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Dark respiration of pines

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Plant respiration is a large, environmentally sensitive component of the carbon balance for pine ecosystems and can consume >60% of the carbon fixed in photosynthesis. If climate, genetics, or carbon allocation affect the balance between assimilation and respiration, respiration will affect net production. Respiration rates for tissues within a tree vary with the number of living cells and their metabolic activity. For pines, foliage and fine roots have similar respiration rates, with rates for seedlings (60 – 420 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C) higher than those for mature trees (20 – 70 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C). Woody tissue respiration is low compared with other tissues (<10 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C, for dormant large stems; and 4–60 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C, for small stems, branches, twigs and coarse roots). Reported annual total respiration for the living parts of pine trees uses 32–64% of the annual total of net daytime carbon fixation. The ratio of annual respiration to photosynthesis increased linearly with stand biomass for young pine stands.

Simulations of respiration and assimilation for *Pinus elliottii* and *P. contorta* forests support the hypothesis that pines growing in warmer climates have lower leaf area index because temperature shifts the canopy compensation point. Simulations of these same stands with increased air temperature in situ suggest that pines growing in cool climates might offset increased foliar respiration and maintain assimilation by reducing leaf area. Future research on the role of respiration in forest productivity should concentrate on producing annual budgets at the stand level.

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Introduction

Photosynthesis supplies energy and reduced carbon compounds to a plant, but respiration converts the sugars and starches to energy and substrate for biosynthesis. Plants use energy from respiration to maintain the integrity of cells, transport sugars throughout the tree, acquire nutrients and build new tissue (Amthor 1989).

Respiration is an important component of the annual carbon balance of plants, because maintenance respiration may have a higher priority for fixed carbon than growth (Ryan 1991a). If so, carbon fixed in photosynthesis and used for maintenance respiration will not be available for growth. In forests, production of leaves, wood and roots uses only 30 to 50% of the carbon fixed in photosynthesis; respiration uses the remainder (Ryan 1991a). However, to know the absolute amount of respiration is less important than to know the balance between photosynthesis and respiration. Determining the importance of respiration to forest productivity is therefore a whole plant problem, rather than a tissue-level problem.

Our knowledge of respiration is limited, particularly for trees and forests in the field (Jarvis and Leverenz 1983, Hagihara and Hozumi 1991, Ryan 1991a, Sprugel and Benecke 1991). In spite of our lack of knowledge about respiration, there is much support for the idea that respiration to a large extent controls productivity or structure in forest ecosystems (Waring and Schlesinger 1985, Landsberg 1986). Respiration may contribute to the low productivity commonly observed in old-growth forests (Yoda et al. 1965, Whittaker and Woodwell 1968), because old forests have more woody biomass and this biomass may require more respiration. Respiration or the ratio of respiration to assimilation may determine differences in the amount of woody or leaf biomass among systems. Also, if global warming occurs, higher respiration costs may cause lower productivity in forests (McGuire et al. 1992, Melillo et al. 1993), but the effect of temperature may be offset by depression of respiration with higher atmospheric carbon dioxide concentrations ($[CO_2]$) (Amthor 1991). These hypotheses have rarely been examined rigorously, yet form the basis for most of our mechanistic models.

In this paper, we will review the literature on dark respiration of pines, summarize respiration rates and annual budgets for whole-stands and use simple models to examine the interaction between climate, respiration and production. First, we will outline conceptual models for understanding respiration of whole plants. Second, we will summarize the literature on respiration rates of pines and discuss possible limitations of these data. Finally, we will use simple models to determine the conditions where a change in the balance between photosynthesis and respiration might affect forest productivity or structure.

The functional model of plant respiration

Forest ecologists and ecophysiologists generally focus on the function of respiration and its importance in the annual carbon budget, not the biochemistry. However, we need a few definitions to avoid misunderstanding. The processes of glycolysis and the oxidative pentose phosphate pathway, the Krebs cycle and electron transport to oxidative phosphorylation are called dark respiration, or in this paper, simply respiration. Photorespiration is the oxidation of ribulose biphosphate catalyzed by ribulose biphosphate carboxylase in the presence of oxygen. Photorespiration alters the amount of net photosynthesis in light and will not be treated here. Cyanide-resistant respiration is an alternate pathway for electron transport which generates only 1 ATP per NADH oxidized, rather than 3 for cytochrome-mediated electron transport (Laties 1982). Cyanide-resistant respiration affects the energy released from respiration, not the CO_2–O_2 balance. To our knowledge, no one has assessed the importance of cyanide-resistant respiration of pines.

The functional model of plant respiration (McCree 1970, Amthor 1989) has been useful for assessing the effect of respiration on the carbon economy of a tree or forest, particularly when the carbon is balanced over a year (Ryan 1991a). The functional model partitions respiration into that used for construction of new tissue and that used for maintenance of existing cells. Sometimes a third component, respiration for nutrient uptake, is also recognized. This model recognizes that even though respiration comes from the same biochemical pathways, the energy is used for different purposes. The model has proved useful for understanding respiration because the carbon cost of constructing a given tissue varies with its chemical makeup, while the energy used for maintenance varies with temperature and perhaps other environmental factors (Amthor 1989).

In equation form, the functional model is:

$$R = \left(\frac{1-Y_G}{Y_G}\right)\frac{dw}{dt} + mW \qquad (1)$$

where R = integrated daily total of respiration (g C d^{-1}), Y_G = biosynthetic efficiency (the ratio of carbon incorporated into structure to carbon used for structure plus energy used for synthesis (g C g C^{-1})), dW/dt = absolute growth rate (g C d^{-1}), W = biomass (g C) and m = the maintenance coefficient (g C (g C biomass)$^{-1}$ d^{-1}). Maintenance respiration represents the costs of protein synthesis and replacement, membrane repair and the maintenance of ion gradients (Penning de Vries 1975), while construction respiration is the cost for new tissue synthesis from glucose and minerals. Construction respiration can be easily estimated from elemental analysis (McDermitt and Loomis 1981); heat of combustion, ash and organic nitrogen (Williams et al. 1987); or carbon content and ash content (Vertregt and Penning de Vries 1987).

The functional model of plant respiration has been applied to understand pollutant effects (Amthor and Cumming 1988), differences in respiration costs between young and old forests (Ryan 1990) and the response of respiration to atmospheric $[CO_2]$ (Reuveni and Gale 1985, Amthor 1991, Amthor et al. 1992, Wullschleger and Norby 1992). Many physiologically-based models of forest production use the functional model, subtracting maintenance respiration from fixed carbon before calculating growth (Running and Coughlin 1988, Friend et al. 1993, McMurtrie 1991). This approach assumes that maintenance respiration has a higher priority for fixed carbon than does growth. Despite the advantages of the functional model, it has not been widely used for understanding respiration in forest ecosystems.

Respiration increases with temperature, because temperature increases the rate of the enzymatic reactions in respiration. Environmental physiologists use a simple exponential model of response to temperature, instead of using the more formal Arrhenius model, because the two agree closely between 0 and 50°C. Respiration rates are often expressed in terms of Q_{10} – the change in rate with a 10°C change in temperature:

$$R = R_0(Q_{10}^{T/10}) \qquad (2)$$

where R_0 is respiration at 0°C. For a wide variety of plant materials, Q_{10} ranges from 1.6–3 but centers about 2 (Amthor 1984).

Respiration rates for pines

The respiration rate for a given tissue reflects the metabolic activity occurring in that tissue at that point in time. Because so many factors affect metabolic activity, interpretation of respiration rates is difficult unless these

Table 1. Respiration rates (R_d) for foliage, fine roots, and woody tissue of various pine species. To convert reported rates to standard rates, we assumed dry matter contained 50% carbon, specific leaf area was 20 m^2 $(kg\ C)^{-1}$ (all-sided), and density of woody material was 0.4 g cm^{-3}. Where O_2 consumption was reported we assumed a respiratory quotient of 1. Standard rates were adjusted to 15°C assuming respiration increases exponentially with temperature; we used Q_{10} given, or assumed 2 if no temperature response was reported.

Species	Tissue	R_d reported	Tissue temperature (°C)	Q_{10}	Season	Rd @ 15°C (nmol C $(mol\ C)^{-1}$ s^{-1})	Notes	Citation
Pinus elliottii	Foliage	0.27 mg CO_2 g^{-1} h^{-1}	20	2.09	All	28	Average canopy, fully expanded foliage	Cropper and Gholz 1991
P. elliottii	Foliage	0.48 mg CO_2 g^{-1} h^{-1}	25		Fall	35	Upper canopy, fully expanded foliage	Cropper and Gholz 1991
P. elliottii	Foliage	0.28 mg CO_2 g^{-1} h^{-1}	25		Fall	20	Lower canopy, fully expanded foliage	Cropper and Gholz 1991
P. contorta	Foliage	0.26 g C g^{-1} yr^{-1}	8	1.9	Yearly average	52	Canopy average, montane stand, calculated from annual total	Benecke and Nordmeyer 1982
P. contorta	Foliage	0.28 g C g^{-1} yr^{-1}	5		Yearly integration	71	Canopy average, subalpine stand, calculated from annual total	Benecke and Nordmeyer 1982
P. radiata	Foliage	3.0 mol m^{-2} yr^{-1}	11	2.26	Yearly average	64	Average of current and 1-yr-old sun foliage	Benecke 1985
P. radiata	Foliage	1.1 mol m^{-2} yr^{-1}	11	2.26	Yearly average	23	Average of current and 1-yr-old shade foliage	Benecke 1985
P. pumila	Foliage	0.4 μmol m^{-2} s^{-1}	10	2.2	July	59	1 yr old	Kajimoto 1990
P. sylvestris	Foliage	0.3 mg CO_2 kg^{-1} s^{-1}	23		Summer	94	From 2-yr-old seedlings	Lorenc-Plucinska 1988
P. taeda	Foliage	0.93 mg CO_2 g^{-1} h^{-1}	20		November	100	Whole shoot of 1st season seedling	Drew and Ledig 1981
P. rigida	Foliage	1.15 mg CO_2 g^{-1} h^{-1}	29		Growth chamber	66	Shoot of 185-d-old seedling	Ledig et al. 1976
P. resinosa	Foliage	2.5 mg CO_2 g^{-1} h^{-1}	19		Summer	287	Current+1 foliage from 4-yr-old seedlings, 10 wks after budbreak	Gordon and Larson 1968
P. contorta	Female cones	2.5 nmol g^{-1} s^{-1}	15		Autumn	60	Average of late autumn values, 19–24 wks after pollination	Dick et al. 1990
P. contorta	Female cones	6.0 nmol g^{-1} s^{-1}	15		Mid-summer	144	Average of mid-summer values, 48–57 wks after pollination	Dick et al. 1990
P. contorta	Male cone-bearing buds	8.0 nmol g^{-1} s^{-1}	15		Early spring	192	Values ranged from 9.9 nmol g^{-1} s^{-1} (spring) to 6.3 nmol g^{-1} s^{-1} (summer)	Dick et al. 1990
P. sylvestris	Female cones	0.9 mg CO_2 g^{-1} h^{-1}	15	2.0	Spring	136	Average of March, April and May, 1-yr-old cones	Linder and Troeng 1981a
P. sylvestris	Female cones	1.7 mg CO_2 g^{-1} h^{-1}	15	2.0	Mid-summer	258	Average of June and July, 1-yr-old cones	Linder and Troeng 1981a
P. contorta	Twig	1.3 μmol m^{-2} s^{-1}	15	linear	Late summer	62	0.5 cm diameter, calculated from regression given in their Fig. 7	Benecke and Nordmeyer 1982
P. contorta	Branch	4.3 μmol m^{-2} s^{-1}	15	linear	Late summer	37	2.8 cm diameter, calculated from regression given in their Fig. 7	Benecke and Nordmeyer 1982

cont.

Table 1. Cont'd.

Species	Tissue	R_d reported	Tissue temperature (°C)	Q_{10}	Season	Rd @ 15°C (nmol C (mol C)$^{-1}$ s^{-1})	Notes	Citation
P. contorta	Stem	6.6×10^{-5} kg C (kg C sapwood)$^{-1}$ d^{-1}	15	2.04	Fall	0.8	40- to 250-yr-old trees, 12–36 cm dbh, dormant	Ryan 1990
P. radiata	Stem	54.9 mol m^{-2} yr^{-1}	11		Yearly average for stem	2.2	25.5 cm diameter	Benecke 1985
P. taeda	Stem	50 mg CO_2 m^{-2} h^{-1}	10	2.9	Winter	0.8	17 cm diameter	Kinerson 1975
P. contorta	Stem	6.5 μmol m^{-2} s^{-1}	15	linear	Late summer	19	8.4 cm diameter, calculated from regression given in their Fig. 7	Benecke and Nordmeyer 1982
P. sylvestris	Stem	1.5 mg CO_2 dm^{-2} h^{-1}	10	2.0	July	5.6	5.7 cm diameter, growing	Linder and Troeng 1981b
P. sylvestris	Stem	0.5 mg CO_2 dm^{-2} h^{-1}	10	2.1	October	1.9	5.7 cm diameter, dormant	Linder and Troeng 1981b
P. densiflora	Stem	6 mg CO_2 dm^{-2} h^{-1}	23		July	8.4	6.2 cm diameter, growing	Negisi 1975
P. densiflora	Stem	6 mg CO_2 dm^{-2} h^{-1}	20		October	10	6.2 cm diameter, dormant	Negisi 1975
P. densiflora	Stem	5 mg CO_2 kg^{-1} h^{-1}	20		March	0.5	10 cm diameter, growing	Yoda et al. 1965
P. cembra	Stem	10 mg CO_2 dm^{-2} h^{-1}	10	2.2	July	8.3	27 cm diameter, growing	Havranek 1981
P. cembra	Stem	4 mg CO_2 dm^{-2} h^{-1}	10	1.8	October	3.0	27 cm diameter, dormant	Havranek 1981
P. sylvestris	Stem	1.5 mg CO_2 dm^{-2} h^{-1}	10		Fall	1.8	18 cm diameter, dormant	Zabuga and Zabuga 1985
P. radiata	Coarse root	40.3 mol m^{-2} yr^{-1}	11	2.3	Yearly average for large root	4.2	10.2 cm diameter	Benecke 1985
P. radiata	Coarse root	31.0 mol m^{-2} yr^{-1}	11	2.3	Yearly average for large root	6.6	5.0 cm diameter	Benecke 1985
P. radiata	Coarse root	25.6 mol m^{-2} yr^{-1}	11	2.3	Yearly average for large root	11	2.6 cm diameter	Benecke 1985
P. sylvestris	Coarse root	1.6 mg CO_2 dm^{-2} h^{-1}	10		July	20	1.7 cm diameter	Linder and Troeng 1981b
P. sylvestris	Coarse root	2.3 mg CO_2 dm^{-2} h^{-1}	10		October	29	1.7 cm diameter	Linder and Troeng 1981b
P. elliottii	Fine roots	0.39 mg CO_2 g^{-1} h^{-1}	20	1.94	Spring and summer	42	From mature stand	Cropper and Gholz 1991
P. taeda	Fine roots	82–829 μl O_2 g-1 h^{-1}	15			23-240	Range for fine roots, excluding root tips	Barnard and Jorgensen 1977
P. taeda	Fine roots	11.0 μg O_2 g^{-1} m^{-1}	17	1.6	Late winter	120	Field-grown seedlings	Boyer et al. 1971
P. echinata	Fine roots	35.8 μl O_2 10 mg^{-1} h^{-1}	27		August	420	Entire system of 45-d-old seedling	Allen 1969
P. rigida	Fine roots	2.0 mg CO_2 g^{-1} h^{-1}	29		Growth chamber	110	180-d-old seedlings	Ledig et al. 1976
P. sylvestris	Fine roots	4.2 mg CO_2 g^{-1} h^{-1}	23		Growth chamber	370	6–12-wk-old seedlings	Szaniawski 1981
P. taeda	Fine roots	2.4 mg CO_2 g^{-1} h^{-1}	20	1.3	December	330	Whole excised root system of <1-yr-old seedlings	Drew and Ledig 1981

factors are known. For example, metabolic activity varies with the environment (because chemical reaction rates increase with temperature), protein content of the tissue (because proteins mediate most chemical reactions and replacing proteins has a high metabolic cost) and phenological status of the tissue (growing tissue respires more). To evaluate the impact of respiration rates on productivity, a carbon budget for at least an entire year must be constructed. The fact that cone production and shoot development require more than a year argues for constructing budgets for several years.

Respiration rates are usually assessed by measuring CO_2 efflux from plant tissue, although O_2 consumption is also used. Measuring CO_2 efflux has the advantage that the budget can be balanced for carbon and photosynthetic rates are almost always measured with CO_2 exchange. Unfortunately, neither CO_2 efflux nor O_2 uptake directly indicates the energy released from respiration and the energy released per unit CO_2 produced varies among sugars, fats and proteins (Penning de Vries et al. 1974) and with the pathway for electron transport (Laties 1982). New methods for measuring respiration in the laboratory can identify CO_2 release, O_2 consumption and energy released allowing an assessment of the efficiency of respiration (Criddle et al. 1990, 1991).

Carbon dioxide efflux is generally measured with portable infrared gas analyzers on small portions of enclosed tissue (Field et al. 1991, Sprugel and Benecke 1991). Both open and closed systems are used and each system has strengths and limitations (Field et al. 1991). Instantaneous respiration rates are generally 5–10% of rates of photosynthesis at the same temperature, so more tissue is generally required to measure rates accurately. In addition, low flows (open systems), or lower chamber volumes and longer response times (closed systems) are also often necessary. Because respiration varies strongly with temperature, the chamber must control temperature or the temperature response must be accurately determined. Respiration rates are generally measured with the tissue shaded to halt photosynthesis. Shading may affect respiration rates for stem and branch respiration, because photosynthesis under the periderm can refix respired CO_2 (Linder and Troeng 1981a, Sprugel and Benecke 1991). Dark respiration rates for foliage estimated by shading foliage in the daytime will likely overestimate night respiration rates at the same temperature (M. G. Ryan and R. Hubbard, unpubl. data).

Rates measured on small tissue samples are difficult to extrapolate to the tree or stand, because respiration rates vary strongly within the canopy (Benecke 1985, Brooks et al. 1991, Cropper and Gholz 1991), among types of woody tissue (Linder and Troeng 1981a, Benecke 1985, Ryan 1990) and from sample to sample of fine roots (Barnard and Jorgensen 1977, Cropper and Gholz 1991). If models correctly account for the variation, then extrapolation becomes more robust. For example, sapwood volume can be used to predict maintenance respiration for woody tissue (Havranek 1981, Ryan 1990, Sprugel 1990). Additionally, tissue N content, because of its close relationship with protein content, may predict maintenance respiration for all tissues (Ryan 1991a). For example, Kawahara et al. (1976) found a strong relationship between dark respiration and nitrogen content in foliage and branches of *Pinus densiflora*. Other techniques offer promise for estimating respiration at a larger scale, but they have not been applied to pine ecosystems. For example, Paembonan et al. (1991) have measured respiration for the entire aboveground parts of a young cedar for 2 years by enclosing a tree in an open-top chamber. CO_2 exchange can also be measured for large areas by the eddy-correlation method (Desjardins 1992, Wofsy et al. 1993), but the method does not separate autotrophic and heterotrophic respiration and the time-scale is frequently small (hours to days).

Respiration rates have been measured for various tissues for a number of pine species (Table 1). Comparing these rates is difficult because growth and maintenance respiration are rarely separated, rates were taken at different temperatures and no common basis for the expression of respiration rates exists. We selected rates for comparison that also reported temperature and favored those studies where respiration was measured in the field. Our list is not exhaustive, but represents the range of rates reported in the literature (see Linder 1979, 1981 for other references and conifers other than pine). To compare rates expressed on a different basis or taken at a different temperature, we estimated respiration at 15°C in nmol C (mol C substrate)$^{-1}$ s^{-1}, using the assumptions listed in Table 1. Respiration measured while tissue is dormant estimates maintenance respiration, while respiration measured when tissue is growing combines growth and maintenance respiration.

Foliage

Respiration rates reported in the literature for foliage range from 20 to 290 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C (Table 1). Rates tend to be higher for seedlings and lower for mature trees in the field. Also, foliage from the lower canopy (shade leaves) respires less than sun leaves from the upper canopy and growing foliage respires more than fully-expanded foliage. Foliage respiration increases exponentially with temperature, with a Q_{10} of 1.9 to 2.3. However, Kajimoto (1990) found a much higher Q_{10} response (2.3 to 3.3) in the fall than in mid-summer (2.2).

Few studies report seasonal patterns of respiration, corrected to constant temperature. Gordon and Larson (1968) report high respiration in seedlings 2 to 3 weeks after bud-break, with rates declining to the end of the study at week 10. Drew and Ledig (1981) found higher total respiration in summer than for the dormant season, to be expected from higher temperatures in summer. No seasonal differences in respiration rates for fully expanded foliage were found in *P. elliottii* (Cropper and Gholz 1991) or *P. radiata* (Benecke 1985).

Plant respiration generally increases in response to ozone, sulphur dioxide, or fluoride exposure, but inhibition can also occur (Darrall 1989). Lack of a consistent response may stem from differences in pre-treatment growing conditions (Darrall 1989) or a failure to separate components of respiration (Amthor and Cumming 1988). Costs to repair damaged tissue or the increased use of the cyanide-resistant pathway may increase maintenance costs, while reduced photosynthesis and growth will decrease total respiration (Amthor and Cumming 1988). In pines, photochemical smog (mostly ozone) had no effect on dark respiration of pine seedlings (Bytnerowicz et al. 1989), but NO_2 increased dark respiration in some varieties of *P. sylvestris* seedlings (Lorenc-Plucinska 1988). Atmospheric [CO_2] can strongly affect (and generally depress) dark respiration (Amthor 1991), but this has not been studied in pines.

Cones

Respiration rates for female and male cones can exceed those of foliage (Table 1). Respiration rates are greater in mid-summer, when the cones greatly increase in weight (Linder and Troeng 1981b, Dick et al. 1990). Photosynthetic activity in the cones mitigates the high rates of dark respiration; for *P. sylvestris*, Linder and Troeng (1981b) found that refixation lowered respiratory use of carbon by 31%. Similarly, in *P. contorta*, Dick et al. (1990) observed a 25% decrease in respiration attributed to refixation.

Cone respiration was estimated to be less than 3% of daily photosynthesis in *P. contorta* (Dick et al. 1990). However, stemwood production was negatively correlated with cone production in *P. monticola* (Eis et al. 1965), so the total carbon used for cones may be important. The carbon cost of cone production together with cone respiration has been calculated by Linder and Troeng (1981b) as 10 to 15% of annual wood production for an old *P. sylvestris* stand.

Woody tissue

Although rates for woody tissue are low compared with those for foliage and fine roots (Table 1), forests contain much woody tissue and the aggregate cost can be high. Rates for twigs, small branches and coarse roots are much greater than rates for larger stems (Table 1), probably because the smaller organs contain a higher fraction of living tissue. Respiration correlates with growth rate in the summer (Havranek 1981, Linder and Troeng 1981a, Zabuga and Zabuga 1985, Ryan 1990, Sprugel 1990) and with sapwood volume in the dormant seasons (Havranek 1981, Ryan 1990, Sprugel 1990). Sapwood contains the majority of living cells associated with woody tissue and the respiring biomass necessary for estimating maintenance respiration can be estimated from sapwood volume (Ryan 1990). Respiration rates measured after growth ceases in the fall estimate maintenance respiration (Ryan 1990). However, since there is some evidence that maintenance rates evaluated at a common temperature are higher in the summer than in the fall (Linder and Troeng 1981a), the use of fall measurements may underestimate total maintenance costs. Total CO_2 efflux from woody tissue increases in the summer, because higher temperatures increase maintenance costs and because cell growth is occurring.

The response of respiration to temperature needs to be resolved before effects of climate change on plant respiration can be accurately predicted. Respiration increases exponentially with temperature and reported Q_{10} values are generally near 2 (Table 1), but some striking exceptions have been reported. For example, both Kinerson (1975) and Ryan (1990) reported some Q_{10}'s approaching 3. Additionally, both Linder and Troeng (1981a) and Benecke and Nordmeyer (1982) report that the daily total CO_2 efflux from stems increases linearly with temperature. High Q_{10} values might occur where the temperature response is calculated from respiration measured over a season, because growth and hence growth respiration is greater at high temperatures.

The rate of flow of sap through wood can also strongly affect CO_2 efflux (Negisi 1975). For example, Negisi (1978) reported that bark respiration was about 25% lower in the day than estimated from a simple temperature model. Apparently, diffusion of CO_2 is low and xylem sap can move CO_2 from wood toward foliage. Atmospheric [CO_2] had no effect on woody tissue maintenance respiration (Wullschleger et al. 1994), even though the [CO2] in stems can be quite high (Hari et al. 1991).

Photosynthesis under bark can refix respired CO_2 and hence lower net respiration rates for stems and branches in light (Linder and Troeng 1980, Benecke 1985, Sprugel and Benecke 1991). Because the periderm blocks light to the photosynthetic machinery, photosynthetic rates are greatest in young branches. Consequently, the effect of bark photosynthesis on net CO_2 efflux from stems declines with stem size and age (Linder and Troeng 1980). For example, refixation in full light lowered net respiration rate by 40% for a 3-yr-old stem section of *P. sylvestris*, but by only 10% for a 12-yr-old stem section (Linder and Troeng 1980).

Fine roots

Respiration rates for fine roots in *Pinus* species range from 23 to 420 nmol C (mol C biomass)$^{-1}$ s^{-1} at 15°C (Table 1). Like foliage, rates for fine roots tend to be higher for seedlings than for large trees in the field. Root systems of older trees probably have fewer live cells per unit mass than seedlings and are probably also less active. Respiration rates for fine roots may be less sensitive to

Table 2. Annual budgets and whole-stand estimates of plant respiration and assimilation in young pine stands. Assimilation (A) is defined as the annual sum of net daylight canopy C fixation; autotrophic respiration (R_a) is the annual sum of respiration for stems, roots and foliage (night only for foliage). Values are given per m² of ground surface area.

Species	Mean annual air temperature (°C)	Above-ground biomass (g C m^{-2})	Stand age (yr)	Respiration (g C m^{-2} yr^{-1})				A (g C m^{-2} yr^{-1})	R_a/A	Source
				Stem + branch	Root	Foliage	Total (R_a)			
P. sylvestris, control	3.6	1384	20	51	99	60	210	637	0.33	Linder and Axelsson 1982, Linder 1985
P. sylvestris, fertilized, irrigated	3.6	3671	20	155	116	135	406	1264	0.32	Linder and Axelsson 1982, Linder 1985
P. contorta	3.6	5600	40	103	250	230	583	911	0.64	Ryan and Waring 1992
P. contorta, montane	8.0	11240	18	1740	980	780	3500	5560	0.63	Benecke and Nordmeyer 1982
P. contorta, subalpine	5.1	9385	21	665	375	620	1660	2920	0.57	Benecke and Nordmeyer 1982
P. taeda	15.6	5778	16	1348	63	657	2068	4140	0.50	Kinerson et al. 1977
P. elliottii	21.6	5300	22	211	246	135	592	1102	0.54	Gholz et al. 1991, Cropper and Gholz 1993

temperature, with reported Q_{10} values often below 2 (Table 1). The lower sensitivity to temperature could reflect the more stable diurnal temperatures found in forest soils. Drew and Ledig (1981) found a strong seasonal pattern in the total CO_2 efflux from fine roots, with values high in early winter and low at the end of summer; however, respiration rates for a given temperature appeared to change little. Cropper and Gholz (1991) found no difference in temperature-corrected respiration rates between spring and summer samples. Barnard and Jorgensen (1977) found that fine root respiration rates were highest for unsuberized meristems (root tips), next highest for mycorrhizal roots (<1 mm diameter) and lowest for larger roots and those not infected with mycorrhizae. How pollutants, nitrogen deposition and atmospheric [CO_2] might affect fine-root respiration has not been assessed. Because high [CO_2] can depress respiration (Amthor 1991) and because [CO_2] in soil greatly exceeds atmospheric levels, respiration rates for roots measured at 360 ppm CO_2 will greatly exceed respiration in situ (Gi et al. 1994).

Whole-stand estimates

Annual carbon budgets have been estimated for a few young, actively growing pine forests. These annual budgets are valuable because we can use them to evaluate how climate and species influence carbon allocation, respiration costs and productivity. Annual carbon budgets evaluated from five separate studies (some with more than one treatment) are summarized in Table 2. Canopy carbon assimilation is reported as the annual sum of net daylight canopy carbon fixation and respiration (R_a) is reported as the annual total for aboveground woody tissues (stem+branch), coarse and fine roots (root) and foliage (night only). Growth and maintenance respiration not distinguished. Net primary production is equal to A minus R_a.

For young pine stands, respiration consumes 32–64% of A annually (Table 2). The ratio R_a/A was similar for the *P. contorta*, *P. taeda* and *P. elliottii* studies, but lower for the studies with the 20-yr-old *P. sylvestris* stands. If construction respiration consumes roughly 25% of carbon allocated to new tissue, then construction respiration for dry matter production is >50% of the total respiration for *P. sylvestris*, but less than 30% for the other studies.

Respiration of stems, roots and foliage (as a proportion of total respiration) varies greatly among sites, perhaps because of differences in aboveground biomass, leaf area index (LAI, all-sided) and climate. However, the value for annual root respiration for *P. taeda* (Kinerson et al. 1977) seems unrealistically low. Additionally, A for the montane *P. contorta* stand exceeds values reported for very productive tropical forests (Edwards et al. 1980). Because these budgets were assembled by extrapolating measurements made on a small portion of a stand's biomass, errors in sampling or extrapolation could cause errors in the annual budgets.

Except for the two New Zealand *P. contorta* stands, differences in R_a/A among studies do not appear to be related to average annual temperature (as suggested by Kinerson et al. (1977)) or to night temperatures during the growing season (as suggested by Hellmers and Rook (1973)). R_a/A increased linearly with stand biomass for these young pine stands (R^2 = 0.60). Further improvements in our understanding of the control of respiration over production are likely to come when annual budgets are validated with whole-system flux measurements obtained through eddy-covariance, by comparison with models of canopy photosynthesis (for example, Forest-BGC (Running and Coughlin 1988) or BIOMASS (McMurtrie et al. 1990)) and by using independent models to estimate respiration (Ryan 1991b).

Potential effects of respiration on forest productivity and structure

Because respiration can consume such a large fraction of assimilation, respiration could control the productivity or structure (LAI or woody biomass) of pine forests. Ideas about the effect of respiration on forest productivity can be condensed into three independent hypotheses: (i) does the low productivity commonly observed in old-growth forests result from a change in R_a/A, because R_a increases with woody biomass and A stabilizes after canopy closure (Yoda et al. 1965, Whittaker and Woodwell 1968)? (ii) does respiration or R_a/A determine differences in LAI or leaf retention, or woody biomass among systems (Waring and Franklin 1979, Cropper and Gholz 1994)? (iii) will global warming enhance respiration costs and reduce productivity (Woodwell 1987)? It has generally been assumed that the answer to all three questions is "yes", but this assumption has rarely been examined rigorously. Yet, these three hypotheses are embedded in many of our mechanistic models (Landsberg 1986, Running and Coughlan 1988, Bonan 1991, McMurtrie 1991, Rastetter et al. 1991, Friend et al. 1993).

Hypotheses about the effect of respiration on forest productivity are difficult to test, because respiration estimates must be compared with the remainder of the forest's carbon budget. Usually, this requires stand-level estimates of A, R_a and growth summed over one to several years – a difficult, but necessary task. In this section, we explore the merits and limitations of the three hypotheses about respiration by examining the literature and using a simple model of assimilation (Forest-BGC, Running and Coughlin (1988)) and respiration (Ryan 1991b).

Respiration and lower productivity in old forests

Net primary production commonly declines after canopy closure and is typically very low for old forests (Whittaker and Woodwell 1968, Jarvis and Leverenz 1983, Waring and Schlesinger 1985, Pearson et al. 1987). A widely accepted hypothesis holds that the low growth in old forests results from respiration of the large number of living cells in woody tissue (Yoda et al. 1965, Whittaker and Woodwell 1967, Waring and Schlesinger 1985). The argument goes as follows: (i) LAI (and assimilation) stay constant after canopy closure, but woody biomass or bole surface area increases with stand age; (ii) because woody-tissue respiration varies with surface area (Woodwell and Botkin 1970, Kinerson 1975) or biomass (Yoda et al. 1965), respiration should increase; (iii) increased respiration will lower the amount of fixed carbon that is available for wood production. There is anecdotal support for this hypothesis (Whittaker and Woodwell 1968, Waring and Schlesinger 1985), but until recently (Ryan and Waring 1992) it had not been rigorously tested (Jarvis and Leverenz 1983, Landsberg 1986, Sprugel and Benecke 1991).

Ryan and Waring (1992) found that respiration costs of woody tissues were similar for an old forest and an adjacent younger stand, even though wood production was substantially lower in the old forest. Their results contradicted the conventional hypothesis probably because they partitioned woody-tissue respiration into the components of maintenance and construction and estimated respiration from sapwood volume (Ryan 1990, Sprugel 1990) and wood production, rather than from surface area.

Why is the distinction between respiration components so crucial in understanding this phenomenon? Maintenance respiration rates for woody tissue are very low (Table 1, Ryan 1990) and maintenance respiration can be a relatively minor component of an annual carbon balance. Annual respiration costs may be overestimated if they are extrapolated from rates measured in the growing season or on young trees only. Summer measurements include both growth and maintenance respiration and would not apply to the entire year. Construction respiration varies linearly with wood production; therefore, because growth is low in old stands, construction respiration would necessarily be low. A better approach is to estimate maintenance respiration after growth ceases in autumn and construction respiration from wood production and wood chemistry (Ryan and Waring 1992).

Using sapwood volume to estimate maintenance respiration overcomes the variability associated with surface-area measurements (Ryan 1990). In addition, sapwood volume might increase less as a stand ages than bole surface area (although the evidence that bole surface area increases with age is equivocal (Sprugel and Benecke 1991)). Because tree leaf area is linearly related to sapwood cross-sectional area (Waring and Schlesinger 1985), if leaf area is static, sapwood volume can only increase if tree height increases. Since most height growth occurs early in stand development, sapwood volume and maintenance respiration may differ little between intermediate and old-growth stands. Ryan and Waring (1992) and Yoder et al. (1994) suggest that low photosynthesis depresses growth in older forests and discuss the consequences for forest growth modeling.

The hypothesis that woody tissue respiration depresses growth in old forests should be examined for other systems. The lodgepole pine stands used by Ryan and Waring (1992) grow in a cool environment (average temperature is 4°C), where respiration may use less carbo-

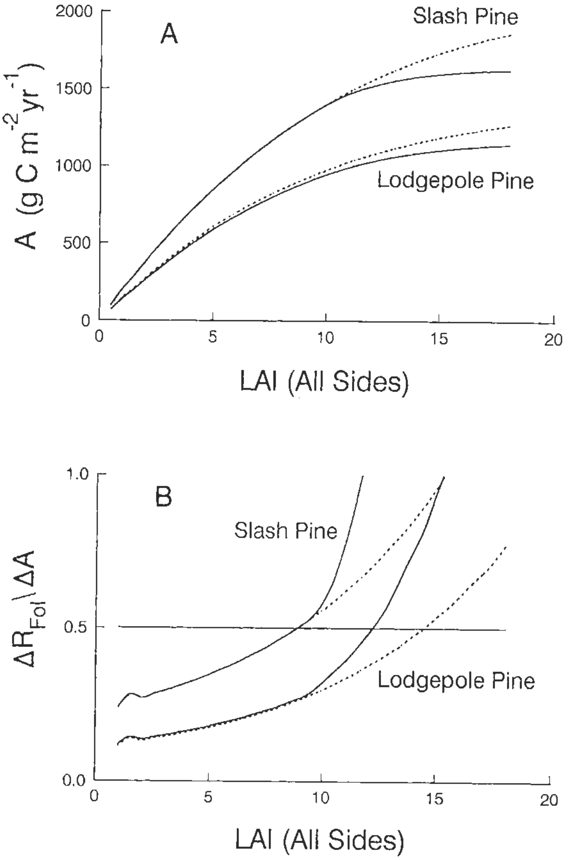

Fig. 1. Carbon assimilation and respiration for lodgepole pine and slash pine stands; (a) net carbon fixation in daylight (A) versus LAI, (b) the incremental change in annual foliage respiration (ΔR_{Fol}) for a 0.5 unit change in LAI relative to the incremental change in A(ΔA) versus stand LAI. Dotted lines summarize model runs where soil moisture was constant; solid lines summarize model runs where climate, LAI and soil characteristics influence soil moisture.

hydrate. Additionally, productivity is low in these forests (Pearson et al. 1987). However, Waring et al. (1994) found that maintenance respiration costs for old and young stands of *Tsuga heterophylla* and *Pseudotsuga menziesii* on highly productive sites were similar and concluded that respiration was probably not responsible for reduced wood production in the old stand.

Respiration and LAI

Foliar respiration rates are typically c. 10% of light-saturated photosynthetic rates at the same temperature. However, light levels can be low near the bottom of dense conifer canopies and respiration might play a role in regulating the LAI that can be carried in a given environment (Schoettle and Fahey 1994). Because light decreases exponentially through a canopy, the marginal photosynthetic return from additional leaf area decreases rapidly. Large LAIs may serve to sequester nutrients and shade competitors, but provide little additional photosynthate (Waring 1991). In a warm climate, respiration costs might force a lower LAI, because high temperatures might increase the canopy's "compensation point".

To examine whether temperature regime might affect LAI, we simulated photosynthesis and respiration for two pine canopies in contrasting climates. We selected a 22-yr-old slash pine stand in Florida and a 40-yr-old lodgepole pine stand in Colorado because (i) neither site typically experiences stomatal closure from low plant water status (pre-dawn water potential >-1.0 MPa); (ii) average annual temperatures were strongly different (4°C for lodgepole pine near Fraser, Colorado, USA and 22°C for slash pine near Gainesville, Florida, USA); (iii) LAI differed considerably (10 to 12 for the Fraser site (Ryan and Waring 1992) versus 3 to 6 for the Gainesville site (Gholz et al. 1991); and (iv) foliar N concentrations were similar (0.8 mg g^{-1}). The similarity in water and nutrients should allow a more even comparison of temperature effects. Ryan and Waring (1992) present more detail about the lodgepole pine stand; the slash pine is described fully in Gholz et al. (1991).

We used the Forest-BGC Model (Running 1984, Running and Coughlin 1988) to estimate the annual total of daytime net photosynthesis (A). We modeled maintenance and construction respiration for the foliage (R_{Fol}) using methods outlined in Ryan (1991b). Further information on the simulations is given in Appendix A.

Forest-BGC estimates greater A for the slash pine site at all LAIs, largely because of its higher air temperatures and longer growing season. Precipitation was lower for the lodgepole pine (680 mm versus 1270 mm), but neither the slash nor the lodgepole pine sites appeared to be limited by soil water availability (Fig. 1a). Differences between A estimated for constant and variable soil water occurred only at high LAIs, where the model predicted that transpiration would influence soil moisture.

The change in respiration for an increment of LAI relative to the change in A ($\Delta R_{Fol}/\Delta A$) estimates the marginal benefit in net carbon for the additional leaf area. Foliage would respire more carbon than it fixes if $\Delta R_{Fol}/\Delta A$ exceeds unity. However, we consider the marginal returns to be closer to 0 at $\Delta R_{Fol}/\Delta A = 0.5$, because additional foliage also requires additional fine roots (with similar respiration rates (Cropper and Gholz 1991)) and additional respiring sapwood.

Simulation results tend to support the hypothesis that site temperature might exert some control over LAI. $\Delta R_{Fol}/\Delta A$ is higher for the warmer slash pine site for all values of LAI and crosses the 0.5 threshold at a much lower LAI than does lodgepole pine (Fig. 1b). For slash pine, $\Delta R_{Fol}/\Delta A$ increases rapidly when LAI exceeds 9. Normal peak LAI for the modeled stand is 5 to 6 (Gholz et al. 1991). However, LAI in the modeled stand increased to 9 after heavy fertilization (Gholz et al. 1991), suggesting that LAI in the modeled stand was nutrient

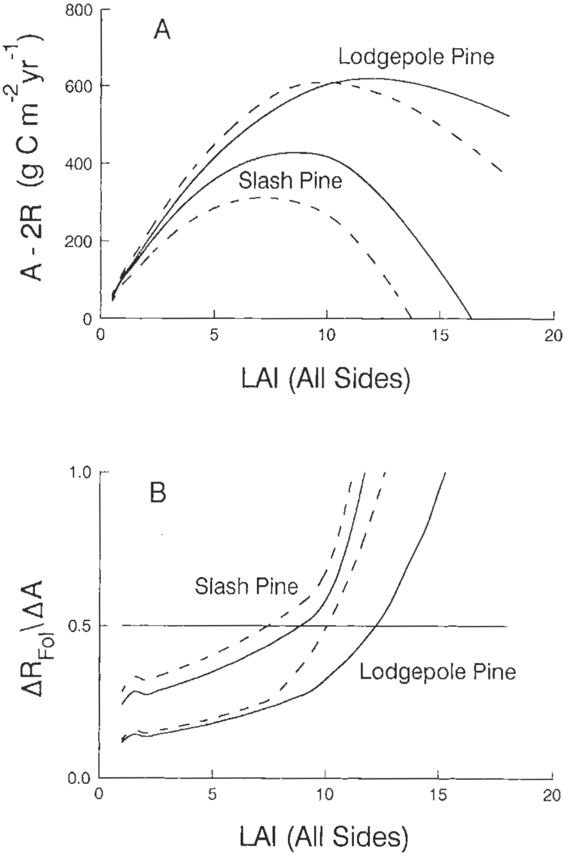

Fig. 2. Modelled effect of a 3°C increase in air temperature on net carbon fixation in daylight (A) and the annual total of foliage respiration: (a) assimilation minus twice foliage respiration ($A - 2R_{Fol}$) versus stand LAI; (b) the incremental change in annual foliage respiration (ΔR_{Fol}) for a 0.5-unit change in LAI relative to the incremental change in A (ΔA) versus stand LAI. Solid lines are for model runs with normal climate; dashed lines summarize model runs where air temperature was increased 3°C. Climate, LAI and soil characteristics influence soil moisture for both the normal temperature and +3°C simulations.

limited. For lodgepole pine, $\Delta R_{Fol}/\Delta A$ increases rapidly when LAI exceeds 13 – roughly the maximum reported LAI for lodgepole pine on similar sites (Kaufmann et al. 1982). The actual stand used in the simulations (normally with an LAI of 12) showed no response to fertilization (D. Binkley pers. comm.), suggesting that better nutrition would not increase LAI.

The simulation results in Fig. 1 suggest that temperature, through its effect on respiration costs, could affect LAI in pine forests. Water, nutrition and perhaps temperature can control LAI and it is difficult to separate multiple, interacting effects. Therefore, it is difficult to use field surveys of LAI to test hypotheses. However, in an extensive study of LAI in *P. taeda* in the southeastern U.S., L. Allen et al. (pers. comm.) found that LAI decreased with higher temperatures. However, rigorous, controlled field testing of the hypothesis is needed.

Climate change and respiration

Because respiration and photosynthesis differ in their response to temperature, global warming could decrease net carbon uptake by plants (Woodwell 1987, McGuire et al. 1992). For most temperate plants, photosynthesis increases approximately linearly between 0 and 15°C and varies little in the range 20 to 40°C (Fitter and Hay 1987). In contrast, respiration increases exponentially from 0 to 40°C before peaking and dropping sharply. If these relationships hold, an increase in the average temperature would increase respiration proportionally more than photosynthesis. However, forests may be able to acclimate to a warmer climate to conserve net primary production. Because conifer forests can support large LAIs, the marginal leaf area is inefficient at supplying carbon (Fig. 1). If LAIs were reduced in a warmer climate, A and $\Delta R_{Fol}/\Delta$ might remain nearly constant. Rates of respiration and photosynthesis can also acclimate to different temperatures (Strain et al. 1976, Drew and Ledig 1981).

We simulated net assimilation and respiration for the slash and lodgepole pine stands described in the previous section to explore whether pine ecosystems could conserve net production in a warmer climate by changing LAI. The Forest-BGC model was run using the parameters and climate described above. For each site, we also ran simulations with temperature increased 3°C; relative humidity, precipitation and short-wave radiation were unchanged. We report results only for simulations where soil moisture was affected by precipitation, runoff, evaporation and transpiration.

Because roots and sapwood also respire and they occur in proportion to foliage, as an index we estimated the net carbon available for dry matter production as assimilation minus twice foliar respiration. Simulation results show that the lodgepole pine forest would be minimally affected by a 3°C temperature increase. Net fixation in lodgepole pine stand with LAIs of 10 to 12 could be preserved if LAI were lowered to 7 to 9 (Fig. 2a). In contrast, $A - 2R_{Fol}$ for slash pine is lower for the +3°C scenario for all LAIs. The uniform lowering of $A - 2R_{Fol}$ for the warmer climate suggests that a shift in LAI could not conserve net production.

Two factors probably cause the lodgepole pine and slash pine sites to respond differently to temperature. First, the relationship between air temperature and the temperature for optimal photosynthesis differs between the two sites. At the slash pine site, temperature for much of the year is near the photosynthetic optimum and adding 3°C reduces photosynthesis. In contrast, at the lodgepole pine site temperatures are often below the photosynthetic optimum and a 3°C temperature rise generally increases photosynthesis. Second, respiration costs are lower and increase less rapidly with increasing LAI at the cooler lodgepole pine site. $\Delta R_{Fol}/\Delta A$ is initially high for slash pine (Fig. 2b) and $\Delta R_{Fol}/\Delta A$ increases rapidly with increasing LAI.

Simulation results, of course, depend on the models used. In the case of the simulations shown in Fig. 2, results are particularly sensitive to the assumed temperature dependencies of photosynthesis and respiration. Species tend to have a photosynthetic optimum near the temperature at which they grow (Larcher 1983). Therefore, a warmer climate may shift the photosynthesis-temperature response upward and increase photosynthesis more than estimated by models such as Forest-BGC. Respiration rates can also acclimate to temperature and acclimation has been observed in *Pinus* seedlings (Drew and Ledig 1981). For example, respiration rates have been shown to stay within a narrow range, regardless of the growing temperature (Fukai and Silsbury 1977, McNulty and Cummins 1987, Amthor 1989). Until we understand physiological acclimation and the longer-term controls on ecosystem productivity (such as feedbacks between production, decomposition and nutrient cycling (Rastetter et al. 1991)), our predictions of ecosystem response to climate change will be uncertain.

Conclusions

We have accumulated much information about respiration rates in pine forests and are beginning to identify the causes of variability in rates among species and within tissues of a given species. The wider availability of robust, portable equipment for measuring gas exchange has encouraged more investigators to measure large trees in the field. These field measurements on large trees are important because field-grown trees and seedlings in growth chambers behave very differently.

To determine how respiration might affect productivity requires estimation of annual respiration and productivity. Approaches such as the use of sapwood volume to estimate maintenance respiration of woody-tissue and the use of tissue nitrogen to estimate maintenance respiration for all tissues, offer promise for computing these annual budgets. However, these approaches must be widely tested using complete carbon budgets assembled in several locations before we gain full confidence in our models.

Despite the success of the functional model of respiration in agronomy (Amthor 1989), it has not been widely applied in forestry. However, rates of maintenance respiration are sensitive to the environment (Ryan 1991a), while construction respiration varies with productivity and tissue chemistry. We believe that the use of the functional model will simplify the interpretation of respiration data and explain some of the variability in observed rates.

The central question about the role of plant respiration in pine ecosystems is: can or does respiration control productivity? The complete carbon budgets described in this paper suggest that the fraction of assimilation used in respiration can vary greatly among stands. This variability in R_a/A among species which are physiologically similar suggests that respiration can indeed alter productivity. From simulation models, we expect that R_a/A will increase with increasing site temperature (e.g. McGuire et al. 1993), but R_a/A did not appear to vary with temperature for the carbon budget studies in pine stands. The challenge for the next generation of field and modelling studies will be to measure R_a/A for a number of sites and species and determine the mechanisms responsible for variability in R_a/A.

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Appendix A – Information on model simulations

We used the Forest-BGC model (Running 1984, Running and Coughlin 1988) to estimate the annual total of daytime net photosynthesis (A). Published parameter values for a generic conifer forest (Running and Coughlin 1988) were used to run the model for both sites, with a few exceptions. We used actual foliar [N] and soil water storage capacity, because Forest-BGC is very sensitive to these parameters. Published values for maximum stomatal conductance to water and CO_2 were lowered 18% for both sites so that A estimated by the model matched independent estimates for the two sites. Parameters for foliage, wood and root respiration were set to 0 so that the program would calculate A instead of A minus respiration. Finally, we used a different temperature-photosynthesis response for the two sites to reflect the higher average temperature at the Florida site.

Forest-BGC requires daily values for maximum and minimum temperatures, relative humidity, shortwave radiation and precipitation. We used weather data collected either on site (lodgepole pine) or from a nearby NOAA weather station (slash pine). Shortwave radiation was estimated by the MTCLIM interpolation program (Running et al. 1987) for both sites.

Preliminary runs showed little year-to-year variability in A. Therefore, we report simulations for an average year (1984 for lodgepole pine, 1985 for slash pine). We varied leaf area index (LAI, all-sided) from 0.5 to 18 and ran the model with i) soil moisture constant and ii) soil moisture affected by precipitation, runoff, evaporation and transpiration. For lodgepole pine forests, LAI was assumed constant throughout the year. Because LAI varies substantially throughout the year in slash pine forests, we adjusted LAI every 15 days to reflect the seasonal dynamics reported by Gholz et al. (1991).

We modeled maintenance and construction respiration for the foliage (R_{Fol}) using methods outlined in Ryan (1991b). Maintenance respiration was estimated from foliar N content (Ryan 1991a) and average annual temperature and construction respiration was estimated assuming 0.25 g C respiration per g C allocated to tissue production. Foliar [N] was assumed constant for all LAIs in the simulation. To estimate construction respiration, foliage production was estimated as a constant fraction of the foliage standing crop (0.12 for lodgepole pine (Schoettle 1989) and 0.50 for slash pine (Gholz et al. 1991)). Maintenance respiration estimated from foliar N was within 12% of that measured at the slash pine site (Cropper and Gholz 1991).