek, 1981), *Pinus contorta* (Benecke and Nordmeyer, 1982; Ryan, 1990; Ryan and Waring, 1992), *Pinus densiflora* (Yoda *et al.*, 1965; Negisi, 1974, 1975, 1979, 1982), *Pinus radiata* (Benecke, 1985), *Pinus sylvestris* (Johannson, 1933a; Linder and Troeng, 1981; Zabuga *et al.*, 1983; Zabuga and Zabuga, 1985), *Pinus*

taeda (Martin, 1992), and *Pinus thunbergii* (Yoda *et al.*, 1965). These studies contain a wide variety of information about respiration in conifer stems (and in a few cases, branches and roots), including seasonal variation, species comparisons, and relation of respiration to volume. Unfortunately, most of the actual respiration rates reported are given as respiration per unit surface area, which is relatively uninformative, because it varies tremendously for different individuals, and even for different locations on the same tree. For example, Sprugel (1990) found that on a single day in June, CO_2 efflux from stems of 28-year-old *A. amabilis* trees (corrected to 15° C) varied from 0.12 μmol/m^2/sec on a small, slow-growing tree to 2.67 μmol/m^2/sec on a large, fast-growing tree. Variation in respiration per unit area of branches was similarly dramatic, ranging from 0.10 to 1.61 μmol/m^2/sec. When respiration per unit area varies by more than 20-fold within a single species on a single site on a single date, trying to compare values among species or sites is relatively futile, and so we have refrained from tabulating such values.

The idea that woody-tissue respiration should be expressed on a per-unit-area basis was apparently based on the assumption that the largest component of woody-tissue respiration was maintenance respiration of the cambium and phloem, so that respiration per unit area might be expected to be relatively constant. The assumption in turn was apparently based on a misinterpretation of the seminal work of Goodwin and Goddard (1940), who measured O_2 uptake by cut stems and found that respiration was highest near the outer surface of the stem. Later authors, reading their work, apparently did not realize that what Goodwin and Goddard were measuring was almost entirely *construction* respiration resulting from the production and maturation of xylem and phloem cells (Havranek, 1981)—and hence highly variable from site to site and season to season, making respiration per unit surface area too variable to be a useful index for species comparisons or scaling. In fact, other studies (Ryan, 1990; Sprugel, 1989, 1990) have shown that when construction respiration is absent (i.e., once the growing season is over), phloem and cambium respiration are insignificant compared with sapwood maintenance respiration—and of course the amount of sapwood under a given area of surface, as well as the rate of new wood production, will vary drastically depending on the size and vigor of the tree. Thus there is no reason to expect respiration per unit surface area to be constant from tree to tree or even within a single tree, and measurements expressed on a surface area basis are of little use for comparisons.

If respiration per unit surface area is too variable to be a useful measure of woody-tissue respiratory activity, it is necessary to ask what units are better. As noted above, Ryan (1990) and Sprugel (1989, 1990) both found that when the growing season is over, stem respiration is strictly

Table II Maintenance Respiration Rates of Conifer Sapwood[a]

Species	Location	Respiration (nmol/g/sec)	Reference
Abies amabilis	Washington	0.05	Sprugel (1990) and D. G. Sprugel, unpublished (1986)
Pinus contorta	Colorado	0.032	Ryan (1990)
Pinus elliottii	Florida	0.020	Ryan *et al.* in review
Pinus ponderosa	Montana	0.020	Ryan *et al.* in review
Pinus resinosa	Wisconsin	0.022	Ryan *et al.* in review
Tsuga heterophylla	Oregon	0.015	Ryan *et al.* in review

[a] All values at 15°C.

proportional to the amount of sapwood present in the sample cuvette, suggesting that at a constant-temperature sapwood maintenance respiration per unit volume (or mass) is relatively constant throughout a stand. And as we have already noted, values of construction respiration per unit sapwood produced should be relatively constant as long as the chemical composition of the wood does not vary too much. Thus the most useful values for comparing woody-tissue respiration rates among species would be values for maintenance respiration per unit sapwood volume or dry weight, and construction respiration per unit of new wood and bark produced.

Unfortunately, only a few estimates of sapwood maintenance respiration are available for conifers (Table II). Those that are available suggest that respiration per gram of wood is relatively constant among conifers, and that there are no immediately obvious patterns of variation with climate. Estimates of the construction cost of conifer wood are somewhat more variable (Table III). Chemical methods (Penning de Vries, 1975a;

Table III Construction Respiration Rates of Conifer Sapwood

Species	Respiration (g C/g C)	Method	Reference
Generic wood	0.25	Chemical pathway analysis	Penning de Vries (1975a)
Abies amabilis	0.42	CO_2 efflux − maintenance respiration	Sprugel (1989) and D. G. Sprugel, unpublished (1986)
Larix decidua	0.87	See text	Havranek (1985)
Pinus elliottii	0.15	Chemical pathway analysis	Chung and Barnes (1977)
Pinus radiata	0.25	CO_2 efflux − maintenance respiration	U. Benecke (unpublished, 1984); cited in Sprugel and Benecke (1991)

Chung and Barnes, 1977; cf. Section V) suggest that the construction cost of wood should be about 0.25 g C/g C. U. Benecke (unpublished, 1984; cited in Sprugel and Benecke, 1991) monitored CO_2 efflux from two locations on a *P. radiata* stem throughout a summer and subtracted estimated maintenance respiration from the total CO_2 efflux, and estimated the construction cost of wood at 0.25 g C/g C, a perfect match to the theoretical value. However, Sprugel (1989 and D. G. Sprugel, unpublished, 1986), using essentially the same technique, measured the construction respiration cost of sapwood production in *A. amabilis* at 0.42 g C/g C. Havranek (1985), using a somewhat more indirect technique based on the differences between measured CO_2 efflux and wood increment in two consecutive years, estimated the respiration cost of wood production in *L. decidua* at 0.87 g C/g C. The fact that these last two estimates based on CO_2 efflux are substantially higher than those based on chemical pathway analysis may mean that there are substantial additional respiration costs involved with tissue production in addition to the direct chemical costs (e.g., the costs of loading and unloading carbohydrates from the phloem), or it could simply reflect experimental error or inaccurate assumptions involved in the calculations. However, the differences are quite striking and suggest that more study of the actual costs of wood production would be valuable.

C. Variation within the Canopy

Woody-tissue respiration varies seasonally, between trees and even between locations on the same tree. The limited data available so far suggest that most of the observed variation in stem respiration reflects variation in the rate of wood production at any given place and time and in the amount of respiring sapwood. Thus, the easiest way to explain intracanopy variation is to partition observed measurements of respiration into construction and maintenance components, and to relate these to the sapwood volume and growth rate.

Efforts to partition respiration into construction and maintenance components, and to use this partition to predict total respiration for whole stands, have proceeded farther in studies of stem respiration than for any other tissue (although still not very far). Techniques for partitioning stem respiration into growth and maintenance components are discussed in some detail by Sprugel and Benecke (1991), and are also reviewed in Martin (1992). The simplest technique for partitioning measurements of respiration into construction and maintenance components is to assume that respiration measured before or after the growing season is solely maintenance respiration, and that higher levels during the growing season represent construction plus maintenance. The summation of construction respiration over the whole growing season then

represents the construction cost of the new wood that was produced that year. The key to this technique is the assumption that maintenance respiration at a constant temperature remains constant throughout the year, or at least for a month or two after growth stops (see discussion in Sprugel and Benecke, 1991). This assumption is necessary for most methods of partitioning respiration, but is virtually impossible to test, because maintenance respiration cannot be measured directly during the growing season. Sprugel (1990) attempted to check this assumption by regressing growing-season respiration against growth rate (with maintenance respiration left as the intercept when growth = 0), and although the results were rather noisy due to sampling variation, they were generally consistent with a constant rate of maintenance respiration.

Partitioning of branch respiration into maintenance and construction components has been less successful than for stem respiration. Sprugel (1990) found that measured branch respiration rates significantly exceeded the levels that would be expected for stems with similar growth rates and sapwood volumes, and that the observed respiration could not be readily partitioned into construction and maintenance components using the same techniques that worked for stems. Because the differences between predicted and measured values were greatest in the spring (when measured values exceeded predicted values by up to four or five times), and branch respiration rates were fairly well correlated with the amount of new growth on the branches, Sprugel suggested that some of the additional respiration might represent the cost of mobilizing carbohydrates stored in the parenchyma. However, little additional work has been done on this question and it basically remains a mystery.

Coarse root respiration has been systematically measured in only two studies (Linder and Troeng, 1981; Benecke, 1985), and in both cases only a single location was monitored. More studies with larger sample sizes will be needed before it is possible to determine the sources of variation in coarse root respiration and the possibility of using the construction : maintenance distinction to scale up to the stand level.

D. Scaling Up to the Stand Level

When stem respiration is partitioned into construction and maintenance components it becomes relatively easy to scale stem respiration measurements up to the stand level. Because maintenance respiration per unit of sapwood volume seems to be relatively constant throughout the main stem (at a given temperature), sapwood volume is a useful index for extrapolating small-scale measurements of stem maintenance respiration up to a stand level (Sprugel, 1989; Ryan and Waring, 1992). Although equations for estimating stem sapwood volume are available

for only a few species (e.g., Ryan, 1989), there are no great technical difficulties in generating equations for estimating sapwood volume as a function of height and sapwood area, which is commonly estimated as an index of leaf area. Similarly, if the construction respiration cost of producing different kinds of tissues is estimated (either from pathway analysis or through measurement of CO_2 evolution), total annual construction respiration for the stems in a stand can be estimated easily from the annual production of stem wood, which is routinely estimated in studies of net primary productivity.

Techniques for scaling branch and coarse root respiration from samples to the stand are less well developed. If it turns out that biomass and growth rate are good indices of branch and coarse root respiration, then it should be possible to tap into a substantial literature on branch and wood biomasses in forests. For example, determination of coarse root biomass is relatively easy because good relationships exist between coarse root biomass and the tree diameter at breast height (Vogt and Persson, 1991). A sizable data base also exists on coarse root biomasses for forests (Cannell, 1982). However, until the nature of local and seasonal variation in branch and coarse root respiration is better understood, scaling these processes up to the stand level will remain difficult.

IV. Fine Root Respiration

In general, root respiration is far more difficult to measure unambiguously than foliage or woody-tissue respiration because of the inaccessibility of roots under natural conditions. All known techniques for measuring root respiration require either removing roots from the soil environment and measuring them under vastly different conditions in the laboratory or the field, or making very significant modifications of the soil, whose effects on root and heterotroph respiration cannot readily be predicted.

Most studies of belowground respiration have concentrated on determining the respiration rates of fine roots because fine roots contribute the bulk of the CO_2 from belowground autotrophic respiration. The following discussion generally considers only fine and small-diameter roots (i.e., roots less than 0.5 cm in diameter); methods used to measure and scale coarse roots are more akin to the methods used for stems and branches, and were considered in the previous section.

A. Measurement Techniques

Singh and Gupta (1977) provide a detailed discussion of the older methodologies used to estimate fine root respiration rates, and these will

Table IV Root Respiration Data for Coniferous Seedlings and Forests Using Indirect and Direct Methods

Species	Respiration[a]	Q_{10}	Temperature (°C)	Size class (cm)	Analysis approach	Reference
			Mass-based measurements			
Abies amabilis	0.6–8.7	—	5–14	0.03–0.1	30-year-old stand, same root sampled monthly (July–November)	K. A. Vogt, D. J. Vogt, and D. Sprugel, unpublished (1986)
	0.8–8.9	—	—	0.1–0.15		
	0.4–6.1	—	—	0.2		
	0.3–3.3	—	—	0.2		
	0.3–3.3	—	—	0.2–0.35		
	0.3–1.6	—	—	0.5		
	0.2–0.6	—	—	0.6		
Abies lasiocarpa	27.1–29.1[b]	1.9	12	Fine	Excised 1-cm root segments from small trees	Sowell and Spomer (1986)
Picea engelmannii	30.0–33.6[b]	2.0	12	Fine	Excised 1-cm root segments from small trees	Sowell and Spomer (1986)
Picea rubens	1.3–3.2	—	—	Fine	Excised roots	Keller, 1967 (in Singh and Gupta, 1977)
Pinus elliottii	2.5	1.94	12	Fine	Intact roots, 22-year-old stand, one-time field reading per root, forest floor only	Cropper and Gholz (1991)
Pinus radiata	3.0	2.8	10	Fine	Excised roots, seedlings	D. Hollinger, unpublished (1991)
	1.5	2.3	10	Fine	Excised soil blocks, mature forest	
Pinus sylvestris	1.1	—	?	<0.2	Excised roots	Ågren *et al.* (1980)
Pinus taeda	5.7–8.0[a]	2.0	17	Fine	Excised roots, field-planted seedlings	Boyer *et al.* (1971)
Pseudotsuga menziesii	2.8	2.7	10	Fine	Excised roots, seedlings	D. Hollinger, unpublished (1991)
	1.2	3.0	10	Fine	Excised soil blocks, mature forest	
			Ground area-based measurements			
Pinus elliottii	0.43	—	—	Fine + coarse	9-year-old stand	Ewel *et al.* (1987)
	0.81	—	—		29-year-old stand; compartmentalized budget	
Pinus taeda	0.06	—	—	Fine + coarse	Excised roots	Kinerson (1975)

[a] Units for mass-based measurements are nmoles/gram/second; units for ground area-based measurements are kilograms carbon/m^2/year.
[b] Converted from O_2 uptake assuming RQ = 1

not be covered here. Interestingly, several of the earlier approaches to measuring fine root respiration are still utilized with slight modifications (Table IV).

Two major approaches have been used to estimate root respiration, which Singh and Gupta (1977) classified as direct and indirect approaches. The direct approach usually involves measuring CO_2 evolution or O_2 uptake of fine roots *in situ* or after they have been removed from the soil. This is by far the most common approach and is discussed in more detail below. The indirect approach typically consists of measuring total CO_2 evolution or O_2 uptake from intact soil surfaces in the field and either comparing different sites with varying root biomass or comparing nonmanipulated sites with sites that have been manipulated by removing all or part of the plants. In this approach the root contribution to total soil respiration is calculated by comparing total soil respiration rates from sites with known variation in root biomass. No studies of this type have been reported for conifer forests.

Only two studies have measured root respiration directly on intact roots in the field (Cropper and Gholz, 1991; K. A. Vogt, D. J. Vogt, and D. G. Sprugel, unpublished, 1986). Although studying the same coarse root throughout a year is very feasible, and the approach can mimic those described for branches (see previous section), respiration of intact fine roots has rarely been measured in the field because it is difficult to isolate fine roots from the soil without disturbing the system or causing the senescence of roots when they are exposed to the atmosphere (Vogt *et al.*, 1989). Cropper and Gholz (1991) measured the respiration rate of intact fine roots of *P. elliottii* in the forest floor using a one-time placement of roots in a chamber followed by harvesting of the roots for dry weight determinations. K. A. Vogt, D. J. Vogt, and D. G. Sprugel, (unpublished, 1986) used the removable chambers described in Vogt *et al.* (1989) to measure short-term respiration rates of intact *A. amabilis* roots monthly over a 5-month period, reburying the roots after each measurement (Table IV) (Vogt *et al.*, 1989). In this cool, damp subalpine stand there appeared to be little loss of vitality when the same fine roots (ranging in diameter from <1 to 6 mm) were measured repeatedly over 5 months.

Most other "direct" measurements of root respiration have been made under laboratory conditions. Two basic methods have been used. In the first, excised roots are collected from plants growing in pots or from the soil of a mature stand, and then CO_2 evolution is measured in the laboratory under controlled conditions. In the second method, CO_2 evolution is measured from intact soil cores collected in the field or the root systems of plants growing in pots in growth chambers, and the measured respiration is then compartmentalized into root (autotrophic) and soil

(heterotrophic) components by separately analyzing the respiration rates of the individual components (Coleman, 1973; Edwards and Sollins, 1973).

All of the laboratory methods mentioned above have considerable problems that may skew the respiration rates measured for roots or for intact soil cores. Excised roots are commonly used to measure respiration rates, but no study has been conducted to compare intact and excised roots in conifers, or to determine whether the root injury that occurs when soil cores are collected alters the respiration rate of the roots in the cores. As noted in Section III,A, there has long been concern that harvesting branches or stem sections could cause significant changes in their respiration rates. These problems are magnified in dealing with roots because the roots are not only wounded and separated from their parent tree, but also in most cases are removed from the dense, CO_2-rich soil environment and placed into a vastly different physical environment (Evans, 1972). Redmann and Abouguendia (1978) (in grasslands) and Medina *et al.* (1980) (in rainforests) both found that when small cores were brought back to the laboratory, there was an immediate increase in CO_2 evolution, although it is not clear how long this response persists. Moreover, Billings *et al.* (1977), found that in the Arctic graminoids *Carex aquatilis* and *Dupontia fischeri* the respiration rate was higher in excised roots as compared with intact roots, and the Q_{10} was also greater. However, Holthausen and Caldwell (1980) found little effect of excision in the desert shrub *Atriplex confertifolia*. Clearly considerably more study is needed before measurements from excised roots or intact soil cores can be confidently assumed to be equivalent to respiration of roots in their natural environment.

When respiration from intact soil cores of whole soils is compartmentalized into root and soil components, there are problems in separating respiration due to roots from the respiration of microbes that are in close association with roots. A significant portion of the respiration in the rhizosphere may also be from microbes utilizing the carbohydrates exuded into the rhizosphere (Wanner, 1970; Hendrickson and Robinson, 1984). Furthermore, the presence of mycorrhizal fungi on fine root tips will modify respiration rates, but by how much is not known. Data of Barnard and Jorgensen (1977) and Harley and Smith (1983) suggest that they will increase respiration rates. It is also not known whether different species of mycorrhizal fungi colonizing root tips will have different effects on root respiration. Any study that separates roots from the surrounding soil may introduce unknown biases by disrupting these rhizosphere relationships and mycorrhizal associations.

Many early studies attempted to compartmentalize soil respiration into root and heterotrophic components either by excluding living roots

from the sites in the field (using small minitrench plots) or by bringing soil cores back to the laboratory and comparing the respiration rates of the total core to the respiration of the components (Wiant, 1967; Schlesinger, 1977; Singh and Shekhar, 1986). Unfortunately, most studies using the small minitrench plot approach never quantified how much living root biomass and decaying root tissue was under the plot where vegetation was excluded. Many studies also used static chemical absorption systems to measure CO_2 evolution from the soil cores or plots; this method has been shown to underestimate CO_2 evolution rates, and so results from these studies must be regarded as questionable (Reiners, 1968).

Several recent studies have utilized new methods based on total carbon budgets (Ågren *et al.*, 1980; Ewel *et al.*, 1987). Ewel *et al.* (1987) subtracted CO_2 attributable to litter-layer roots and soil organic matter decomposition from total soil CO_2 evolution to obtain root respiration rates. Edwards and Harris (1977) used standing crops of litter, small and large roots, and their decay rates to partition C transfers. These carbon-budget-based approaches are useful for estimating maximum root respiration rates, but this approach is confounded by the usual problems of estimating ecosystem components by subtraction (Kaufmann and Landsberg, 1991); errors in estimating the other C components of an ecosystem accumulate and can result in an error in estimating root respiration that vastly exceeds the proportional error of the other components.

B. Rates

Published (and some unpublished) estimates of conifer root respiration are summarized in Table IV, along with the diameter sizes measured and the methods used. Those studies reporting only the percentage of total soil respiration attributed to roots (i.e., without reporting actual rates) were not included in Table IV, but can be found in Singh and Gupta (1977). Unfortunately, it is difficult to draw any significant conclusions by comparing values from different studies because (1) there are few data on how the different methods used to obtain these estimates affect the values observed, (2) only a few species have been analyzed, and (3) basic information on patterns of variation in root respiration have not been established (see Section IV,C).

C. Variation within the Rooting Zone

Root respiration may vary with temperature, soil moisture, season, root diameter, presence of mycorrhizal fungi on root tips, and possibly tree age and distance from the parent tree. The broad outlines of some of these patterns of variation are known, but few quantitative data are available.

As noted in Section I,B, temperature is well known to have an important effect on respiration in all tissues. However, studies in rainforest trees and in grasslands have shown that day and night respiration rates may not vary in a consistent direction (Medina *et al.*, 1980; Grahammer *et al.*, 1991). If soil cores are being used, then soil moisture variation must also be accounted for, because soil water content also influences the rate of soil respiration (Grahammer *et al.*, 1991). It has been suggested that under water stress conditions the fraction of soluble carbohydrates allocated to root growth increases as roots become a greater sink for carbohydrates compared to shoots, resulting in higher root respiration rates (Grahammer *et al.*, 1991). In addition, root respiration is apparently directly dependent on current photosynthate, which suggests that anything affecting shoot photosynthesis activity will feed back on root respiration levels. For example, Szaniawski and Adams (1974) found that root respiration rates were highest for *Tsuga canadensis* seedlings when the shoots were photosynthesizing, suggesting a dependence on current photosynthesis.

The few studies that have examined changes in fine root respiration rates by diameter show definite increases in respiration with decreasing diameters. For example, in *A. amabilis* (see Table IV), roots <2 mm in diameter consistently had higher respiration rates compared to larger roots. Few other data exist comparing roots of different sizes in conifers, but Cox (1975) found that smaller diameter excised roots from yellow poplar seedlings had higher respiration rates than did larger diameter roots (see Table IV) when measured at 20°C using a differential respirometer. Using similar methods, Chapman (1979) found that root respiration increased significantly with decreasing diameter of roots from coarse (5–7 mm) to very fine (<0.5 mm) in lowland *Calluna* heathland. Chapman (1979) recorded the highest respiration rates in roots <1 mm in diameter.

The stage of plant development may also affect the respiration rates of root tissues. Root respiration has been determined mainly on seedlings, but as stands mature, the carbon allocation patterns will change and should be reflected in the respiratory demands of tissues (Sprugel and Benecke, 1991). D. Hollinger (unpublished, 1991) found that in both *P. radiata* and *P. menziesii*, root respiration rates of seedlings were consistently higher than respiration rates for mature trees of the same species (Table IV). This suggests that great caution must be used in extrapolating from seedling measurements to mature stands to estimate fine root respiration (D. Hollinger, unpublished, 1991).

It is not clear if root respiration rates might change with increasing distance from a tree bole. Boyer *et al.* (1971) measured no differences in fine root respiration rates of root tips compared to root segments located

several centimeters from the tips. In an *A. amabilis* stand (Table IV) in Washington, roots of similar diameters (~5 mm) at different distances from the bole did not have different respiration rates. Thus current evidence seems to suggest that distance from tree bole is not an important factor to consider, but further studies are needed.

D. Stand-Level Conversions

Converting fine root respiration data to a stand level is more difficult than for many other types of tissues because fine root biomass data are scarce for forest ecosystems (Vogt, 1991) and would have to be specifically collected on the site being studied. Moreover, so little is known quantitatively about the sources of variation in fine root respiration that it is not even obvious what kinds of data should be collected in many cases. For example, fine root biomass data have been collected using a great variety of root diameter size classes, depending on the question being asked (Vogt and Persson, 1991). For scaling purposes, fine roots should probably be separated into functional diameter classes that reflect their respiration rates. It may be necessary to collect fine root biomass data in at least three different diameter classes (e.g., <2, 2–5, and 5–10 mm) and measure respiration rates specifically by these diameter class groupings. This type of sorting is very time consuming, but it may be essential if we are to have accurate estimates of root respiration at a stand level. Even with careful sorting, though, it is often difficult to tell the difference between roots that are senescing and those that are not, especially when mycorrhizal fungi are present (Vogt and Bloomfield, 1991). Thus at the present time, both a lack of information on factors affecting root respiration and great difficulties in collecting appropriate stand-level data on root characteristics present critical barriers to scaling respiration measurements realistically from the sample level to the stand.

V. Proxy Methods for Estimating Respiration without Tissue-Specific Measurements

We study autotrophic respiration (R_a), among other reasons, because (1) carbon used for respiration may vary with the environment, type of vegetation, and successional stage; (2) the balance between photosynthesis and autotrophic respiration determines dry matter production; and (3) fluxes from respiration are important in determining the global carbon budget. Instantaneous fluxes of CO_2 from plant respiration indicate current physiological status, but are difficult to obtain and are not generally useful for determining the role or importance of respiration in

ecosystem energetics. For this reason estimates of autotrophic respiration need to be placed in the context of the entire carbon budget, and examined over one to several years.

Fuller understanding of the role of autotrophic respiration in regulating ecosystem productivity will come only when we have assembled carbon budgets from many different ecosystems and different successional stages. Toward this goal, for estimating respiration we outline methods that can be applied without detailed physiological measurements. In this section, we describe methods for estimating instantaneous fluxes and annual budgets of CO_2 from respiration for whole ecosystems. First, we examine some of the disadvantages of the use of tissue-specific rates, and present evidence that element concentrations (primarily N and C) of tissues can provide estimates of respiration. Next, we discuss a method for estimating belowground autotrophic respiration, and its limitations. Finally, we discuss eddy correlation as a technique useful for estimating CO_2 fluxes, and derive equations for estimating instantaneous respiration for forests. The methods described may be useful where tissue-specific rates or annual budgets are lacking, and also serve as an independent estimate where detailed measurements have been made.

A. Estimating R_m from Tissue N Content

Several physiologically based models of forest production use the functional model of R_a outlined in Section I and tissue-specific rates to estimate R_a for forest ecosystems [for example, Forest-BGC (Running and Coughlin, 1988; Running and Gower, 1991), HYBRID (Friend, 1991; Friend *et al.*, 1993), BIOMASS (McMurtrie *et al.*, 1990; McMurtrie, 1991, and GEM (Rastetter *et al.*, 1991)]. Typically, these models estimate net canopy photosynthesis in the light (equivalent to a cuvette measurement), sum photosynthesis for a period, subtract maintenance respiration, and determine dry matter production from the remainder. However, the use of tissue-specific rates to estimate respiration may lead to uncertain estimates because of the high variability in respiration rates per unit biomass or surface area (see previous discussions). Also, using tissue-specific respiration rates precludes feedback with other ecosystem processes. Maintenance respiration and tissue nitrogen content are strongly correlated within a species [see, for example, Jones *et al.* (1978) and Irving and Silsbury (1987) for crop plants, and Kawahara *et al.* (1976) for conifers]. This relationship exists because most of the organic nitrogen in plants is in protein and roughly 60% of maintenance respiration supports protein repair and replacement (Penning de Vries, 1975b). Ryan (1991a) recently derived a relationship between maintenance respiration and tissue N content using a variety of crop, shrub,

and tree species:

$$R_m = 2.95 \cdot 10^{-6} N, \quad (3)$$

where R_m (moles C/sec at 20°C) is maintenance respiration and N is Kjeldahl N content of plant tissue (moles). The relationship is linear over the range of tissue nitrogen contents normally encountered (about 0.04–6% of dry weight). In conifers, Kawahara *et al.* (1976) showed that tissue N content could account for much of the variability in respiration rates among tissues in a *P. densiflora* forest. This relationship estimated annual maintenance respiration costs for a *P. elliottii* stand within 10% of the value reported in Cropper and Gholz (1991) that was estimated from detailed chamber measurements.

To the extent that tissue N is correlated with respiration, using N to estimate maintenance respiration offers several advantages over the use of tissue-specific rates. First, photosynthesis has been strongly linked with foliar N content (Field and Mooney, 1986; Evans, 1989, 1993a,b), and the use of N to estimate respiration would provide a strong link between the two processes. However, this relationship is strongest in fast-growing and somewhat weaker in slow-growing evergreen sclerophylls. Second, a close relationship between N and respiration would make it easier to predict how respiration could respond to the nutrient status of ecosystems, changing as climate, atmospheric deposition of N, or succession changed tissue nutrient contents. Third, N content, photosynthetic capacity, and respiration decrease from the top to the bottom of the canopy (Brooks *et al.*, 1991), and N might be a more conservative estimator of canopy processes than an average canopy rate. Finally, modeling respiration in different ecosystems might be simpler, because in many cases tissue N contents are simpler to measure than respiration rates.

Although the relationship between respiration and nitrogen has been shown to exist in *P. densiflora* (Kawahara *et al.*, 1976), we lack evidence for this relationship for other conifers. In crop plants, R_m per unit of plant nitrogen varies with growth rate (McCree, 1982; McCree and Amthor, 1982), species (McCree, 1983), and tissue type (Szaniawski and Kielkiewicz, 1982), perhaps because protein content and protein turnover are not strictly related. However, variability in maintenance rates per unit tissue nitrogen is small when compared to the range of respiration rates expressed on a dry weight basis. M. G. Ryan and R. M. Hubbard, (unpublished, 1993) found a positive correlation between dark respiration rates and foliar N content in *P. ponderosa*, *P. radiata*, *P. resinosa*, and *Tsuga heterophylla*.

As noted in Section II, in a N-rich environment such as a fertilized forest, N in plant tissues may be present as amino acids rather than protein (van Dijk and Roelofs, 1988). Because the relationship between fo-

liar N and maintenance respiration depends on the N being in protein, if N is in amino acids or storage proteins, tissue N will likely not be a good predictor of maintenance respiration. Similar problems have been noted for the relationship between photosynthesis and foliar N content (e.g., Reich and Schoettle, 1988).

B. Estimating R_c from Elemental Composition

Synthesis of organic compounds requires both carbon skeletons and energy, and the total carbon cost of synthesis is the sum of these two components. Construction respiration (R_c) is the energetic cost of biosynthesis. The value of R_c varies among molecules because of their complexity, the energy contained within chemical bonds, and the energy used in synthesis. For example, construction of 1 g of lignin requires 2.5 g glucose (R_c = 0.49 g C respired/g C in product), whereas 1 g of cellulose requires only 1.2 g glucose (R_c = 0.07 g C/g C) (Williams *et al.*, 1987).

Penning de Vries *et al.* (1974) pioneered the use of anabolic biochemical pathways to obtain quantitative estimates of R_c. Because this approach requires very detailed knowledge of the molecular composition of plant tissue, it is impractical for most models or growth studies. However, other researchers developed practical empirical relationships for estimating R_c (McDermitt and Loomis, 1981; Vertregt and Penning de Vries, 1987; Williams *et al.*, 1987) that correlate well with values derived from pathway analysis. These methods assume a value for conversion efficiency of about 0.88 g glucose into structure/g glucose substrate, and use elemental analysis (McDermitt and Loomis, 1981), heat of combustion and ash and organic nitrogen (Williams *et al.*, 1987), or carbon content and ash content (Vertregt and Penning de Vries, 1987) to estimate R_c.

For the fruits of various crop plants with a wide variety of chemical compositions, Vertregt and Penning de Vries (1987) found that R_c (g C/kg dry matter synthesized) was

$$R_c = (12/44)[4.24C_{dm} + 1.17\ \text{Ash} - 1744], \tag{4}$$

where C_{dm} and Ash are the carbon and ash contents of tissue (dry matter) in grams/kilogram. For tissue with a C content equal to 50% of dry weight and 0.5% ash, Eq. (4) calculates R_c as 0.21 g C/g C in dry matter. For comparison, Chung and Barnes (1977) used biochemical pathway analysis to estimate R_c for slash pine as 0.26 g C/g C for needles and 0.15 g C/g C for stems.

The method of Williams *et al.* (1987) includes the energy to reduce nitrogen, which may be important if NO_3^- is the N source:

$$C' = \{(0.06968 \cdot \Delta H_c - 0.065)(1 - A) + (kN/14.0067)(180.15/24)\}(1/E_G), \tag{5}$$

where C' is construction cost in grams glucose/gram dry weight, ΔH_c is the ash-free heat of combustion in kilojoules/gram, A is the ash fraction, k is the oxidation state of nitrogenous substrate (-3 for ammonium, $+5$ for nitrate), N is the Kjeldahl organic nitrogen fraction, and E_G is the conversion efficiency (0.89). If dry matter (DM) is assumed to be 50% carbon, R_c (in g C/g C dry matter synthesized) is

$$R_c = [C'(72 \text{ g C}/180.15 \text{ g glucose})(2 \text{ g DM}/1 \text{ g C})] - 1. \quad (5a)$$

With this method, estimates of R_c ranged from 0.23 to 0.40 g C/g C for chaparral leaves (Williams *et al.*, 1987). If nitrate can be reduced inside leaves (Smirnoff *et al.*, 1984; Smirnoff and Stewart, 1985) from reductant generated directly in photosynthesis (Abrol *et al.*, 1983; Wallsgrove *et al.*, 1983), nitrogen would not affect R_c. However, gymnosperms show lower nitrate reductase activities in leaves than do other woody plants, and may reduce nitrate in roots using ATP or energy derived from respiration (Smirnoff and Stewart, 1985).

All of these methods, incidentally, assume that glucose is broken down through the cytochrome-mediated pathway; if the energy required by biosynthesis were derived from cyanide-resistant respiration, all estimates would have to be increased substantially.

To use the methods described above requires knowing dry matter production and chemical composition. For aboveground production in a study plot, this information can be obtained with routine sampling. For belowground production, or for estimating costs over large areas, obtaining the information is more problematic.

C. Estimating Belowground Respiration Costs

Belowground respiration costs are difficult to estimate, either directly or indirectly. To use tissue N to estimate R_m and fine root production to estimate R_c requires knowing fine root biomass and turnover—estimates of which are uncertain and difficult to obtain. Recently, Raich and Nadelhoffer (1989) described a method for indirectly estimating the total amount of carbon allocated belowground for root production and maintenance. This method can be adapted to estimate respiration costs, if the ratio of R_a to production is assumed constant.

Raich and Nadelhoffer (1989) found that total belowground allocation (estimated as the difference between soil CO_2 efflux and aboveground litter input) was strongly correlated with aboveground litter production over a range of litter production (L_f) of 70–500 g C/m^2/year. (However, the strength of the correlation was derived in part from the wide range of the data used; at any given point, and especially in the less productive sites, there was a severalfold range in the values of CO_2 efflux associated

with a given litterfall level.) Belowground allocation (B_{p+c+m}, g C/m^2/year) is given by

$$B_{p+c+m} = 130 + 1.92L_f. \quad (6)$$

If fine root production is known, R_c for roots can be estimated with Eq. (4) or (5), and R_m can be estimated by difference. If fine root biomass and N content are known, R_m can be estimated with Eq. (3), and production of fine roots and R_c can be estimated by difference. If neither production or biomass is known, R_a can be assumed to be 50% of B_{p+c+m} (Amthor, 1989). Examples of applying this method to conifer forests are given in Ryan (1991b).

D. Estimating Whole-Stand Respiration Fluxes Using Eddy Correlation

Extrapolating fluxes measured in small enclosures to ecosystems is difficult, particularly for forests. Conditions in chambers are different than those outside. Estimated fluxes vary among samples because of differences in tissue chemistry, metabolic activity, and sampling technique. Gradients of light, temperature, humidity, and wind speed exist within canopies; these gradients and their effect on fluxes can be modeled, but estimates are uncertain. To overcome some of these problems, direct measurement of CO_2 exchange between a forest and the atmosphere by eddy correlation can provide an independent, system-level estimate of fluxes (e.g., Valentini *et al.*, 1991).

Using micrometeorological theory, it is possible to measure the flux of CO_2 by averaging the product of fluctuations of horizontal wind, vertical wind, and atmospheric [CO_2]. In practice, the method requires placing fast-response sensors above the canopy in such a way that the sensors do not disturb airflow. Campbell (1977) and Baldocchi *et al.* (1988) provide a good introduction to the theory and practice. Sensors placed on towers integrate fluxes over tens to hundreds of meters, whereas aircraft-based sensors can measure flux over tens to hundreds of kilometers (Desjardins, 1992). Reliable fast-response sensors are available but costly, and the technique has not yet been widely applied (Desjardins, 1992).

The advantages of eddy correlation are that fluxes are integrated over a large area, total flux is measured, and vegetation is not disturbed by measurement. Eddy correlation thus provides the most direct estimate available of net ecosystem productivity (assimilation minus autotrophic and heterotrophic respiration). However, technical problems often limit applicability of eddy correlation (Baldocchi *et al.*, 1988). For

example, flux estimates are very dependent on measurement height, sensor response time, and averaging period and are currently limited to gently sloping, even terrain (Baldocchi *et al.*, 1988). Also, large variations in CO_2 over the averaging period yield unreliable flux estimates (Baldocchi *et al.*, 1988). Direct estimates of ecosystem respiration can therefore be problematic because large fluctuations in CO_2 concentration occur only at night. Finally, fluxes are measured with eddy correlation for hours or days or at most weeks or months, but annual budgets are needed to increase ecological understanding.

Despite limitations, eddy correlation can increase our understanding of ecosystem processes by providing realistic estimates of total flux (Valentini *et al.*, 1991). These estimates can be used to set bounds on predictions from current models, and perhaps to derive new empirical models. Additionally, diurnal and seasonal variations in CO_2 flux can be linked with variations in radiation, temperature, soil moisture, and humidity to "decompose" the flux trace and validate component models for photosynthesis and respiration.

E. Estimating Instantaneous Fluxes of CO_2 from R_a

Fluxes estimated with eddy correlation sum assimilation, autotrophic respiration, and heterotrophic respiration. To interpret these fluxes, models for estimating instantaneous fluxes for the separate components are required. Below, we outline theory for estimating instantaneous fluxes of CO_2 from R_a, using Eqs. (3)–(5).

Instantaneous CO_2 flux from R_a can be estimated as the sum of maintenance and construction respiration. Instantaneous R_m can be estimated from tissue nitrogen [Eq. (3)] and tissue temperature using the common exponential model of R_a response to temperature (Amthor 1989):

$$R_m = (7.4 \cdot 10^{-7})N \exp(\beta T), \tag{7}$$

where R_m is in units of moles C/second, N is moles of Kjeldahl nitrogen in living biomass, and β is 0.07 for R_a that doubles with a 10°C increase in temperature.

Instantaneous R_c can be estimated by assuming (1) current growth will be the same as in the previous growing season and (2) that growth will vary exponentially with temperature over the growing season. (This last assumption might be questionable, especially in areas where drought limits growth during a substantial part of the warm season.) For a growing season of n days, construction respiration is approximately αD, where D = annual dry matter production in grams of C and α is calcu-

lated from Eq. (4) or (5):

$$\alpha D = \sum^{n \text{ days}} R_0 \exp(\beta T) I_0(\beta A), \tag{8}$$

where T is average daily temperature in °C, A is daily temperature amplitude [(max − min)/2], $I_0(0.07A)$ corrects for amplitude effects on the integration of what is approximately exp(sin x) (Ågren and Axelsson, 1980), and R_0 is construction respiration at 0° C. Solving for R_0 and using a simple exponential model for temperature response, instantaneous R_c (for the growing season only) is

$$R_c = \{\alpha D / [86400 \cdot 12 \sum^{n \text{ days}} R_0 \exp(\beta T) I_0(\beta A)]\} \exp \beta T, \tag{9}$$

where R_c is in units of moles C/second. For a daily temperature amplitude of 5° C, $I_0(0.07A)$ is approximately 1.05. For a mature lodgepole pine forest, maintenance respiration summed for the entire year was about 70% of total CO_2 flux from R_a (Ryan and Waring, 1992).

The approach outlined estimates R_m from the standing crop of N, but requires knowledge of past growth to estimate R_c. However, if a model of canopy assimilation is validated for conifer ecosystems, R_c can be estimated from photosynthesis and R_m (e.g., Running and Coughlin, 1988; Bonan, 1991).

VI. Conclusions

The status of efforts to estimate respiration of conifers varies sharply from one tissue to another. There have been numerous measurements of foliage respiration in conifers, but relatively few measurements of within-stand variation in reference to parameters that might be used for scaling. However, a number of logical models for scaling have been proposed (e.g., light, age, or N) and general directions for future research seem well established. There are far fewer measurements of woody-tissue respiration that might be useful for scaling, but some consensus seems to have developed that the use of sapwood biomass and growth rates as indices may provide the key to scaling woody-tissue respiration up to the stand level. Root respiration is still bogged down by a plurality of methods, each of which seems to have some serious disadvantages, so that even the nature of within-stand variation is poorly known. Successful and believable scaling of root respiration from tissue-specific measurements to the stand level seems to be far in the future. Finally, proxy measurements such as litterfall and N concentration can and have been used to estimate respiration for whole stands without measuring tissue-

specific rates at all, but all of these techniques require assumptions that need further testing before they will be generally accepted.

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