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Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate

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Abstract. Autotrophic respiration (R_a) in forest ecosystems can be $>50\%$ of the carbon fixed in photosynthesis and may regulate productivity and carbon storage in forest ecosystems, because R_a increases with temperature. We estimated annual R_a from chamber measurements in aspen, black spruce, and jack pine forests in Canada for 1994. Mean foliage respiration at 10°C for expanded leaves was 0.21–0.95 μmol m^{-2} (leaf surface) s^{-1} for all species and differed little from May to September. Wood respiration at 15°C (0.2–1 μmol m^{-2} (stem surface) s^{-1} for all species) was strongly seasonal, with high rates in midsummer that coincided with wood growth. Fine root respiration at 10°C was 2.5–7.7 μmol kg^{-1} s^{-1} for all species and declined throughout the growing season for the conifers. Annual costs of R_a for foliage, wood, and roots (overstory and understory) were 490, 610, and 450 g C m^{-2} (ground) yr^{-1} for aspen, black spruce, and jack pine (old) in northern Manitoba and 600, 480, and 310 g C m^{-2} yr^{-1} for aspen, black spruce, and jack pine (old) in central Saskatchewan. Carbon use efficiency (CUE), the ratio of net production to production plus R_a, averaged 0.44, 0.34, and 0.39 for aspen, black spruce, and jack pine (old) for all tissues and 0.61, 0.36, and 0.44 for aboveground tissues. Differences in CUE between the northern and the southern sites were small for all species, and CUE did not vary with stand biomass. Species differences in CUE suggest that models assuming a constant CUE across species may poorly estimate production and carbon balance for any given site.

Introduction

Net primary production (NPP) of forests controls forest growth and ultimately the storage of carbon (C) in forest ecosystems. However, NPP is only 25–60% of the carbon fixed in photosynthesis; autotrophic respiration (R_a) used for maintenance and tissue construction consumes the rest [*Edwards et al.*, 1980; *Sprugel and Benecke*, 1991; *Ryan*, 1991a; *Ryan et al.*, 1994, 1996a]. Because R_a and photosynthesis respond differently to the environment [*Larcher*, 1995], changes in climate could alter the balance between photosynthesis and R_a and modify NPP.

Fluxes of C from R_a are large and a substantial portion of ecosystem respiration (which also includes respiration from heterotrophs (R_h)). For example, in a young *Pinus radiata* plantation [*Ryan et al.*, 1996a], respiration of foliage at night (r_f), woody tissues (r_w), and roots (r_r) varied from 10.5 to 17.8 Mg C ha^{-1} yr^{-1} (2.8–4.7 μmol m^{-2} s^{-1} averaged over the year); R_h (estimated as soil respiration minus root respiration) varied from 2.6 to 7.1 Mg C ha^{-1} yr^{-1} (0.7–1.9 μmol m^{-2} s^{-1} averaged over the year). Fluxes of C for R_a are controlled by the amount of living biomass, biomass nutrient content (especially nitrogen), cellular activity or growth (in turn controlled

by the supply of sugars from photosynthesis), and temperature [*Amthor*, 1989; *Ryan*, 1991a]. R_h is controlled by substrate quality (especially the concentration of lignin and nitrogen in litter), moisture, and temperature [*Melillo et al.*, 1982]. Because of the different controls on R_a and R_h it is important to measure and model these components separately.

R_a is often partitioned into the functional components of construction and maintenance [*Amthor*, 1989] to interpret fluxes and for modeling. Construction respiration varies with the amount of biomass grown and with the complexity and energy status of the chemical compounds in the biomass [*Vertregt and Penning de Vries*, 1987; *Williams et al.*, 1987]. Maintenance respiration largely varies with enzyme content (closely related to tissue N) and temperature [*Ryan*, 1991a]. Most process-based models of biogeochemical cycling estimate maintenance respiration first, subtract it from net photosynthesis as a tax, and allocate the remaining carbon to production, construction respiration, and storage (see *Ryan et al.* [1996b] and *VEMAP* [1995] for model descriptions and comparisons).

Fine-scale models of respiration are needed to interpret flux measurements from eddy covariance [e.g., *Baldocchi et al.*, 1988; *Baldocchi and Vogel*, 1996; *Lavigne et al.*, this issue]. For longer timescales (e.g., annual) we seek to understand whether species or climate alter the balance between NPP and R_a or the carbon use efficiency (CUE = NPP/(NPP + R_a) of the

Table 1. Characteristics of Vegetation in Study Plots [*Gower et al.*, this issue; *NASA*, 1993; *Steele et al.*, 1977]

Site	Age of Overstory Trees, years	Overstory Leaf Area, $m^2 m^{-2}$	Trees, ha^{-1}	Height of Dominant Trees, m	Basal Area, $m^2 ha^{-1}$	Sapwood Volume, $m^3 ha^{-1}$	Understory Stem Plus Foliage, kg C ha^{-1}	Coarse Roots, kg C ha^{-1}	Fine Roots, kg C ha^{-1} 0–2 mm	Fine Roots, kg C ha^{-1} 2–5 mm
NSA-OBS	150	4.9	5450	9	32	83	NA	9680	850	3285
NSA-OJP	63	2.2	1280	10	17	55	579	4885	1025	1690
NSA-OA	53	2.2	1960	14	34	196	629	10095	790	2430
NSA-YJP	<25	1.8	5700	7	10	13	309	NA	NA	NA
SSA-OBS	115	5.6	6350	7	36	61	514	8385	385	2570
SSA-OJP	63	2.5	1190	13	13	57	143	6515	450	980
SSA-OA	68	3.3	980	20	27	327	1419	10605	395	2890
SSA-YJP	14	2.8	4056	5	9.1	26	NA	NA	NA	NA

ecosystem [*Gifford*, 1994; *Ryan et al.*, 1996a]. If CUE varies little between species, or with climate and forest age, then photosynthesis and respiration are tightly linked, and NPP will vary in concert with photosynthesis. If CUE does vary between sites, then knowledge of the variation in response to climate, species, and forest age are essential, particularly for "epsilon" or production efficiency models [e.g., *Prince*, 1991; *Prince and Goward*, 1995; *Landsberg et al.*, 1996].

The Boreal Ecosystem-Atmosphere Study (BOREAS) offered the opportunity to assess R_a in the context of an annual C budget for several species growing in different climates. In this study we estimate annual budgets for R_a of young and mature jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and aspen (*Populus tremuloides*) growing near the southern and northern boundaries of the boreal forest biome, place R_a in the context of other components of the carbon balance, and determine species and climate effects on CUE.

Methods

Study Sites

We estimated annual budgets of R_a for the overstory and understory of the mature spruce (old black spruce (OBS)), mature pine (old jack pine (OJP)), young pine (young jack pine (YJP)), and mature aspen (old aspen (OA)) sites in the northern (NSA) and southern (SSA) study areas of the Boreal Ecosystem–Atmosphere Study. In the SSA the OA site is in Prince Albert National Park, Saskatchewan, Canada (55° 34'N, 106° 14'W), and the OBS, YJP, OJP sites are near Nippawin, Saskatchewan (53° 53'N, 104° 53'W). In the NSA the sites are 30–60 km west of Thompson, Manitoba, Canada (55° 53'N 98° 20'W).

Sites in the southern area are 30–100 km north of the southern boundary of the boreal forest and, in the north, are close to the northern limit of the closed-crown boreal forest. The study sites experience a strong seasonal variation in solar radiation, with cool summers and extremely cold winters [*NASA*, 1993]. Based on 13 years of record in the NSA and 38 in the SSA, average temperature in the SSA is 0.1°C, 4.0°C warmer than in the NSA. For the same record, growing season temperatures (May to September) averages 13.4°C in the SSA and 10.7°C in the NSA [*NASA*, 1993]. Annual precipitation averages 390 mm at Prince Albert and 542 mm at Thompson; about 40% of the precipitation falls as snow [*NASA*, 1993]. Further details about the sites are given by *Sellers et al.* [1995] and [*NASA*, 1993].

To aid measurements of surface fluxes with eddy covariance, vegetation in study sites was relatively homogeneous and the terrain nearly flat. The overstory trees (black spruce (*Picea*

mariana), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*)) were dominant at their respective study sites, but understory vegetation was a significant component at the aspen sites. Hazel (*Corylus cornuta*) comprised 40% of the leaf area at the SSA aspen site, and alder (*Alnus crispa*) was 20% of the site leaf area in the NSA aspen site. Alder was also a small but important component of the jack pine stands. The understory of the spruce stands was dominated by moss (*Hylocomium* spp.; *Sphagnum* spp.) and Labrador tea (*Ledum groenlandicum*). In the spruce sites, the majority of the area measured by eddy covariance (nominally 500 m radius around the tower) had spruce 5–15 m tall, with >50% crown closure. However, significant portions of the spruce sites consisted of poorly drained soils with a high water table, low spruce density, and trees <7 m tall. At the spruce sites, plots to estimate biomass, productivity, and R_a for this study were in the better-drained soils with taller trees. Characteristics of the vegetation for individual sites are in Table 1.

Gas Exchange

We measured foliage respiration rates (r_f) for the overstory in 1994 in June, July, August, corresponding to the BOREAS intensive field campaigns (IFCs) [see *Sellers et al.*, 1995]), at OBS, OJP, and OA in the northern and southern study areas. At the aspen sites, r_f was also measured for *Corylus cornuta* in the SSA and *Alnus crispa* in the NSA in July and August. We estimated r_f as CO_2 efflux from foliage at night (2300–0300 LST). We accessed the canopy with scaffolding towers that were relocated for each IFC in the NSA, but remained in place throughout the summer in the SSA. For the overstory, r_f was sampled by canopy position (canopy thirds) and foliage age; 15–30 samples were measured at each site for each IFC, distributed among the accessible trees. From each scaffold tower we could sample 3–8 trees. For the understory, we measured flux from five Sun and five shade leaves. Foliar CO_2 efflux was measured in the SSA using a closed system [*Field et al.*, 1991] LI-COR 6200 (LI-COR, Inc., Lincoln, Nebraska) and in the NSA using an open system [*Field et al.*, 1991] ADC LCA3 or LCA4 (Analytical Development Company, Hoddeston, Herts., U.K.). The LI-COR and the ADC systems were compared prior to the experiment and fluxes agreed within 4%. Foliage temperature was measured concurrently with a fine-wire thermocouple.

Immediately after sampling, foliage was removed from the branch, stored at <2°–5°C for 10–48 hours and measured for leaf area. For aspen, alder, and hazel, leaf area was determined with a leaf area meter. For spruce and pine, leaf area was determined by volume displacement [*Chen et al.*, this issue].

The samples were then dried at 65°C for 48 hours, weighed, and stored for analysis of nutrients (N and P) and carbohydrates. In expressing flux rates, leaf area is given as hemisurface area (one half of the total surface area) [Chen et al., this issue].

Temperature response of r_f was measured in July for the overstory species in the NSA. We harvested five shoots of each species from midcanopy at about 0300, recut the stems under water, and stored samples in the dark at 15°C for about 6 hours. Temperature response was determined by measuring r_f at 5°, 15°, and 25°C with a temperature-controlled cuvette [Hubbard et al., 1995]. We did not measure temperature response in June and August because previous studies with conifer r_f showed that temperature response varied little throughout the growing season (M. G. Ryan, unpublished data, 1992).

Wood respiration rates (r_w) were measured for the overstory several times at each site from early June to the end of September 1994. At each site, we sampled 16–20 trees (10 at NSA-YJP) distributed across the range of tree diameters. Chambers were 1–2.5 m above the ground; at the NSA sites, four trees were also measured at 6 m above the ground. For the SSA sites (1) all measurements were taken with an automated manifold system [Lavigne, 1996] that measured flux from each chamber every 1.75 hours; (2) measurements were taken for 3–4 days for each sample period in May to September 1994: early, middle, and late growing season and after growth had ended; (3) chambers were clear acrylic, enclosed all of the stem circumference on small trees or part of the stem circumference on large trees, and remained in place (vented) between measurements. For the NSA sites, (1) eight trees were measured with an automated manifold system each hour over 3–6 days during the early, middle, and late portions of the growing season; (2) 20 trees (including the 8 on the automated system) were measured manually every 2–3 weeks from late May to September; (3) for the OA, OJP, and OBS sites, chamber plates were attached to the stem with putty, chambers were clear acrylic and removed from the plates after sampling; for the YJP site, chambers enclosed the stem.

All wood respiration measurements were made using an open system [Field et al., 1991]; the equipment used was a LI-COR 6252 in the SSA and a LCA2, LCA3, or LCA4 in the NSA. For each measurement we also recorded stem temperature from a thermocouple inserted 1–2 cm into the sapwood. Temperature response of r_w was determined from the manifold samples for each sample period, using sapwood temperature measured about 2 hours earlier [Lavigne et al., 1996]. At the end of the study we either cut disks from the smaller trees or extracted two cores from the larger trees to determine sapwood volume and growth for the wood associated with the chamber. After measurement, cores were dried at 65°C for 48 hours, weighed, and stored for analysis of nutrients (N and P) and carbohydrates. Further details about the sampling methodology are given by Lavigne and Ryan [1997].

Fine root (<2 mm diameter) respiration rates (r_r) were measured once during each IFC on 10–20 samples per site. Measurements were made on intact fine roots 1–5 cm below the surface of the litter. Fine roots (0.1–0.3 g) were carefully separated from the surrounding litter and soil with small brushes and water. Because CO_2 concentration alters CO_2 efflux rate of fine roots [Qi et al., 1994], CO_2 concentration in the cuvette was 500–1400 $\mu l\ L^{-1}$, approximately that of the soil air surrounding the roots before sampling. CO_2 efflux was measured using a closed system [Field et al., 1991] LI-COR 6200 in the SSA or a CID C-301 (CID Inc., Moscow, Idaho) in

the NSA. Fine root temperature was assumed to be that of the surrounding soil, measured with a thermocouple. Temperature response was determined by measuring r_r at 5°, 15°, and 25°C with a temperature-controlled cuvette [Hubbard et al., 1995] on five samples in July at the NSA sites. After the respiration measurements the sample was harvested, dried at 65°C for 48 hours, weighed, and stored for analysis of nutrients (N and P) and carbohydrates.

Coarse root (1–4 cm diameter) r_r was measured during July (IFC-2) and August (IFC-3) only for the NSA plots (6–10 samples/plot). Split Plexiglas chambers (15–25 cm in length) enclosed the intact, excavated root, and gas exchange was measured using an open system [Field et al., 1991] ADC LCA3 or LCA4. We assumed temperature of the coarse roots was the temperature of the surrounding soil. After the August sample, samples were harvested, and measured for sapwood and heartwood area; samples were then dried at 65°C for 48 hours, weighed, and stored for analysis of nutrients (N and P) and carbohydrates.

Alder r_w was measured in June, July, and August 1994 on five stems at the NSA-OA site. Sampling and analysis were the same as given for coarse roots, except we assumed stem temperature was equal to air temperature.

Biomass and NPP

Tree sapwood volume, overstory leaf area, understory leaf mass or area, understory woody biomass, and fine and coarse root biomass were used to extrapolate chamber flux measurements to the site. Leaf area and sapwood volume for the site were estimated by (1) establishing allometric relationships of leaf area or sapwood volume and tree diameter for each site (10 trees per site), (2) measuring the diameter of each tree in three 900 m^2 plots at each site, and (3) using the tree diameters and allometric equations to estimate plot means for sapwood volume and leaf area [Gower et al., this issue]. Aboveground net primary productivity (ANPP) of wood was estimated from a site-specific allometric relationship of woody biomass and tree diameter and diameter growth from tree-ring samples [Gower et al., this issue]. ANPP of foliage was estimated from the increment in foliage standing crop derived from allometric relationships of leaf area with stem diameter plus litterfall [Gower et al., this issue]. Fine root biomass (0–2 mm and 2–5 mm wet diameter) was estimated from 20 cores in September 1994 [Steele et al., 1997]; coarse root biomass was estimated from allometric equations [Steele et al., 1997]. Fine root NPP was estimated from minirhizotrons and coarse root NPP was estimated from allometric equations and the difference in annual stem diameter [Steele et al., 1997]. Understory biomass and ANPP were determined by harvesting small plots [Gower et al., this issue]. Values of biomass, sapwood volume, or leaf area used to extrapolate chamber measurements are given in Table 1.

Site Estimates and Annual Budgets

Our goal was to calculate daily and annual budgets of wood, foliage, understory and fine and coarse root respiration for each site in 1994, using the chamber measurements of respiration, the plot biomass estimates, and the fewest possible assumptions. Chamber measurements had been distributed to represent the stand or canopy. We allocated a greater amount of our effort to determine the biomass and measure respiration fluxes for tissues that comprised the greatest percentage of the total vegetation biomass (tree wood) or had the highest respiration rates (tree foliage and fine roots) and less effort to other

tissues (coarse roots, understory foliage, and understory stems). For each sample period and site, each chamber measurement was adjusted to a reference temperature (10°C for foliage and fine roots, 15°C for overstory and understory stems and coarse roots) using species-specific and (for overstory stems only) species- and time-specific estimates for the response of respiration to temperature. These temperature-corrected respiration rates were then averaged to give an estimate of respiration rate for a given site, time, and tissue.

To estimate respiration rates between sample days, we used linear interpolation and assumed that rates measured in the autumn applied throughout the winter and for the previous spring. Because wood growth initiated in the YJP stands before we sampled, we assumed that wood growth initiated on day 134 in the SSA and day 140 in the NSA. Foliage respiration was estimated separately for expanding (<1 season old) and mature foliage. We estimated leaf expansion and senescence separately by species, based on measurements of phenology at a mixed-species site in the NSA.

Respiration was not measured on all components at all sites. Foliage respiration was not measured at the YJP sites in both the NSA and the SSA; we assumed r_f equaled that of the OJP stands. Coarse root and shrub (alder) r_w was only measured in the NSA; we assumed the same rates for the SSA sites for *Corylus*. Additionally, we did not measure respiration for the understory in the conifer sites, because understory biomass was <1% of the aboveground biomass in each conifer stand. For these sites we assumed that r_f and r_w for the understory equaled that of the associated conifer foliage or wood in August, that the foliage was deciduous, and that biomass was equally partitioned between foliage and wood. We assumed that the understory biomass of NSA-OBS (not measured) was equal to that of SSA-OBS and that of SSA-YJP (not measured) equaled that of NSA-YJP to estimate understory respiration. Our fine root r_r measurements were taken on roots 0–2 mm; to estimate respiration for roots 2–5 mm in diameter, we assumed that respiration was equal to that of coarse roots and converted biomass to volume, assuming a specific gravity of 0.25. Our assumption was based on two studies that reported a sharp linear or exponential decline in fine root respiration as sample weight increased [*Cropper and Gholz*, 1991; *Ryan et al.*, 1996a]; both studies noted that large sample weights corresponded to samples with larger diameter roots. Respiration was not estimated for the roots of YPJ stands, because biomass was not measured for these components. The source for respiration rates for all components and all sites is in Table 2.

The temperature response of r_f and r_r in the SSA were assumed to be equal to those of the species in the NSA. Where temperature response was not measured, we assumed a Q_{10} of 2.

Using the interpolated, temperature-corrected chamber means and plot mean leaf area, biomass, and sapwood volume, we estimated respiration for the ecosystem (ground area basis) for expanding and fully expanded overstory foliage, understory foliage, overstory wood, understory biomass, fine roots (0–2 mm), fine roots (2–5 mm), and coarse roots for 1994. For each component, respiration was estimated every 15–60 min from site-specific air temperature records with the equation

$$R_t = M_t r_B e^{\beta(T - T_B)} \tag{1}$$

where R_t is respiration for component t; r_B is mean tissue respiration rate at the base rate of 10° or 15°C; M_t is mean biomass, foliage area, or sapwood volume per unit ground area; β is the species- and tissue-specific coefficient for re-

sponse to temperature; T is tissue temperature (°C); and T_B is 10° or 15°C. Foliage dark respiration for the understory and overstory were estimated both for night (periods when photosynthetically active radiation was less than 50 μmol m^{-2} s^{-1}) and for 24-hour days. Stem and root respiration were estimated for 24-hour days. We also estimated the maintenance component of respiration for stem and overstory only, by assuming that the dormant season respiration rates applied to the entire year.

Canopy, stem, understory, and soil temperatures used to force the respiration models were assembled from a variety of sources (Table 3). For SSA-OA, SSA-OJP, and NSA-OJP, temperatures were taken from the regional weather stations located on site. The SSA-OJP regional site was also used for SSA-YJP, because the site was within 5 km and on similar soil. The NSA-OJP regional site was used for NSA-OA, because the site was close (within 10 km) and no weather measurements were made on site. For other sites, measurements from the eddy flux tower were used when available; otherwise, we estimated temperatures from the nearest regional weather station, using a linear regression developed when both sites had data (Table 3). For the OJP, YJP, and OBS sites in the NSA, stem temperature was estimated with site-specific regressions of stem temperature and either canopy or under canopy (2 m) temperatures. For the NSA-OA site, we assumed stem temperature was equal to that of the NSA-OJP site. For the SSA sites, we assumed the same relationships as at the NSA sites.

Results

Foliar Respiration

Mean r_f for the overstory was 0.21–0.64 μmol m^{-2} s^{-1} for black spruce, 0.37–0.61 μmol m^{-2} s^{-1} for jack pine, and 0.34–2.0 μmol m^{-2} s^{-1} for aspen (Figure 1, Table 4). For the two conifers, r_f showed little seasonal variability, with the exception of black spruce for IFC-2. For aspen, r_f was substantially greater in IFC-1 than for IFC-2 and IFC-3, especially in the NSA, but did not change even as the leaves began to senesce in IFC-3. Temperature response for the NSA overstory species in July was similar among species ($p = 0.09$). The response coefficients were 0.076 (SE = 0.002) for black spruce, 0.068 (SE = 0.005) for jack pine, and 0.073 (SE = 0.005) for aspen. These correspond to Q_{10} of 2.1, 2.0, and 2.1, respectively. Mean r_f for the understory was 0.34 μmol m^{-2} s^{-1} for alder and 0.42 μmol m^{-2} s^{-1} for hazel. Average foliar N concentration was greater ($p < 0.01$) in the SSA than in the NSA for spruce (0.92% versus 0.68%) and mature jack pine (1.1% versus 0.90%) but not for aspen (2.7% versus 2.6%). However, foliar N per unit leaf area was significantly greater for SSA aspen than for NSA aspen ($p < 0.01$, 0.19 mol m^{-2} versus 0.11).

Wood Respiration

Wood respiration showed a strongly seasonal pattern (Figure 2), with higher r_w in the middle of the growing season. During midsummer, r_w was 2–3 times greater than in early summer or autumn for all species; however, r_w was similar among species and sites (0.2–1 μmol m^{-2} s^{-1} at 15°C). Rates per unit sapwood volume (corrected to 15°C) differed substantially among species, and mean rates were higher for black spruce and young jack pine than for aspen and mature jack pine at both the NSA and the SSA (Table 4). Differences between species in rates per unit sapwood volume were not caused solely by differences in growth, because dormant-

Table 2. Source for Respiration Data Used to Derive Annual Total Respiration in Eight Boreal Forest Stands

Site	Foliage, Night	Aboveground Wood	Fine Root, 0–2 mm	Fine Root, 2–5 mm	Coarse Root	Understory Foliage	Understory Stems
NSA-OBS	separate rates for expanding and fully expanded foliage, linearly interpolated between measurements	average rate every 2–4 weeks linearly interpolated between measurements	Figure 3, linearly interpolated between measurements	coarse root rate, assuming a density of 0.25 g cm^{-3}	average rate	dormant season rate for spruce, only for days 145–260	dormant season rate for spruce stem sapwood
NSA-OJP	same as above	same as above	same as above	same as above	same as above	dormant season rate for pine, only for days 145–260	dormant season rate for pine stem sapwood
NSA-OA	same as above	same as above	same as above	same as above	same as above	average rate for alder, linearly interpolated between measurements	average rate for alder, linearly interpolated between measurements
NSA-YJP	NSA-OJP	same as above	NA	NA	NA	dormant season rate for pine, only for days 145–260	dormant season rate for pine stem sapwood
SSA-OBS	separate rates for expanding and fully expanded foliage, linearly interpolated between measurements	average rate 4–6 × through growth season, linearly interpolated between measurements	Figure 3, linearly interpolated between measurements	coarse root rate for NSA-OBS, assuming a density of 0.25 g cm^{-3}	average rate for NSA-OBS	dormant season rate for spruce, only for days 135–260	dormant season rate for spruce sapwood
SSA-OJP	same as above	same as above	same as above	coarse root rate for NSA-OJP, assuming a density of 0.25 g cm^{-3}	average rate for NSA-OJP	dormant season rate for pine, only for days 135–260	dormant season rate for pine sapwood
SSA-OA	same as above	same as above	same as above	coarse root rate for NSA-OA, assuming a density of 0.25 g cm^{-3}	average rate for NSA-OA	average rate for hazel	average rate for NSA-alder, linearly interpolated between measurements
SSA-YJP	SSA-OJP	same as above	NA	NA	NA	dormant season rate for pine, only for days 135–260	dormant season rate for pine sapwood

Table 3. Source of Temperature Data Used to Force Respiration Models

Site	Overall	When Missing	Canopy	Stem	Understory	Roots
NSA-OBS	eddy flux tower	estimated from BOREAS NSAOJP	average of T_{air} at 2 and 10 m	$T_w \times 1.02$–0.75, from on-site measurements	T_w	T_{soil} at 10 cm
NSA-OJP	BOREAS-NSAOJP		T_c	$T_w \times 1.066$–0.983, from on-site measurements	T_w	T_{soil} at 20 cm
NSA-OA	BOREAS-NSAOJP		T_c	$T_w \times 1.066$–0.983	T_w	T_{soil} at 20 cm
NSA-YJP	eddy flux tower	estimated from BOREAS NSAOJP	T_{air} at 517 cm	T stem	T_{air} at 160 cm	NA
SSA-OBS	eddy flux tower	estimated from BOREAS SSAOJP	T_c estimated from 24 m T_{air}	$T_w \times 1.02$–0.75	T_c estimated from 24 m T_{air}	T_{soil} at 20 cm
SSA-OJP	BOREAS-SSAOJP		T_c	$T_c \times 1.066$–0.983	T_w	T_{soil} at 20 cm
SSA-OA	BOREAS-SSAOA		T_c	$T_c \times 1.066$–0.983	T_w	T_{soil} at 20 cm
SSA-YJP	BOREAS-SSAOJP		T_c	$T_c \times 1.066$–0.983	T_w	NA

BOREAS data sets were compiled largely from meteorological stations at the listed sites, with data substituted as necessary to give a complete 15-min data set for 1994. T_c, T_w, T_{air}, T_{soil} are canopy infrared temperature, within canopy (2 m) air temperature, air temperature, and soil temperature, respectively.
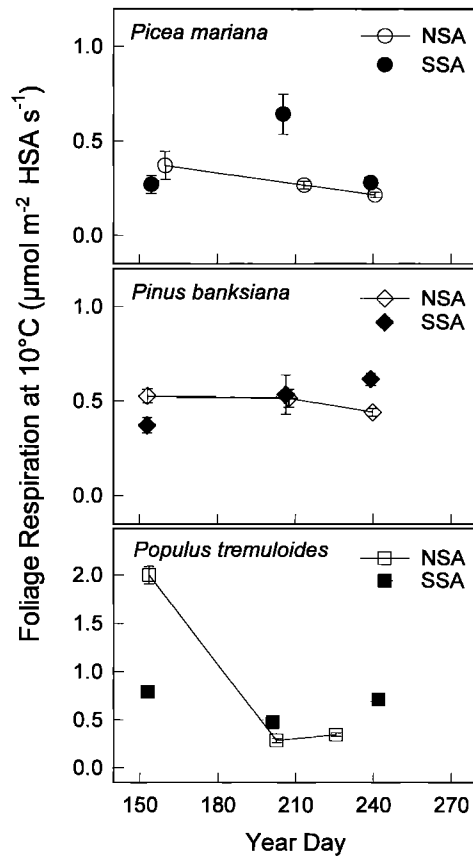
Figure 1. Foliage respiration rates in 1994 for black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*) trees at OBS, OJP, and OA sites in northern (NSA) and southern (SSA) study areas. Rates are expressed per unit hemisurface area [*NASA*, 1994] and represent the average of 15–30 samples distributed in the top, middle, and lower thirds of the canopy. Error bars are standard errors.
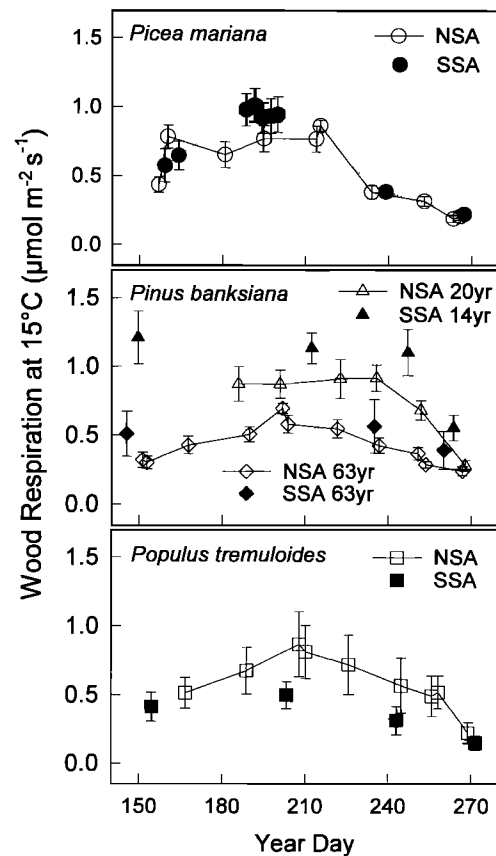

Figure 2. Stem wood respiration rates in 1994 for black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*) trees at OBS, OJP, and OA sites in NSA and SSA. Rates are expressed per unit stem surface area and are the average of 16–24 samples distributed across the range of tree sizes in the stand. Error bars are standard errors. For *Pinus banksiana*, "NSA 20 yr" and "SSA 14 yr" are the young jack pine stands and "NSA 63 yr" and "SSA 63 yr" are the old jack pine stands.

season respiration rates differed as well. In middle to late September 1994, respiration rates were 9, 40, 14, and 45 μmol $m^{-3} s^{-1}$ for aspen, black spruce, jack pine (old), and jack pine (young) in the northern study area and 9, 33, 20, and 50 μmol $m^{-3} s^{-1}$ for aspen, black spruce, jack pine (old), and jack pine (young) in the southern study area. Species with the greatest differences in respiration rates between the dormant and the growing seasons had the highest per tree growth rates. [*Lavigne and Ryan*, 1997]. Alder stem respiration at 15°C was 73 μmol

$m^{-3} s^{-1}$ in June, 194 μmol $m^{-3} s^{-1}$ in July, and 203 μmol m^{-3} s^{-1} in August.

The response of r_w to temperature differed between aspen and the conifers ($p < 0.01$), with Q_{10} (the increase in respiration with a 10°C increase in temperature) averaging 1.3 for aspen and 1.7 for the conifers. Temperature response of r_w

Table 4. Average Respiration Rates in Eight Boreal Forest Stands

Site	Expanding Foliage (Night) (μmol $m^{-2} s^{-1}$) at 10°C	Fully Expanded Foliage (Night) (μmol $m^{-2} s^{-1}$) at 10°C	Aboveground Wood (μmol $m^{-3} s^{-1}$) at 15°C	Fine Root (0–2 mm) (μmol $kg^{-1} s^{-1}$) at 10°C	Coarse Root (μmol $m^{-3} s^{-1}$) at 15°C	Understory Foliage (μmol $m^{-2} s^{-1}$) at 10°C	Understory Stems (μmol $m^{-3} s^{-1}$) at 15°C
NSA-OBS	0.41 (0.07)	0.24 (0.16)	76 (41)	5.4 (4.2)	170 (150)		
NSA-OJP	0.83 (0.19)	0.44 (0.14)	26 (13)	5.6 (3.8)	74 (32)		
NSA-OA	2.0 (0.41)	0.32 (0.11)	21 (16)	4.0 (2.4)	140 (87)	0.34 (0.11)	260 (280)
NSA-YJP			110 (53)				
SSA-OBS	0.93 (0.71)	0.30 (0.15)	56 (20)	3.9 (2.1)			
SSA-OJP	0.83 (0.70)	0.46 (0.23)	23 (8.2)	3.6 (2.1)			
SSA-OA	0.79 (0.20)	0.59 (0.22)	18 (12)	5.1 (3.5)		0.42 (0.18)	
SSA-YJP			88 (30)				

Numbers in parentheses are standard deviations.

within a species differed little within the growing season and between the growing and the dormant seasons.

Root Respiration

Rates of r_r for roots <2 mm diameter were similar for the mature spruce and jack pine stands (2.5–7.7 μmol kg^{-1} s^{-1} at 10°C, Table 4), and r_r declined at the end of the growing season (Figure 3). For the mature spruce and jack pine stands, fine root r_r was lower in IFC-1 and IFC-2 at the southern study area. With the exception of the IFC-2 sample in the southern study area, r_r of aspen fine roots was lower than that of the conifers (3.5–4.2 μmol kg^{-1} s^{-1} at 10°C) and constant throughout the growing season. Per unit biomass, r_r for aspen fine roots was lower than that of aspen foliage (about 10 μmol kg^{-1} s^{-1} at 10°C) but greater for conifer fine roots than for conifer foliage (about 3 μmol kg^{-1} s^{-1} at 10°C). Temperature response of r_r did not differ among species ($p < 0.15$) and the average Q_{10} was 1.9.

Coarse root r_r was generally greater than that of stem wood. Corrected to 15°C, r_r averaged 0.36 μmol kg^{-1} s^{-1} for aspen, 0.43 μmol kg^{-1} s^{-1} for mature black spruce, and 0.19 μmol kg^{-1} s^{-1} for mature pine. Rates per unit of sapwood volume averaged 144 μmol m^{-3} s^{-1} for aspen, 174 μmol m^{-3} s^{-1} for mature black spruce, and 74 μmol m^{-3} s^{-1} for mature pine (Table 4). Rates did not differ between July and August samples ($p > 0.44$).

Figure 4. Annual course of aboveground autotrophic respiration (understory, wood, and overstory foliage at night) at OBS, OJP, YJP, and OA sites in NSA and SSA. Rates are expressed per unit ground area and are the average of 15- to 60-min estimates for the day. The top line is the average total respiration. The white area under the top line is foliage night respiration; the black area is wood respiration; the bottom white area is understory respiration. Respiration was estimated using site-specific respiration rates for foliage, wood, and understory (extrapolated to an entire year), site-specific values of understory and overstory leaf area, and biomass or sapwood volume, and site-specific measurements or estimates of air temperature.
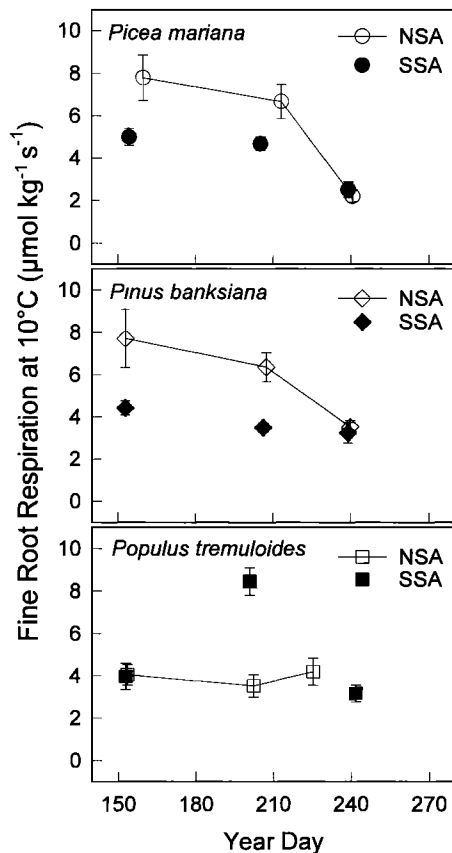

Figure 3. Respiration rates of fine roots (0–2 mm wet diameter) in 1994 for black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*) trees at OBS, OJP, and OA sites in NSA and SSA. Rates are expressed per unit fine root dry mass and are the average of 15–25 samples per site. Error bars are standard errors.
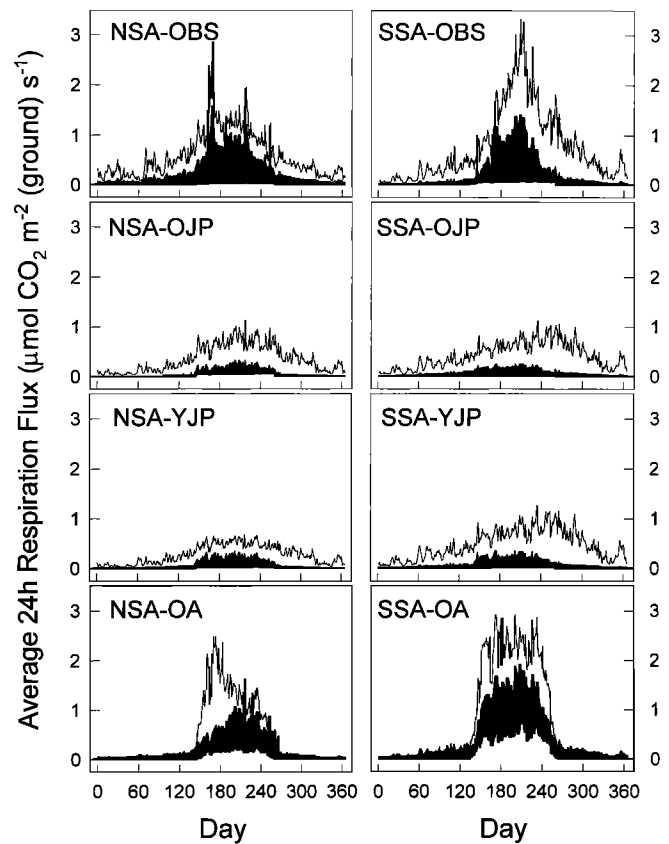
Site Estimates and Annual Budgets

Site differences in the annual course of aboveground R_a (Figure 4) are caused by differences in tissue respiration rates and their seasonal pattern, biomass, and climate. The highest fluxes for aboveground R_a were in black spruce and aspen in midsummer, where large foliar and wood biomass and (for spruce) high R_w gave an average daily aboveground flux of CO_2 of >2 μmol m^{-2} (ground) s^{-1}. Fluxes of C for wood plus foliage respiration for jack pine were generally below 1 μmol m^{-2} s^{-1} throughout the year, as were fluxes from aspen and black spruce outside of the growing season. Understory respiration exceeded 5% of above ground R_a only in the aspen stands.

Fluxes for foliage respiration for the ecosystem (R_f) generally exceeded those for wood (R_w, Figure 4, Table 5), except for mature spruce in the NSA and aspen in NSA at the end of the growing season. Foliage has a positive carbon balance in the day when radiation exceeds the compensation point, but the CO_2 efflux from wood respiration occurs throughout the

Table 5. Annual Autotrophic Respiration (g C m^{-2} yr^{-1}) by Component in Eight Boreal Forest Stands

Site	Overstory Foliage (Night)	Above-ground Wood	Understory Wood Plus Foliage (Night)	Total Above-ground	Fine Root, 0–2 mm	Fine Root, 2–5 mm	Coarse Root	Total Root	Total Auto-trophic	Overstory Plus Understory Foliage, 24 hours	Total Autotrophic (Including 24-hour Dark Foliage Respiration)
NSA-OBS	121	103	5	229	162	78	143	382	611	345	830
NSA-OJP	106	22	6	135	267	17	30	314	450	313	651
NSA-OA	75	77	19	171	147	47	122	316	486	345	741
NSA-YJP	74	27	4	105	NA	NA	NA	NA	NA	180	NA
SSA-OBS	195	87	9	291	51	47	95	192	483	504	785
SSA-OJP	129	30	2	161	93	11	47	151	312	354	535
SA-OA	105	123	62	290	100	65	149	314	604	464	908
SSA-YJP	142	38	4	184	NA	NA	NA	NA	NA	381	NA

day and night. Therefore fluxes of CO_2 from foliage at night are 2–5 times larger than those from wood. At night the sum of R_f and R_w was 30–60% of ecosystem respiration [*Lavigne et al.*, this issue].

Construction respiration, calculated by subtracting maintenance respiration from the total (maintenance was estimated using rates for the dormant season for the entire year), averaged 45% of the total for wood and 23% of the total for foliage. Wood construction respiration was lowest for the slow growing OJP sites (26% of the total) and highest at the OA sites (51%). Foliage construction respiration was greatest at the aspen sites (44% of the total). Wood construction respiration for the eight sites was not significantly different (p = 0.30) from construction respiration estimated as 0.25 times wood NPP [see *Ryan*, 1991b], but there were large differences for individual species (construction respiration was 1.6–3.6 times greater than 0.25 times wood NPP for black spruce and young jack pine and 0.4–0.8 times less for old jack pine). For foliage, construction respiration for the eight sites was significantly greater than construction respiration estimated as 0.25 times foliage NPP (28 g C m^{-2} yr^{-1} versus 15 g C m^{-2} yr^{-1}, $p < .01$).

During the growing season, root respiration for the ecosystem (R_r) was about 70% of aboveground respiration for the mature spruce and aspen sites but was equal to or exceeded aboveground respiration at the mature jack pine sites (Figure 5). R_r in autumn, winter, and spring were generally greater than aboveground fluxes. At NSA-OBS and NSA-OJP, R_r during the growing season was 74 and 71%, respectively, of surface ("soil") respiration measured in dark chambers (estimated from static chambers and soil temperature at 10 cm depth [see *Lavigne et al.* [this issue] for details of the surface respiration models).

Even in the strongly seasonal boreal forest, a substantial fraction of R_a occurred outside of the growing season. For the conifer sites, 27–42% of the annual total of aboveground R_a occurred outside of the 120- to 150-day growing season, compared with 12–14% for deciduous aspen. For conifers and aspen, 27–51% of R_r occurred outside the growing season.

On an annual basis, fluxes of C from R_a were 54–71% of the plant carbon balance (Tables 5, 7) (dry matter production (NPP, Table 6) comprised the remainder). Aboveground R_a for conifer sites (OBS, OJP, YJP) was larger than aboveground dry matter production; for aspen, aboveground R_a was roughly equivalent (Tables 5, 7). Overstory and understory night R_f was 67% of the aboveground total and a higher percent for the conifer stands (74%) than for the aspen stands (54%). Foliage

night R_f was 21% of aboveground plus root respiration in NSA and 37% in SSA. If we assume dark R_f has the same rate during the day, night R_f averaged 30% of 24-hour R_f. Both night R_f and aboveground R_w were similar for the young and mature jack pine sites in both the SSA and the NSA.

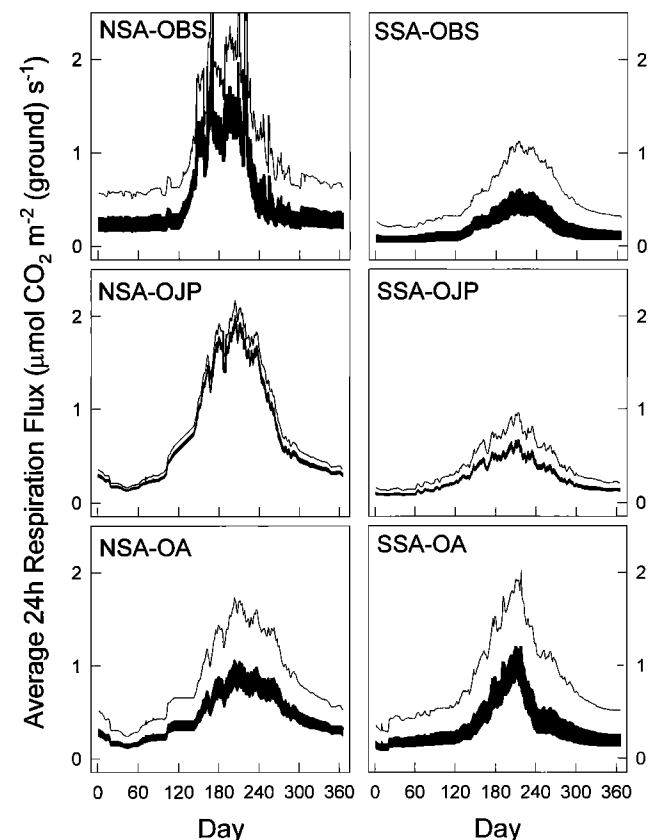R_r averaged 34% of the total in NSA and 53% in SSA.

Figure 5. Annual course of root respiration for overstory trees at OBS, OJP, YJP, and OA sites in NSA and SSA. Rates are expressed per unit ground area and are the average of 15- to 60-minute estimates for the day. The top line is the average root respiration. The white area under the top line is coarse root respiration; the black area is 2–5 mm root respiration; the lower white area is fine root (0–2 mm) respiration. Respiration was estimated using site-specific respiration rates for fine roots and coarse roots for NSA, site-specific values of root biomass, and site-specific measurements or estimates of soil temperature.

Table 6. Annual Net Primary Production (g C m^{-2} yr^{-1}) by Component for Eight Boreal Forest Stands

Site	Overstory Wood	Foliage Increment	Litter	Total Overstory	Understory	Aboveground	Coarse and Fine Roots	Total
NSA-OBS	73	5	45	123	9	132	120	252
NSA-OJP	65	5	34	104	11	115	114	229
NSA-OA	214	0	98	312	30	342	74	416
NSA-YJP	17	4	23	44	NA	NA	NA	NA
SSA-OBS	80	2	51	139	9	147	160	307
SSA-OJP	59	8	48	108	7	115	122	237
SSA-OA	176	0	119	295	66	361	79	440
SSA-YJP	38	1	53	92	NA	NA	NA	NA

Net production data for aboveground and below-ground tissues are from *Gower et al.* [this issue] and *Steele et al.* [1997], respectively.

Averaged over all sites (excluding YJP, where root biomass was not measured), R_r for roots <2 mm in diameter was 49% of total R_r. However, R_r for roots <2 mm was a much larger percentage of total R_r in the mature jack pine sites (74%) than in the mature spruce or aspen sites (37%).

The sum of dark R_f, R_w, R_r (Table 5) and aboveground and below-ground NPP estimates net photosynthesis [*Ryan et al.*, 1994], assuming losses to herbivory are minor. Similarly, the sum of 24-hour R_f, R_w, R_r, and aboveground and below-ground NPP estimates gross photosynthesis or GPP [*Ryan*, 1991b]. Annual net and gross photosyntheses were similar for the NSA and the SSA; average net photosynthesis was 810 g C m^{-2} yr^{-1} in NSA sites and 790 g C m^{-2} yr^{-1} in SSA sites; average gross photosynthesis was 1000 g C m^{-2} yr^{-1} in NSA sites and 1100 g C m^{-2} yr^{-1} in SSA sites (Table 7). For both the NSA and the SSA, estimated gross net photosynthesis was highest for the aspen sites and lowest for the jack pine sites.

Carbon use efficiency estimates the efficiency at which carbon allocated to a tissue or the ecosystem is converted into biomass. For the aboveground tissues, CUE averaged 0.43 (SE = 0.05) for all sites (Table 7). However, the aboveground CUE of the aspen sites (0.61) was much higher than that of the conifer sites (0.37). CUE of roots was low (0.30), lowering overall efficiency to an average of 0.39 (SE = 0.03), averaged for the mature black spruce, mature pine, and aspen sites. CUE (for aboveground tissues and for total) did not vary substantially between the northern and the southern study areas for spruce and pine but did differ for aspen. CUE did not vary significantly with stand biomass for either aboveground tissues (p = 0.13) or all tissues combined (p = 0.26). The ratio of NPP to GPP (the efficiency of using gross photosynthesis) was lower than CUE (average of six sites was 0.29 (SE = 0.02)), because of the substantial cost estimated for R_f

during the day. NPP:GPP was also much greater for the aspen stands (0.35) than for the mature spruce and jack pine stands (0.27).

What is the uncertainty associated with our flux estimates? We identified five potential sources of error in the estimates: (1) respiration rates (standard errors were 5–25% of the mean); (2) distribution of the samples in space (we selected our samples to be representative for the canopy, wood, and roots, but the cuvette samples represent only a very small fraction of total biomass); (3) extrapolation of rates throughout the year (linear interpolation may cause error, and the assumption that autumn or spring rates applied throughout the winter may be incorrect); (4) estimates of biomass for stands (standard errors were 2–20% of the mean); and (5) temperature response (standard errors were 2–8% of the mean). We could not estimate the error associated with (2) and (3), but recalculating the fluxes using the upper and lower 95% confidence intervals for respiration rates, biomass components, and temperature response gave an approximate uncertainty estimate of 33–62% of the mean for the 15- to 60-min flux estimates. Respiration rates do not include respiration of moss, which could be important for the spruce sites (where moss can have high respiration rates [*Goulden and Crill*, 1997]).

Discussion

Foliar Respiration

Foliar respiration is higher for expanding foliage, because of the large contribution of growth respiration [*Ryan et al.*, 1994]. For black spruce and jack pine, however, expanding foliage is a small fraction of the total foliar biomass (10–14% for black spruce and 16–28% for jack pine). Because of this and because new foliage of conifers was too small to measure in IFC-1, r_f

Table 7. Estimated Net and Gross Photosynthesis (g C m^{-2} yr^{-1}) and Carbon Use Efficiency (CUE = NPP/(NPP + R_a)) for Eight Boreal Forest Stands

Site	Estimated Net Photosynthesis	Estimated Gross Photosynthesis	CUE Aboveground	CUE Roots	CUE Total	NPP/GPP Aboveground	NPP/GPP Total
NSA-OBS	860	1080	0.37	0.24	0.29	0.22	0.23
NSA-OJP	680	880	0.46	0.27	0.34	0.24	0.26
NSA-OA	900	1160	0.67	0.19	0.46	0.42	0.36
NSA-YJP	NA	NA	0.30	NA	NA	0.17	NA
SSA-OBS	790	1090	0.34	0.45	0.39	0.19	0.28
SSA-OJP	550	772	0.42	0.45	0.43	0.22	0.31
SSA-OA	1040	1350	0.55	0.20	0.42	0.33	0.33
SSA-YJP	NA	NA	0.34	NA	NA	0.18	NA

Net and gross photosyntheses are estimated as the sum of annual net primary production and annual autotrophic respiration; gross photosynthesis includes foliage dark respiration during the day.

showed little seasonal variability. Aspen, in contrast, showed very high r_f when the foliage was expanding in late May in the northern study area. The IFC-1 measurement for aspen foliage in the southern study area was made after foliar expansion and construction respiration had slowed. Our model for estimating foliage growth and respiration of expanding foliage apparently overestimates respiration, because estimated construction respiration was nearly 2 times that estimated from foliage production. Estimates for foliage construction respiration and foliage expansion are poor because much of the foliar growth occurred between IFC-1 and IFC-2, when r_f was not measured. Poor estimates of construction r_f and foliage expansion will likely have little effect on estimates of annual R_a, because construction r_f is <8% of the total for any site.

Within a species, r_f was generally higher in the southern study area, likely reflecting the greater foliar N [Ryan, 1995]. For this study, r_f was similar to that measured in 1993 on the same species [Ryan, 1995] and within the range of those reported elsewhere for conifers [Sprugel et al., 1995]. In the NSA, r_f for conifers was about 10% of that reported for photosynthesis under nonlimiting light and high humidity [e.g., Dang et al., 1997]; r_f for aspen was about 5% reported maximum photosynthesis rates.

Wood Respiration

In this study, r_w was slightly higher than reported elsewhere for conifers and lower for aspen than for other deciduous trees. For example, dormant season r_w was 7–13 μmol m^{-3} s^{-1} at 15°C for temperate conifers [Ryan et al., 1994] and 15 and 74 for sugar maple (Acer saccharum) and red oak (Quercus rubra) [Gower et al., 1991]. Dormant season respiration for aspen may be low because of the ability of the photosynthetic bark to fix carbon and offset respiratory losses [Foote and Schaedle, 1976, 1978]. Age or growth rate also influence dormant season (maintenance) r_w, because r_w per unit of sapwood volume was much lower for the older, slower growing jack pine in both the NSA and the SSA [Lavigne and Ryan, 1997]. The agreement between the two methods of estimating construction respiration suggests that on average, estimates of annual respiration may be derived from dormant season rates and measurements of production. However, the approach may give incorrect estimates for individual species, because Lavigne and Ryan [1997] found that construction cost (carbon efflux per gram of carbon incorporated into structural matter) differed substantially among species.

Aboveground R_a did not differ appreciably for the different-aged jack pine forests. Increased respiration costs for the larger woody biomass in older stands is a common (but likely incorrect) explanation for the universally observed decline in NPP with forest age [Gower et al., 1996; Ryan et al., 1997]. In this study, R_w was a low fraction of the total R_a and similar for the young and old jack pine stands in both the northern and the southern study areas. In both the dormant and the growing seasons, r_w reflected the overall growth of the trees (relatively fast for young jack pine and slow for old jack pine), so higher respiring biomass in the older stands was offset by lower r_w [Lavigne and Ryan, 1997].

Root Respiration

Fine root r_r (0–2 mm) were somewhat lower than those reported elsewhere for temperate conifers [e.g., Ryan et al., 1994; Sprugel et al., 1995; Ryan et al., 1996a; Zogg et al., 1996], perhaps because we measured fine root respiration at the CO_2

concentration of soil or litter where they were located (2–4 times atmospheric levels), and elevated CO_2 decreases respiratory CO_2 efflux [Qi et al., 1994]. Respiration for coarse roots was similar to those of pine roots of the same diameter [Ryan et al., 1996a].

Site Estimates and Annual Budgets

Results of this study support the concept that R_a is a large component (>50%) of the annual carbon budget [Edwards et al., 1980; Sprugel and Benecke, 1991; Ryan et al., 1994]. Additionally, R_a in the dormant season is >25% of the annual total (perhaps higher for root respiration), and these dormant season fluxes are important in determining annual carbon balance. Measurements of net ecosystem carbon fluxes by eddy covariance show that dormant season respiration fluxes (both R_a and R_h) influence the annual C balance for boreal forests [e.g., Goulden et al., this issue].

Fluxes determined from extrapolated chamber measurements are quite uncertain because of the many steps in the process and the uncertainties associated with each step. R_r is particularly uncertain because fine root biomass is highly variable, r_r for 2–5 mm fine roots was not measured, and coarse root biomass was estimated from off-site allometric equations. Greater sampling of r_r and root biomass will reduce the uncertainties for R_r, but it is unlikely that these uncertainties can be reduced for aboveground fluxes, as this effort represents the largest spatial and temporal sampling of which we are aware. Modeled estimates of R_a with the BIOME-BGC model were within −36 to +38% of our values [see Kimball et al., 1997].

Estimates of respiration extrapolated from chambers at night (including soil respiration) were 25–50% (mean 35%) greater than ecosystem flux measurements made using eddy covariance at six conifer sites (OBS, YJP, OJP in NSA and SSA [Lavigne et al., this issue]). Except for the mature spruce sites where the biomass plots may slightly overestimate biomass for the eddy covariance "footprint," Lavigne et al. [this issue] were unable to identify a systematic source of bias in the chamber extrapolations. A similar chamber-eddy covariance comparison in a deciduous forest found that the extrapolated chamber measurements were also about 25% greater than the nocturnal eddy flux measurements [Goulden et al., 1966].

Carbon use efficiency estimates the efficiency at which carbon fixed in photosynthesis is converted to dry matter on an annual basis and can be used to assess the impact of respiration on productivity [Gifford, 1994; Ryan et al., 1996a]. The consistent differences among species (both NSA and SSA sites) suggest that species differences are real and important. CUE for aspen is likely greater than that of the conifers because of its deciduous habit (no foliar respiration outside of the growing season) and because chlorophyll in the bark mitigates losses from wood respiration [Foote and Schaedle, 1976, 1978]. CUE for black spruce is low because it retains a high foliar biomass relative to NPP (wood NPP per unit of leaf area in black spruce is 50–60% of that in the mature jack pine stands). The high foliar biomass in black spruce stands stores nutrients in the canopy instead of in soil organic matter where they are largely unavailable to the plant. The low aboveground CUE for young jack pine likely results from an incorrect estimate of the NPP. NPP was estimated as biomass/stand age [Gower et al., this issue]. However, biomass growth increases exponentially with stand age (until canopy closure); therefore actual NPP for 1994 is likely higher than estimated.

Because the long-term average temperature differed be-

Table 8. Carbon Use Efficiency (CUE = NPP/(NPP + R_a)) for Forest Stands

Species	Average Annual Temp., °C	Aboveground biomass, g C m^{-2}	CUE Aboveground	CUE Total	NPP/GPP	Reference
Pinus contorta	3.6	5600	0.50	0.36		Ryan and Waring [1992]
Pinus contorta, montane	8.0	11240	0.39	0.37		Benecke and Nordmeyer [1982]
Pinus contorta, subalpine	5.1	9390	0.41	0.43		Benecke and Nordmeyer [1982]
Nothofagus solandri, montane	8.0	13670	0.49	0.45		Benecke and Nordmeyer [1982]
Nothofagus solandri, subalpine	5.1	14260	0.55	0.57		Benecke and Nordmeyer [1982]
Pinus taeda	16.0	5780		0.50		Kinerson et al. [1977]
Pinus elliottii	22.0	5300		0.46		Gholz et al. [1991], Cropper and Gholz [1993]
Pinus radiata, control	13.0	6010	0.50		0.43*	Ryan et al. [1996a]
Pinus radiata, irrigated	13.0	7160	0.55		0.50*	Ryan et al. [1996a]
Pinus radiata, irrigated + fertilization	13.0	11310	0.54		0.48*	Ryan et al. [1996a]
Pinus banksiana, north	−3.9	2330	0.46	0.34	0.19	this study
Pinus banksiana, south	0.1	3090	0.42	0.43	0.21	this study
Populus tremuloides, north	−3.9	5630	0.67	0.46	0.35	this study
Populus tremuloides, south	0.1	9260	0.55	0.42	0.32	this study
Picea mariana, north	−3.9	5630	0.37	0.29	0.17	this study
Picea mariana, south	0.1	4820	0.34	0.39	0.20	this study

NPP is annual above plus below-ground net primary productivity, GPP is annual gross photosynthetic C fixation, not including photorespiration.
*Aboveground only.

tween the northern and the southern study areas, we expected differences in CUE between study areas for a given overstory species. In 1994, temperature differences were much less than normal, and the NSA had a record warm year. Average annual temperature in 1994 was still cooler in the NSA (−2.3 versus 0.2°C), but most of the temperature difference occurred in winter. For May to September, average temperature in the NSA was only slightly lower than in the south (13.1 versus 14.0). Given the response of R_a to temperature, the 0.9°C growing-season temperature difference would only change R_a by 6% and have a negligible effect on CUE. Therefore 1994 was inadequate to test whether climate can alter CUE. We suspect that variation in CUE is not related to climate, because we found large differences between species in this study (with similar climate), and Ryan et al. [1994] found no relationship between CUE and average annual temperature for pine forests.

Total CUE for jack pine and aspen stands in this study was similar to values estimated elsewhere for entire stands (Table 8). In contrast, CUE for the mature spruce forests was lower than for other conifer stands growing in warmer climates (Pinus taeda, Pinus elliottii, Table 8) but similar to conifers growing in cooler climates (e.g., Pinus contorta). Differences in CUE among species exist (Table 8) and are likely important for estimating carbon budgets for a given site. Overall, however, CUE tends to be conservative for stands over a wide range of aboveground biomass and average annual temperature (Table 8). Average aboveground and total CUE were 0.48 and 0.42, respectively (CV = 18%) for the studies in Table 8, and neither aboveground nor total CUE was correlated with biomass or average temperature.

For a given species, and perhaps among species, CUE should be fairly conservative, because growth, respiration, and photosynthesis are strongly linked [Amthor, 1994; Gifford, 1994]. Dry matter production depends on the supply of carbohydrate from photosynthesis [e.g., Cannell, 1989], and respiration is used to synthesize the compounds and supply energy for biomass production [Amthor, 1989]. Both photosynthesis and respiration (especially the maintenance component) increase with increasing tissue N content in foliage [Field and Mooney,

1986; Ryan, 1991a, 1995]. Nitrogen content in foliage is correlated with N in wood and roots, so as maintenance respiration costs rise, they are balanced by an increase in photosynthetic capacity in leaves.

Because of the strong link between R_a and production, changes in environment will likely produce offsetting changes in photosynthesis and R_a. For example, if temperature increases (and moisture is available), maintenance respiration will increase, but so will photosynthesis. If moisture is unavailable, photosynthesis will decline, but so will growth and construction respiration (although maintenance respiration may increase). Because maintenance respiration may also vary with cellular activity (independent of N content) [Lavigne et al., 1996], lowered photosynthesis may also reduce maintenance respiration. Large differences in temperature [Gifford, 1994] and N status [Ryan et al., 1996a] did not alter CUE in other studies.

Conclusions

Autotrophic respiration is an important component of the annual carbon balance, consuming 54–71% of annual net photosynthesis and 64–77% of annual gross photosynthesis. Estimated gross and net photosynthesis and CUE were similar for stands of the same species growing in the two different study areas. This study showed that species clearly differ in CUE, perhaps because of differences in foliage biomass, or the ability of photosynthetic bark to refix respired C. These differences in CUE among species will be important in estimating carbon budgets for individual stands. However, this study and others in the literature suggest that CUE is conservative over a wide range of annual air temperature and aboveground biomass.

Notation

R_a autotrophic respiration.
R_h heterotrophic respiration.
r_f foliage respiration, μmol m^{-2} (leaf) s^{-1}.
r_w wood respiration, μmol m^{-2} (stem) s^{-1}.

r_r root respiration, μmol kg^{-1} s^{-1}.

R_f foliage respiration for ecosystem, μmol m^{-2} (ground) s^{-1}.

R_w wood respiration for ecosystem, μmol m^{-2} (ground) s^{-1}.

R_r root respiration for ecosystem, μmol m^{-2} (ground) s^{-1}.

NPP net primary production (typically g C m^{-2} (ground) yr^{-1}).

GPP gross primary production (typically g C m^{-2} (ground) yr^{-1}).

CUE carbon use efficiency, NPP/(NPP $+ R_a$) = NPP/net photosynthesis.

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