

Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence

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Received March 3, 2004; accepted June 11, 2004; published online October 1, 2004

Summary We quantified the contributions of root respiration (RC) and heterotrophic respiration to soil surface CO₂ flux (R_S) by comparing trenched and untrenched plots in well-drained and poorly drained stands of a black spruce (*Picea mariana* (Mill.) BSP) fire chronosequence in northern Manitoba, Canada. Our objectives were to: (1) test different equations for modeling R_S as a function of soil temperature; and (2) model annual R_S and RC for the chronosequence from continuous soil temperature measurements. The choice of equation to model R_S strongly affected annual R_S and RC, with an Arrhenius-based model giving the best fit to the data, especially at low temperatures. Modeled values of annual R_S were positively correlated with soil temperature at 2-cm depth and were affected by year of burn and trenching, but not by soil drainage. During the growing season, measured RC was low in May, peaked in late July and declined to low values by the end of the growing season. Annual RC was < 5% of R_S in the recently burned stands, ~40% in the 21-year-old stands and 5–15% in the oldest (152-year-old) stands. Evidence suggests that RC may have been underestimated in the oldest stands, with residual root decay from trenching accounting for 5–10% of trenched plot R_S at most sites.

Keywords: *autotrophic respiration, boreal forest, heterotrophic respiration, modeling, trenched plots.*

Introduction

Boreal forests have been studied intensively in relation to the global carbon (C) cycle. Circumpolar and composed primarily of spruce, pine and larch, these forests contain one of the largest terrestrial C reserves, while accounting for only ~25% of the world's forested area (Post et al. 1982, Schlesinger 1997). The disproportionate C content of the boreal forest is due to several factors, including low temperatures, frequent permafrost, poor soil drainage and the relative importance of *Sphagnum* and feather mosses, which retard the decay of forest litter, including dead roots (Harden et al. 2000, Hobbie et al. 2000, Kasischke 2000).

Soil surface CO₂ flux (R_S) is the second largest flux in the global C cycle (Raich and Schlesinger 1992). It is sensitive to

soil temperature (Lloyd and Taylor 1994, Boone et al. 1998), and water content (Moore and Knowles 1989), resource quality (Raich and Tufekcioglu 2000, Robinson 2002), and current photosynthetic rate (Högberg et al. 2001, Kuzyakov and Cheng 2001). Soil surface CO₂ flux is overwhelmingly comprised of hetero- (R_H ; microbes and soil fauna) and autotrophic (R_A ; root) respiration components. Three primary methods have been used to separate R_H and R_A : direct measurements of root respiration or soil incubations, plots with and without roots, and stable or radioactive isotope techniques (Hanson et al. 2000).

Published estimates of the contribution of root respiration (RC) to R_S vary, with mean values of 45–50% for forest ecosystems (Hanson et al. 2000). Here we follow many previous studies in using the terms “root respiration” and “autotrophic respiration” interchangeably, but note that there are heterotrophic contributions to what we refer to as “root respiration,” e.g., rhizospheric respiration of symbiotic mycorrhizal fungi (Keltling et al. 1998). There is, however, no standard practice of including rhizospheric respiration in soil microbial respiration or in autotrophic root respiration (Keltling et al. 1998, Hanson et al. 2000).

Partitioning the heterotrophic and root sources of R_S is difficult but important. Net primary production (the balance between gross primary production and total autotrophic respiration of the ecosystem) includes R_A losses (Gower et al. 2001), but knowledge of heterotrophic losses is required to calculate net ecosystem production and allow comparison with eddy flux measurements. In addition, R_H and R_A may respond differently to environmental variables (Boone et al. 1998, Widén and Majdi 2001), implying different flux behaviors at a variety of time scales. Thus, the contribution of each component must be known in order to understand the effects of climate change (Melillo et al. 2002), forest age and disturbance regime on soil C cycling and respiration. Partitioning R_S sources during stand development is particularly important in boreal forests because the dominant disturbance is wildfire, a factor that strongly influences stand and landscape age structure, species composition, biogeochemical cycles, net primary production and net ecosystem CO₂ exchange (Goldammer and Furyaev 1996, Gower et al. 2001).

The response of R_S to temperature has been described by various models (Fang and Moncrieff 2001) with diverse theoretical bases. Linear, logistic and quadratic equations have been used, but the most commonly employed are exponential and Arrhenius equations, both of which describe an increase in R_S with temperature, but with different behaviors at low and high temperatures. The temperature sensitivity of R_S (Q_{10}) is constant in the exponential model, but declines at high temperatures in the Arrhenius model. Several studies (Lloyd and Taylor 1994, Hess and Schmidt 1995, Fang and Moncrieff 2001) have examined the fitting of these and other models to various data, but few have explored the consequences of model choice on calculating annual R_S and RC in field settings as opposed to laboratory incubations.

Few studies partitioning R_S have been performed in boreal forests, and we are unaware of any studies with a chronosequence design that examine changes in RC during stand development. In this study, we quantified the contributions of RC and heterotrophic respiration to R_S by comparing trenched and untrenched plots in well-drained and poorly drained stands of an age sequence (wildfire chronosequence) of black spruce (*Picea mariana* (Mill.) BSP)-dominated stands. The objectives of the study were to: (1) test different equations for modeling R_S as a function of soil temperature; and (2) model annual R_S and RC for the chronosequence from continuous soil temperature measurements.

Materials and methods

Site descriptions

The study was conducted west of Thompson, Manitoba, Canada, near the BOREAS Northern Study Area (55°53' N, 98°20' W), in two soil drainages nested within seven different-aged black spruce forests. The stands included in this chronosequence grew after stand-killing wildfires in 1850, 1930, 1964, 1981, 1989, 1995 and 1998. All stands are within a 40 km² area except the two most recently burned stands, which are located in Leaf Rapids, Manitoba, ~100 km northwest of the older stands. Annual mean temperature and precipitation were 0.8 °C and 438.5 mm, respectively. The 14 stands have been studied extensively and differ in their species mix, leaf area (Bond-Lamberty et al. 2002b), soil and woody debris CO₂ fluxes (Bond-Lamberty et al. 2002a, Wang et al. 2002), C distribution (Wang et al. 2003), net primary production (Bond-Lamberty et al. 2004b) and net ecosystem exchange (Litvak et al. 2002).

The study chronosequence was established in May 1999 by locating one "dry" (well drained) and one "wet" (poorly drained) stand in each burn area. Stands at the wet and dry sites are identified by the letters "D" and "W", respectively, plus the year of burn. Stands were classified as wet or dry depending on edaphic condition and species composition. In the boreal forests of northern Manitoba, common wet-site species include a *Sphagnum* (*Sphagnum* spp.) ground cover, a bog birch (*Betula glandulosa* var. *hallii*) and Labrador tea (*Ledum groenlandicum* Oed.) understory, with a tamarack (*Larix laricina* (Du Roi) C. Koch.) and black spruce overstory. Common species in

the drier stands include a feather moss (usually *Ptilium*, *Pleurozium* or *Hylocomium* spp.) ground cover and *Vaccinium* spp. understory. The stands were dominated by trembling aspen (*Populus tremuloides* Michx.), black spruce and jack pine (*Pinus banksiana* Lamb.). Early successional deciduous tree species give way to black spruce in the older chronosequence stands; the black spruce canopy closure, at about 50 years, is associated with drastic thinning of the understory and growth of thick feather mosses in the well-drained stands.

So far as possible, study sites were matched for soil type. Generally, soils are composed of sedimentary materials deposited by glacial Lake Agassiz. The dry stands are located on moderately drained montmorillonite clay soils classified as Gray Luvisols (Boralfs), whereas the wet stands are located on poorly drained clay soils, underlain with discontinuous permafrost at 100–150 cm, and generally classified as Luvic Gleysols (Aqualfs). One poorly drained stand with deep peat (the 21-year-old wet stand) has Fibrisols, Mesisols and organic Cryosols; the 7-year-old stands were derived from morainal deposits of sand and gravel.

Replicate plots and measurement collars

Replicate plots (5 × 10 m) were established in each stand, located at least 200 m from the edge of a burn. Four plots in the well-drained stands were located randomly, while five plots in the poorly drained stands were oriented end-to-end, because of the design limitations imposed by a concurrent study at the same site. We do not address the statistical problems associated with this end-to-end design, because the flux and model errors reported below are not based on plot-to-plot variability. In 1999, two polyvinyl chloride (PVC) collars (33 cm inside diameter, 5 cm tall) were inserted to a depth of 2–4 cm in the soil, at random locations, in each replicate plot; we avoided severing visible roots in the process. The collars had a beveled lower edge to facilitate insertion with minimal soil compaction and were left undisturbed throughout the study. Two additional randomly sited collars were added to each plot in the summer of 2000. Around each new collar, the outside edges of a 1 × 1 m square were excavated to a depth of 50 cm, below which few roots exist in these cold clay soils (Strong and La Roi 1983, Wang et al. 2003). Trenches were lined with 6-mil clear plastic film and backfilled, after which these "trenched" plots were carefully weeded to remove aboveground vegetation with minimal soil disturbance. Moss (primarily feather mosses in dry sites, *Sphagnum* in wet sites) was not removed because of the disturbance this would cause to the underlying mineral soil. Throughout the study, weeding of the entire trenched plot was performed at least 24 h before soil surface CO₂ flux measurements were made. Trenched plots were allowed to equilibrate for 10 months before soil surface CO₂ measurements began. A total of 18 trenched plots were dug in each of the seven different-aged sites, eight and 10 in each dry and wet stand, respectively.

Soil surface CO₂ flux and soil temperature

Soil surface CO₂ flux was measured with a Li-Cor 6200 portable CO₂ infrared gas analyzer (IRGA; Li-Cor, Lincoln, NE) equipped with a 33-cm inside diameter, clear acrylic chamber.

Soil surface CO₂ flux was measured monthly during the growing season between May 2001 and August 2002 with the IRGA (flow rate 1100 cm³ s⁻¹, one measurement every 30 s, five measurements in total). Collars were covered with an opaque black cloth during measurements to eliminate the effects of moss photosynthesis on R_S measurements. The IRGA was calibrated daily with 395 ppm CO₂ (± 5%, balance N₂; Scott Specialty Gases, Plumsteadville, PA). The five measurements were averaged to produce a mean R_S for the collar. For each replicate plot, R_S of the trenched (R_{trench}) and control (R_{control}) collars was measured within 10 min, and RC calculated as 1 - R_{trench}/R_{control}, assuming that the difference between R_{trench} and R_{control} was attributable entirely to the absence of root respiration.

Soil temperature was measured both discretely and continuously. Discrete measurements were made at 2- and 10-cm depths next to each collar with a digital long-stem thermometer (15-078K, Fisher Scientific, Pittsburgh, PA), while R_S was being measured. Soil temperatures were measured continuously at the same depths with a Campbell Scientific CR10X data logger (Campbell Scientific, Logan, UT) attached to three sets of copper-constantan thermocouples.

Effects of live moss

Measurements made with a set of small (15-cm inside diameter) PVC collars tested the effects of live moss on R_S measurements. Five pairs of collars were randomly located at the 72-year-old burn site, where the bryophyte layers in the chronosequence were thickest (~30 and ~60 cm of total moss at the dry and wet stands, respectively). All live moss (about the top 6 cm) was clipped in one collar of each pair, and R_S in each collar measured on July 6, July 21 and August 1, 2001.

Data analysis

Discrete soil temperature measurements made during the R_S measurements were used to model the relationship between R_S and soil temperature (T), whereas continuous soil measurements were used to estimate annual R_S from all stands. The continuous and discrete T measurements fitted each other well (data not shown). In four stands (W1995, W1981, D1850, W1850) where no data loggers were installed, discrete measurements of T were fit by linear regression to the continuous T measurements from the other stands in order to predict continuous T values. Wang et al. (2002) detailed these model fits.

To relate T to R_S, four model forms, both linear and nonlinear in their parameters, were examined: a first-order exponential in a form frequently used to describe biological systems, R_S = ae^{bT} (Landsberg and Gower 1997); a second-order exponential, R_S = ae^{bT + cT²} (O'Connell 1990, Wang et al. 2002); an Arrhenius-type model of the form R_S = ae^{-E₀/(T - T₀)} (Kavanau 1951, Lloyd and Taylor 1994); and a power model with a minimum temperature (Fang and Moncrieff 2001) of the form R_S = a(T - T_{min})^b. Model parameters with the smallest sum of squares were estimated for each model type by the iterative Gauss-Newton algorithm of PROC NL MIXED in SAS OnlineDoc Version 8.2 software (SAS Institute, Cary, NC). Soil drainage, stand age and trenched or control status

were treated as fixed effects; replicate plots within a site were treated as a normally distributed random effect. Model fit (adjusted R²), residual distribution and number of required parameters were compared to assess overall model suitability. Empirical models relating R_S to T were developed for each soil drainage class × stand age × trench/control combination; approximate R² values for the site-specific models were computed by fitting the same models without the random effects specified above.

Annual C flux was modeled with the continuous, site-specific soil temperature data and the fitted site-specific R_S models. A paired t-test was used to test for the effects of live moss on R_S.

Results

Choice of model form and independent variable

Soil surface CO₂ flux was positively correlated with soil temperature at both 2-cm (T₂) and 10-cm (T₁₀) depths. Models based on T₂ produced better fits than models based on T₁₀ (R² = 0.77–0.79 versus 0.71–0.75; the Schwarz's Bayesian Criterion metric was also superior); thus, T₂ was selected as the primary predictor variable. Discrete T₂ measurements varied between 1.1 and 29.4 °C; measured R_S (total n = 1082) ranged from 0.18 (Day 267, 3-year-old dry stand) to 8.46 μmol m⁻² s⁻¹ (Day 175, 21-year-old wet stand).

Models based on exponential, second-order exponential, Lloyd and Taylor (1994), Arrhenius (L&T) and the Fang and Moncrieff (2001) minimum-temperature (F&M) functions all provided good fits to the data (site-specific models had R² = 0.68–0.95, with mean R² values of 0.86–0.88 for all model types). All residual distributions were satisfactory (data not shown), and the models produced similar results for the temperature range 10–20 °C. Nonetheless, the models exhibited considerable differences (Figure 1), particularly when extrapolated outside of the measured temperature range. With only two parameters, the exponential model had limited flexibility and predicted high R_S values (1–2 μmol m⁻² s⁻¹) when T₂ ≈ 0. From previous year-round R_S measurements in this chronosequence (Wang et al. 2002), these values were known to be too high by an order of magnitude. The second-order exponential model produced low R_S at low T₂ but also had, at most sites, an optimal temperature (T_{opt}) for R_S at ~15 °C, after which the R_S response declined quickly with increasing temperature (Figure 1). This response prediction was usually driven by a few highly variable measurements and seemed unlikely to be correct (see Discussion). Furthermore, the parameters of this model are difficult to interpret—e.g., one must calculate the first derivative to determine T_{opt}.

The L&T and F&M equations exhibited similar behavior, with the latter being more responsive than the former at low temperatures. Two related problems arose with these models: the parameter-estimation algorithm failed to converge (Bates and Watts 1981) for a number of stands, and because our measurements were confined to the growing season (when normally T₂ > 5 °C), the T_{min} and T₀ parameters frequently converged to unrealistic site-specific values between 0 and 5 °C.

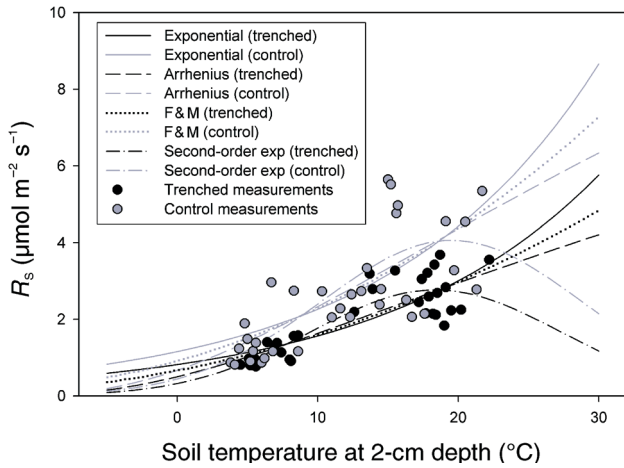


Figure 1. Model fits and measured soil surface CO₂ flux (R_S) for one black spruce stand in the chronosequence (20-year-old dry stand) by model type (exponential, Arrhenius, Fang and Moncrieff (2001) minimum-temperature power (F&M) and second-order exponential). Black lines are models for trenched plot data; grey lines are for control plot data. Model descriptions are given in text.

(R_S is zero and undefined when T_{\min} and T_0 are zero, respectively.) Although the F&M equation has a simpler form and its parameters have more obvious meaning (Fang and Moncrieff 2001), we chose the L&T equation because its low-temperature response better matched the previously measured winter R_S values in this chronosequence (Winston et al. 1997, Wang et al. 2002).

Effects of temperature, trenching and moss on R_S

In the overall R_S - T_2 model, fit with the L&T equation $R_S = ae^{-E_0/(T-T_0)}$, year of burn and trenching both had significant effects on the E_0 parameter ($T_{125} > 3.00$, $P < 0.001$ for both). Soil drainage had no significant effect on either a ($T_{125} = -0.96$, $P = 0.340$) or E_0 ($T_{125} = 1.67$, $P = 0.097$). No fixed effect was significant in the estimation of T_0 , which was 251 K (SE = 9.3 K) or -22 °C. To address the convergence problems noted above, this value of T_0 was subsequently “fixed” into the model (i.e., T_0 was not allowed to vary between stands when calculating site-specific models, where nonconvergence or in-

appropriate values had been seen). The site-specific equation thus became the two-parameter model $R_S = ae^{-E_0/(T_2 + 251)}$; the implications of this change are discussed below.

Model parameters for each burn year are given in Table 1. Site-specific Q_{10} values, calculated as simple linear estimates in each temperature range, varied from 1.4 to 7.3 at low (5–15 °C) temperatures and 1.2 to 3.1 at higher (15–25 °C) temperatures. Values of Q_{10} for the entire data set were 1.5 for 5–15 °C and 1.3 for 15–25 °C. Removal of live moss at the 72-year-old stands had no effect on measured R_S during the summer of 2001 ($T_{53} = -1.32$, $P = 0.19$).

Annual soil surface CO₂ flux and its components

Modeled annual C respired from the control plots was 85–570 g C m⁻² year⁻¹, with the highest values in the 21-year-old dry and wet stands (Table 2). With one exception (discussed below), these values were consistent with values calculated by Wang et al. (2002) from year-round R_S measurements at these same sites. Growing season (May 15–September 15) emissions comprised 54–90% of annual R_S (Figure 2). Annual C from the trenched plots was 76–385 and 134–498 g C m⁻² year⁻¹ in the well-drained and poorly drained stands, respectively.

Root contribution (RC) to R_S increased from about 0% in the recently burned stands to 35–40% in the 20-year-old stands, and declined to 5–15% in the oldest stands (Figure 3). The error bars in Figure 3 show the substantial effect of choice of model type on RC. In the dry stands, measured RC was relatively low in May, peaked around day of year 210 (late July), and declined markedly by the end of the growing season (Figure 4). There was no consistent seasonal pattern of RC in the wet stands (data not shown).

Discussion

Choice of statistical model and its effects

Once basic regression assumptions are satisfied, model choice has the greatest effect because of different model behaviors at the extremes of most measured data sets, for statistical, biological and environmental reasons. Statistically, regression confidence intervals are narrowest in the middle of the data

Table 1. Equation parameters for best fits of the Lloyd and Taylor (1994) Arrhenius-based model, by black spruce stand age. Equations are of the form $R_S = ae^{-E_0/(T_2 - T_0)}$, where R_S is soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), E_0 is activation energy, T_2 is soil temperature (K) at 2-cm depth and T_0 was fixed at 251 K (-22 °C) as described in the text. All model fits were significant ($P < 0.001$). Number of observations (n) and approximate adjusted R^2 values are given.

Age (years)	Trenched					Control				
	n	a	E_0	T_0	R^2	n	a	E_0	T_0	R^2
4	80	17.45	93.96	251.0	0.82	68	14.47	90.71	251.0	0.80
7	53	9.79	71.72	251.0	0.75	69	31.13	107.56	251.0	0.78
13	82	7.00	55.54	251.0	0.84	77	13.98	67.27	251.0	0.88
21	67	19.04	80.34	251.0	0.80	73	30.73	82.60	251.0	0.83
38	96	24.75	85.60	251.0	0.91	112	26.97	80.93	251.0	0.91
72	92	12.72	65.10	251.0	0.90	90	11.55	53.01	251.0	0.88
152	62	5.10	40.27	251.0	0.90	60	6.89	44.56	251.0	0.86

Table 2. Modeled CO₂ efflux (g C m⁻² year⁻¹) for trenched and control plots of black spruce, by soil drainage and stand age.

Age (years)	Growing season		Annual	
	Trench	Control	Trench	Control
<i>Well-drained stands</i>				
4	174	166	262	255
7	57	76	76	85
13	152	253	285	425
21	246	351	385	551
38	213	281	378	484
72	226	289	394	540
152	206	236	329	375
<i>Poorly drained stands</i>				
4	88	84	134	137
7	273	301	498	513
13	155	211	239	337
21	258	408	354	570
38	225	265	330	397
72	168	204	290	338
152	169	213	352	375

set—more precisely, when $(x - \bar{x})^2$ is small—and largest when the regression line is far from the sample mean \bar{x} . In addition, when annual fluxes are calculated from fitted R_S models, extrapolating outside of the range of measured data is common (e.g., Bowden et al. 1993, Epron et al. 1999, Buchmann 2000), despite the inherent problems with such extrapolation (Chatterjee and Price 1991). Biologically, the exponential response of R_S to T means that fluxes at high temperature constitute a greater fraction of annual R_S than would be expected from the annual frequency of such high-temperature days. There is a complementary effect in the errors in cold-weather fluxes, as R_S is small at low temperatures, but boreal winters are long: in this chronosequence, $T_2 < 0$ °C for 40–60% of the year, depending on site, with this time period constituting 20–40% of annual CO₂ flux (Wang et al. 2002,

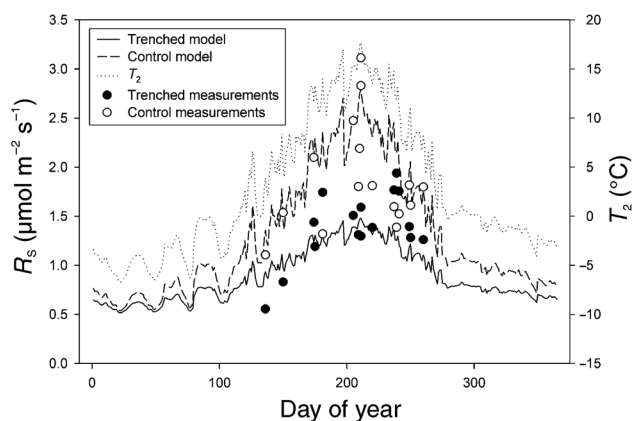


Figure 2. Annual measured and modeled soil surface CO₂ flux (R_S), in trenched and untrenched (control) plots of the 13-year-old dry black spruce stand. Soil temperature at 2-cm depth (T_2) is plotted on the right-hand y-axis.

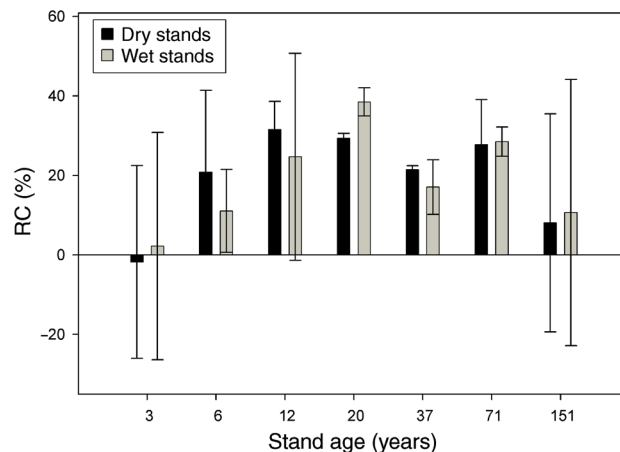


Figure 3. Annual percentage of root contribution (RC) to soil surface CO₂ flux for all chronosequence well-drained (dry) and poorly drained (wet) stands. Error bars indicate the range of RC computed with alternative model types (minimum-temperature power, exponential, second-order exponential) instead of the Arrhenius-based model employed.

O'Connell et al. 2003). Thus, for R_S modeling, the choice of statistical model is particularly important at the temperature extremes, particularly when these extremes are under-represented in the measured data. If annual environmental conditions greatly exceed the measurement range used to assess temperature– R_S relationships, the collection of more data is the best solution.

Fixing the T_0 parameter in the L&T (1994) equation $R_S = ae^{-E_0/(T-T_0)}$, as done here, reduces this three-parameter model to a two-parameter model—effectively to the original Arrhenius model on which it is based—with a concomitant loss in fitting flexibility. Fang and Moncrieff (2001) found,

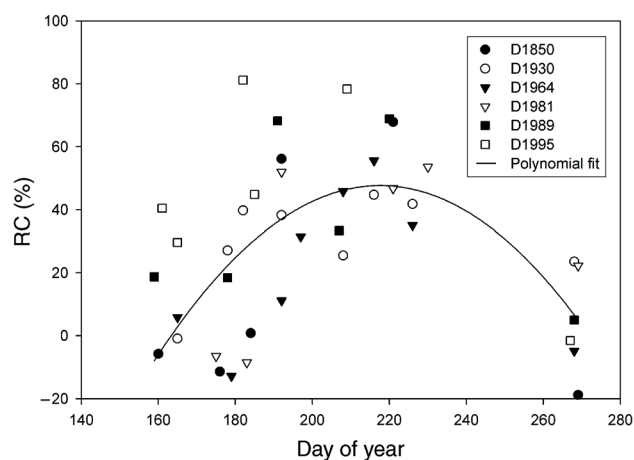


Figure 4. Seasonal change in root contribution (RC) to soil surface CO₂ flux by day of year for the six well-drained stands with vegetation present. Site names in the legend are composed of “D” (dry) plus year of wildfire at the stand. The polynomial shown ($y = -7.18 + 0.07x - 0.0002x^2$) was fitted to all values; stand-specific fits are similar.

however, that the extra T_0 in the L&T model did not provide a better fit. In addition, there are situations, as in this study, where allowing the T_0 parameter to vary freely results in biologically unlikely or impossible results (i.e., no respiration at 0 °C). This is an inadequacy of the data set and not inherent in the equation, but should not be ignored when selecting the appropriate model form. Finally, fixing T_0 at 251 K may seem extreme: does R_S not reach zero until soils reach -22 °C? Measurements of wintertime respiration in the field (Winston et al. 1997, Wang et al. 2002) are inconclusive; soil temperatures never drop as low as -22 °C (even when air temperature is less than -50 °C), and measured R_S is always above zero. In the laboratory, Elberling and Brandt (2003) observed microbial respiration at -18 °C in an incubation of arctic soil. More generally, large (and insulated) reservoirs of deep soil C in boreal forests clearly contribute significantly to R_S (Trumbore and Harden 1997, Hirsch et al. 2002). Thus fixing $T_0 = 251$ K seems statistically and biologically reasonable.

Annual R_S and its root contribution

The R_S values for the control plots are in the normal range reported for boreal forests (Wang et al. 2002 and references therein, Gower 2003). The control plot R_S values reported here are somewhat higher than R_S calculated for the same sites by Wang et al. (2002), but quite well correlated with those values ($R^2 \approx 0.63$). The one exception was the 7-year-old dry stand (412 versus 85 g C m⁻² year⁻¹). Differences in precipitation patterns between the two study periods may have made a significant difference in this sandy-soil site. In addition, Wang et al. (2002) used a second-order exponential equation with an optimal temperature T_{opt} of ~14 °C for this stand. As noted above, it is highly unlikely that this relatively low temperature is a true R_S optimum; most studies have found far higher temperature optima (though in non-boreal systems) for T_{opt} (Parker et al. 1983, O'Connell 1990, Thierron and Laudelout 1996). The 7-year-old dry stand had a relatively sandy soil and high annual T_2 (B. Bond-Lamberty, unpublished observa-

tions), exacerbating the declining- R_S effect caused by the equation choice of Wang et al. (2002). Nevertheless, our R_S values for this site should be treated with caution, particularly given the R_S decline implied from the 4- to 7-year-old dry stands; this may imply high measurement error or a failure in chronosequence site selection.

Seasonal variation has been seen in the response of R_S to temperature, and in the relative auto- and heterotrophic contributions to R_S . Widén and Majdi (2001) reported RC values of 33–62% in May, decreasing to 12–16% in October, for a mixed *Picea abies* (L.) Karst.–*Pinus sylvestris* L. forest; O'Connell et al. (2003) found that RC was positively correlated with T_{10} for a southern boreal *P. mariana* forest; Rayment and Jarvis (2000) measured declines in R_S and Q_{10} during the growing season in the same forest. The changes in measured RC seen here (Figure 4) agree with the results of Rayment and Jarvis (2000), and the Q_{10} values are similar to published values (Raich and Schlesinger 1992, Boone et al. 1998, Rayment and Jarvis 2000, Widén and Majdi 2001, Wang et al. 2002). Understanding why the relationship between R_S and temperature changes is important, particularly in fire-prone boreal systems, where wildfire affects both biophysical (O'Neill et al. 2002) and structural (Pietikäinen and Fritze 1993) properties of the soil.

Root contribution to R_S varies over the course of forest succession, especially after a stand-killing event such as wildfire. Hanson et al. (2000) summarized 37 studies of RC in forest systems, and reported that RC values were normally distributed with a mean of 49%, but made no attempt to examine the relationship between RC and stand age. Our RC values, reported for a variety of stand ages, are lower than the mean reported by Hanson et al. (2000), but are similar to other published data for boreal forests (Table 3). In our study, the lowest RC values were for the youngest and oldest stands. The youngest stands had little live vegetation, so R_S was not expected to differ between the control and trenched plots. The low RC values in the oldest stands are more surprising (see discussion of

Table 3. Summary of published estimates of annual root contribution (RC) to soil surface CO₂ flux in boreal forests. Stand age, measurement time (GS = growing season only; A = annual) and method (1 = paired trenched/control plots; 2 = paired clear-cut or burned/control plots; 3 = laboratory incubation; 4 = root respiration measured in situ; 5 = mass balance or other subtraction method; and 6 = manipulation of photosynthate supply) are given.

System type (location)	Age (years)	Time	Method	RC (%)	Reference
<i>Picea abies</i> , <i>Pinus sylvestris</i> (Sweden)	34–50	GS	4	~31	Widén and Majdi (2001)
<i>Pinus sylvestris</i> (Sweden)	45–55	GS	6	54	Högberg et al. (2001)
<i>Pinus banksiana</i> (Canada)	70	A	2	35	Striegl and Wickland (1998)
<i>Populus tremuloides</i> (Canada)	70	GS	5	60	Russell and Voroney (1998)
<i>Picea abies</i> , <i>Pinus sylvestris</i> (Sweden)	105	GS	4	~24	Widén and Majdi (2001)
<i>Picea mariana</i> (Canada)	115	GS	3	54	Uchida et al. (1998)
<i>Picea mariana</i> (Canada)	120	A	1	17–22	O'Connell et al. (2003)
<i>Picea mariana</i> (Canada)	120	GS	5	24	Malhi et al. (1999)
<i>Picea mariana</i> (Alaska)	125	GS	3	~80 ¹	Flanagan and Van Cleve (1977)
<i>Picea mariana</i> , <i>Pinus banksiana</i> , <i>Populus tremuloides</i> (Canada)	7–152	GS	1	5–40	This study

¹ Top 20 cm of soil only.

errors below). Vegetation type and species strongly influence root dynamics (Vogt et al. 1996, Gower et al. 2001), and evergreen forests generally have higher belowground C allocation than deciduous forests (Gower et al. 1995). Understory fine root mass peaks, relative to overstory fine root mass during stand reinitiation (Landsberg and Gower 1997). In this chronosequence, C allocation to fine roots peaks, in relative and absolute terms, in the 72-year-old stands (Bond-Lamberty et al. 2004b), whereas understory biomass (Wang et al. 2003), leaf area index (Bond-Lamberty et al. 2002b) and net primary production peak concurrently with RC, in the younger stands. We did not separate the contribution of the (largely deciduous) understory roots to soil surface R_A flux; in view of the almost total lack of understory in the oldest stands of the chronosequence, contribution of understory roots may help explain the observed RC pattern. Other preliminary results for RC, based on the C isotopes of soil surface CO_2 flux sampled across this chronosequence (S. Trumbore, University of California, Irvine, CA, unpublished observations), exhibit a similar pattern to that found in this study.

Soil drainage at the stand level had no significant effect on measured R_S in the control or trenched plots. This contrasts with the findings of Wang et al. (2002), who used a much larger year-round data set, and reported a significant effect of soil drainage on R_S . This discrepancy highlights a potential problem with the design of our study: we did not make soil water potential measurements while sampling R_S . In arid ecosystems, soil water is a significant predictor of R_S (Raich and Schlesinger 1992, Raich et al. 2002). However, many researchers report only a minimal predictive effect of soil water on forest R_S once temperature is accounted for (Buchmann 2000, Raich et al. 2002, Bolstad et al. 2004), particularly in boreal systems not subject to severe water stress (Rayment and Jarvis 2000, O'Neill et al. 2002).

Potential sources of error

Several direct and indirect lines of argument suggest that the RC values reported in this study should be treated as minimum values. The use of trenched plots inevitably raises questions about the disturbances created by trenching, although in a meta-analysis, Bond-Lamberty et al. (2004a) found no difference between results obtained with trenched plots and results obtained by other methods. In particular, there is often a transient CO_2 flush as severed fine roots inside the plot decompose, whereas large severed roots may decompose over longer time periods, raising the measured R_S of the trenched plot. We allowed our trenched plots to equilibrate for almost a year before beginning measurements, assuming that this is adequate time for the transient CO_2 flush to dissipate (Ewel et al. 1987, Bowden et al. 1993, Haynes and Gower 1995). However, Epron et al. (1999) used root biomass assays to estimate root decay in trenched plots (in a temperate deciduous forest, with a 6-month delay after trenching) as 60–100 g C m⁻² year⁻¹, or 14–24% of the trenched plot CO_2 efflux. A rough calculation of root decay in these chronosequence sites may be performed, using the root biomass numbers of Wang et al. (2003) and published decay rates of 0.05–0.35 year⁻¹, depending on root size

(McCaugherty et al. 1984, Landsberg and Gower 1997). This suggests that fine and coarse root decay could account for 5–30 g C m⁻² year⁻¹ (5–10%) of measured trench plot R_S at most sites. At the two oldest dry stands, however, where it was impossible to avoid severing some large roots because of tree size and density, the decay contribution was probably higher—40–60 g C m⁻² year⁻¹, or 15–20% of the total trenched plot flux. We estimate that the decline in RC seen in the two oldest well-drained stands could be an artifact of unmeasured coarse root decay, but that the numbers for the young stand are much less affected by the decay of severed roots.

Trenching can also affect soil biophysical conditions—especially soil water—of the trenched plots. In our study, trenching raised soil temperatures slightly in the dry and wet 13-year-old stands, probably because, at this site, we were forced to disturb woody debris in order to install and access the PVC measurement collars, allowing more sunlight to reach the forest floor. This temperature change would not have directly affected calculated RC (because annual flux estimates were based on the continuous data logger data), but may have changed soil microbial population size or composition (Fritze et al. 1993). Finally, trenching in the oldest stands may have disturbed the insulating moss layer. The magnitude of these effects is unknown but would tend to increase soil surface CO_2 flux in the trenched plots, thus raising calculated R_H and lowering RC.

Because of the difficulty of making belowground measurements, the large variation in reported values of RC (Hanson et al. 2000) may be due as much to methodological problems as to underlying variability among factors such as species, ecosystems and stand age. Thus, it is worthwhile to explore possible proxies for the hetero- and autotrophic sources of soil respiration; ideally, measurements that are relatively straightforward to make and can be used to indirectly partition the R_S source fluxes. There was a strong relationship between R_H and aboveground litterfall (Bond-Lamberty et al. 2004b) in the dry stands ($n = 7$, $R^2 = 0.60$, $P < 0.01$), but not in the wet stands ($n = 7$, $R^2 = 0.01$, $P = 0.81$); this relationship is not surprising given the known correlation of litterfall and R_S on a global scale (Raich and Nadelhoffer 1989). Heterotrophic soil surface CO_2 flux was also strongly correlated to R_S for all the sites ($n = 14$, $R^2 = 0.81$, $P < 0.01$; soil drainage was not significant). There was little or no significant correlation between R_H and fine root net primary production (NPP_{FR}), R_A and stand leaf area index (Bond-Lamberty et al. 2002b), or R_H and total detritus (litterfall + NPP_{FR}). Some significant relationships might be explored further; in particular, Bond-Lamberty et al. (2004a) found that R_A and R_H were strongly correlated to each other (and thus to R_S) on a global scale, providing a useful method of constraining C budgets and estimating RC.

In conclusion, the contribution of hetero- and autotrophic sources to soil surface CO_2 flux changed dramatically across a boreal black spruce wildfire chronosequence, with the highest root contribution occurring 12–20 years after stand reinitiation. Calculated fluxes are sensitive to the statistical model employed in estimating R_S as a function of temperature,

and caution is needed when extrapolating with these equations outside the of the fitted data. Linking soil respiration to its source physiological processes, as opposed to deriving it from empirical models, should provide more accurate estimates of R_s and will help elucidate the relationship between the heterotrophic/autotrophic partitioning and stand age, species composition and soil biophysical conditions.

Acknowledgments

This research was supported by grants from NASA (NAG5-8069) and the National Science Foundation (Integrated Research Challenges in Environmental Biology, DEB-0077881) to S.T. Gower. Ben Bond-Lamberty was supported by a University of Wisconsin CALS Thomsen Fellowship. Carol Goranson, Lisa Kruger, Karen Nielsen and Wayne Kirkland assisted in the onerous tasks of trenching and weeding. We are grateful to the Nisichawayasihk First Nation for permission to work on tribal land.

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