

Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching

M. B. LAVIGNE,^{1,2} R. J. FOSTER¹ and G. GOODINE¹

¹ Natural Resources Canada, Canadian Forest Service - Atlantic Forestry Centre, Fredericton, NB E3B 5P7, Canada

² Corresponding author (mlavigne@nrcan.gc.ca)

Received April 7, 2003; accepted September 13, 2003; published online February 2, 2004

Summary Soil respiration (r_s), soil temperature (T_s) and volumetric soil water content were measured in a balsam fir (*Abies balsamea* (L.) Mill.) ecosystem from 1998 to 2001. Seasonal variation in root and microbial respiration, and covariation in abiotic factors confounded interpretation of the effects of T_s and soil water potential (Ψ_s) on r_s . To minimize the confounding effect of temperature, we analyzed the effect of Ψ_s on r_s during the summers of 1998–2000 when changes in T_s were slight. Soil respiration declined 25–50% in response to modest water stress (minimum Ψ_s of –0.6 to –0.2 MPa), and between years, there was substantial variation in the relationship between r_s and Ψ_s . In the summer of 2000, 2-m² plots were subjected to drought for 1 month and other plots were irrigated. The relationship between summertime r_s and Ψ_s in the experimental plots was similar to that estimated from the survey data obtained during the same summer. In late spring and early autumn of 2001, 2-m² trenched and untrenched plots were subjected to drought or exposed to rainfall. It was dry in the early autumn and there was severe soil drying (Ψ_s of –10 MPa in untrenched plots and –2 MPa in trenched plots). In spring, r_s in untrenched plots responded more to modest water stress than r_s in trenched plots, indicating that root respiration is more sensitive than microbial respiration to water stress at this time of year. The response to abiotic factors differed significantly between spring and autumn in untrenched plots but not in trenched plots, indicating that root activity was greater in early autumn than in late spring, and that roots acclimated to the sustained, severe water stress experienced before and during the autumn.

Keywords: *Abies balsamea*, abiotic control, interannual variation, seasonal variation, trenched plots.

Introduction

Soil respiration (r_s) will play a major role in the response of forests to global warming (Raich and Schlesinger 1992, Grace and Rayment 2000, Valentini et al. 2000), but a better understanding of biotic and abiotic controls over r_s is required to predict the significance of this role. Soil respiration varies with soil temperature (T_s), leading to the concern that r_s will in-

crease more than gross primary production in response to global warming, thereby reducing sequestration of carbon by forests (Kirschbaum 1995). However, if turnover of soil organic matter is relatively insensitive to T_s , the positive feedback of global warming on carbon turnover in forest soils will be limited (Giardina and Ryan 2000, Trumbore 2000). Soil water content is the second abiotic factor that exerts a strong influence over r_s (Schlentner and Van Cleve 1985, Hanson et al. 1993, Davidson et al. 1998, Law et al. 1999, 2001, Irvine and Law 2002, Rey et al. 2002, Janssens et al. 2003).

Soil respiration is the sum of root respiration and respiration by soil microorganisms. The latter is often referred to as heterotrophic respiration. The components of soil respiration can have different responses to T_s and soil water content (Boone et al. 1998). These differences add to the difficulty of forecasting the response of r_s to global warming.

Measurements of r_s of root-free soil samples indicate that heterotrophic respiration is sensitive to short-term variation in T_s , but the response to variation in soil water content is modest in many soils (Orchard and Cook 1983, Howard and Howard 1993, Kirschbaum 1995, Bowden et al. 1998, Lomander et al. 1998, Zak et al. 1999). Similarly, r_s of intact soil monoliths collected in a Sitka spruce plantation was sensitive to changes in T_s but responded only modestly to changes in soil water content (Fang and Moncrief 2001). The response of heterotrophic respiration to soil water content may depend on the relative importance of fungi in the decomposer community, as there is evidence to suggest that fungi are less responsive to moderate water stress than bacteria (Orchard and Cook 1983).

Root respiration is sensitive to temperature and soil water content (Boone et al. 1998, Burton et al. 1998, Atkin et al. 2000, Pregitzer et al. 2000, Maier and Kress 2002, Burton and Pregitzer 2003); however, predicting responses is complicated by seasonal variation (Vose and Ryan 2002) and acclimation to the prevailing environmental conditions in some (Atkin et al. 2000), although perhaps not all (Burton and Pregitzer 2003), species. Moreover, changes in root respiration in response to environmental stress may, in part, reflect increased root mortality (Espeleta and Eissenstat 1998, Pregitzer et al. 2000).

Trenched plots provide a means of partitioning r_s into root and heterotrophic respiration (Hanson et al. 2000). The use of

trenched plots may, therefore, bridge the gap between simple correlative field studies of the relationship between r_s and environmental variables and studies that examine root respiration and heterotrophic respiration separately.

Between 1998 and 2001, we measured r_s , T_s and volumetric soil water content (from which soil water potential (Ψ_s) was estimated) in a New Brunswick balsam fir (*Abies balsamea* (L.) Mill.) ecosystem. In 2000, a drought treatment was imposed and, in 2001, both drought and trenching treatments were imposed.

In southern New Brunswick, potential evapotranspiration can exceed precipitation during the growing season (Lavigne et al. 2003), which means that Ψ_s at our experimental site can vary substantially over the course of the summer, whereas T_s varies relatively little. We therefore analyzed summer data for evidence of effects of Ψ_s on r_s unconfounded by covariation in T_s (Davidson et al. 1998). In summer 2000, we subjected small plots to drought to obtain a wider range of Ψ_s values for correlative analyses of the relationship between r_s and Ψ_s . In 2001, we imposed drought on trenched and untrenched plots to test the hypothesis that root respiration is more sensitive to drought than heterotrophic respiration in a typical balsam fir ecosystem. We imposed drought in late spring and again in early autumn to obtain data over wide ranges of T_s and Ψ_s to better test the fitting of a model that predicts r_s responses to T_s and soil drying simultaneously. Because earlier work suggested that r_s and the relative contribution of roots to r_s are both greater in autumn than in spring (Lavigne et al. 2003), we hypothesized that r_s would be more sensitive to soil drying in autumn than in spring.

Materials and methods

Site description

Measurements were taken at a 40-year-old balsam fir site on the Acadia Research Forest near Fredericton, New Brunswick, Canada (46°02' N, 66°23' W) (Bernier et al. 1999). The soil is a humo-ferric podzol, with a sandy loam texture (57% sand, 34% silt, 9% clay), a stone content (> 2 mm) of 42% by volume, and a compacted layer at a depth of 50 cm. In 1998, mean tree height was 10 m, mean diameter was 11.2 cm, there were 2700 trees ha⁻¹, and estimated leaf area index (half total leaf area) was 14.9 based on allometric relationships with sapwood cross-sectional area (M.B. Lavigne, unpublished data). Between 1998 and 2001, mean annual air temperature at the site was 5.6 °C, mean annual soil temperature at 5 cm depth was 6.1 °C, and mean growing season (May 1–October 30) precipitation was 453 mm.

Air temperature was monitored 1.5 m above ground with a Campbell Scientific (Logan, UT) CS500-L temperature probe and soil temperature was recorded at a depth of 5 cm in three locations with copper-constantan thermocouples. Precipitation was measured above the canopy with a TE525M tipping bucket rain gauge (Texas Electronics, modified by Campbell Scientific). Soil water content (θ_s) in the upper 30 cm was measured with a CS615 water content reflectometer (Camp-

bell Scientific) inserted vertically at the surface. Observations were taken every 5 s and 30 min means were stored in the data logger.

Soil respiration

Carbon dioxide efflux from the soil was measured with a portable photosynthesis system (LI-6200, Li-Cor, Lincoln, NE) attached to a closed, dynamic soil respiration chamber (Li-Cor, Model 6000-09). The respiration chamber was placed on a thin-walled polyvinyl chloride collar, 10 cm in diameter, inserted into the soil. Each collar was 5 cm deep, with a sharpened edge that was inserted 2–3 cm into the soil. Collars were left in place for a year. Herbaceous vegetation was removed from collars when encountered. Standard procedures (Norman et al. 1992) were followed in measuring soil respiration: air entering the chamber was partially scrubbed of CO₂ to reduce the concentration to below ambient before starting a sequence of four measurements during the course of which CO₂ concentration rose continuously in the closed gas exchange system. The measurement yielding a mean CO₂ concentration closest to ambient was selected for subsequent analyses. A thermocouple was inserted 5 cm into the soil to record T_s during the measurement of r_s .

Survey data

During 1998, 1999 and 2000, we measured soil respiration on 45 days at 20 undisturbed locations scattered throughout the site. Volumetric soil water content was measured on the same days, but only in the vicinity of the weather station. In 1998, measurements were taken on 14 days between July 8 and December 9, during which time T_s varied between 0.7 and 16.3 °C, and θ_s varied between 12.5 and 33.9%. Measurements were made on 17 days in 1999 between April 23 and December 3, with a T_s range of 0.1 to 16.0 °C, and a θ_s range between 8.7 and 31.5%. In 2000, measurements were made on 14 days between May 16 and October 23; T_s varied between 5.3 and 15.1 °C, and θ_s varied between 10.6 and 22.0%. Covariation in T_s and θ_s (Davidson et al. 1998) makes it difficult to assess the independent effects of these factors on r_s . We therefore adjusted r_s for temperature and analyzed data for each season separately, to assess variation in the response of r_s to θ_s .

Drought and irrigation experiments

Experiment 1 This experiment, which examined the relationship between r_s and θ_s , was conducted in July and August when T_s varied little. In 2000, five wooden frames, 2 × 2 m, were constructed and fixed on posts 1–1.5 m above ground. Clear plastic sheeting was affixed to the wooden frames on June 30 and left in place until August 11. Frames were constructed and installed such that rainwater drained toward one corner, where it was collected in a tub. A soil respiration collar was installed near the center of each drought-treated (D) plot. Ten soil collars were installed 20 m or more from the nearest D plot, and the soil in and around the collars was irrigated (I plots) on July 24 with water collected in tubs from the D plots. Soil water content in the upper 30 cm of soil (including surficial organic layers) was measured in the D plots and in five of the I plots by time do-

main reflectometry (Water Point Model MP-917, Environmental Sensors, Victoria, B.C., Canada) with 30-cm-long, single-diode, single-segment probes (Model SDP-30 cm) left in place for the season. Soil respiration, T_s and θ_s were measured on 13 days during 2000 in the D and I plots.

Experiment 2 In 2001, measurements were again made in the five D plots and 10 I plots established for Experiment 1. In addition, two trenched and drought-treated (TD) plots, and two trenched and irrigated (TI) plots were also measured. Each trenched plot was 2 m². Trenches were 30 cm deep and severed most or all roots entering the plot. The trenches were backfilled after lining with landscaping fabric to prevent root ingrowth. Measurements taken in the trenched plots during 1999 and 2000 have been reported previously in a study of the partitioning of r_s between root and heterotrophic respiration (Lavigne et al. 2003). In the current experiment, trenched and untrenched plots were compared to assess whether the response to θ_s differs between root and heterotrophic respiration. Differences in r_s between trenched and untrenched plots in response to changes in θ_s were assumed to be due to root activity. We did not attempt to partition r_s because of the small number of trenched plots per treatment; consequently, it was unnecessary to account for the additional heterotrophic respiration in trenched plots arising from decomposition of roots killed by trenching.

Soil water probes were installed in three D plots, three I plots, both TD plots, and both TI plots. Volumetric soil water content was recorded manually at the same time that r_s was measured.

Because root and soil microbial contributions to r_s vary during the year (Lavigne et al. 2003), drought and irrigation treatments were applied in late spring and early autumn to determine whether responses of r_s to θ_s differed among seasons. Rain was excluded from the D plots between June 6 and June 29, and again between September 2 and October 31, and from TD plots between June 18 and July 9, and again between September 2 and October 31. The I and TI plots were watered on June 21. All plots were watered on July 12, several days after opening up the drought-treated plots to receive rainfall. Measurements were taken on 39 days during and between drought periods in 2001.

Calculation of water potential

Soil water potential was computed from measured θ_s based on the equations of Saxton et al. (1986), which relate soil texture to parameter values needed for calculating Ψ_s from θ_s .

Data analysis

Between droughts, during July 2001, r_s in the five D plots was 20% less than in the 10 I plots, and r_s in the two TD plots was 27% greater than in the two TI plots, reflecting the variability in the stand. Accordingly, we increased all measured values of r_s in D plots by 20% and decreased all measured r_s values in TD plots by 27%, to facilitate combining treatments for analyses of the relationship between r_s and Ψ_s .

Regression analyses

Equation 1 was used to describe the relationship between respiration and temperature in each year of the survey data:

$$\hat{r}_s = ae^{b(T_s-10)} \quad (1)$$

where \hat{r}_s is predicted soil respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), T_s is soil temperature ($^{\circ}\text{C}$) at 5 cm depth, and a and b are coefficients estimated by nonlinear regression. Janssens et al. (2003) and Janssens and Pilegaard (2003) have shown that the exponential equation is at least as effective as alternative equations for describing the relationship between T_s and r_s . The coefficient b provides an estimate of Q_{10} ($=e^{10b}$). Because 10 is subtracted from T_s , the coefficient a is an estimate of r_s at 10 $^{\circ}\text{C}$ (\hat{r}_{10}). Interannual differences in r_s were assessed based on comparisons of coefficients by one-way analysis of variance and t -tests.

To examine reasons for variations in r_s other than variations in T_s in the survey data and in Experiment 1, we estimated a value of r_{10} for each observation by reworking Equation 1 as:

$$r_{10} = \frac{r_s}{e^{b(T_s-10)}} \quad (2)$$

where b is set at 0.0693 (corresponding to $Q_{10} = 2.0$; the rationale for selecting this value of b is explained in the Discussion), and r_s is observed soil respiration. Soil respiration at 10 $^{\circ}\text{C}$ can vary seasonally or in response to Ψ_s . These sources of variation were examined by plotting r_{10} versus Ψ_s separately for spring, summer and autumn. A narrow range of T_s was observed during Experiment 1 (less than 4 $^{\circ}\text{C}$) and for summer measurements in the survey database, making it inappropriate to analyze these data for simultaneous responses to T_s and Ψ_s . Therefore, the following equation was used to investigate the effect of Ψ_s on r_s in Experiment 1 and during the summer periods of the survey:

$$\hat{r}_{10} = ce^{d\Psi_s} \quad (3)$$

where \hat{r}_{10} is predicted soil respiration at 10 $^{\circ}\text{C}$, and c and d are coefficients estimated by nonlinear regression. Interannual variability of responses to soil water in the survey data was assessed by one-way analysis of variance.

The effects of T_s and Ψ_s were assessed simultaneously in Experiment 2 with the following equation, derived by substituting Equation 3 for coefficient a in Equation 1:

$$\hat{r}_s = (ce^{d\Psi_s})e^{b(T_s-10)} \quad (4)$$

where coefficients are estimated by nonlinear regression. Values of coefficients were estimated for trenched locations by pooling data from TD and TI plots and for untrenched locations by pooling D and I plots. Values of coefficients were compared by t -tests to assess seasonal variation and compare locations having little or no root respiration with locations having normal root respiration.

Results

Annual variation in climate

Soil temperature rose rapidly between late April and mid-June, remained relatively constant from late June until late August, and declined slowly between September and December (Figure 1); however, variations about this general pattern caused annual climatic statistics to vary among years (Table 1). Mean growing season T_s was highest in 1999 because T_s between mid-July and late September was higher than observed in other years (Figure 1). In comparison, in 1998, the mean growing season T_s was almost as high as in 1999 because the soil began warming about 2 weeks earlier and remained warmer in May and June than in other years. Mean growing season T_s was lowest in 2000 because of comparatively low temperatures between late May and late June.

Two days with high rainfall in September of 1999 (Figure 1) caused that year to be the wettest (Table 1), despite rainfall being below average for most of the growing season. Rain fell frequently during each growing season, but periods of 1–3 weeks without precipitation occurred in all years. Periods with little or no rainfall were shortest and least common in 2000. Year 2001 was driest because there were no days with more than 40 mm of rainfall, and there were extended periods with little or no rainfall in July, August and September. The soil at this site is well drained, with limited capacity to store water and, therefore, θ_s declined rapidly in the days following rain (Figure 1). There were four periods of 1 week or more with low θ_s in 2001 and one in 1999. In 1999 and 2001, there was a trend of decreasing θ_s between May and September, but this trend was less pronounced in 2000.

Soil temperature varied little diurnally or weekly (Table 2). Minimal diel and weekly variation of T_s occurred during win-

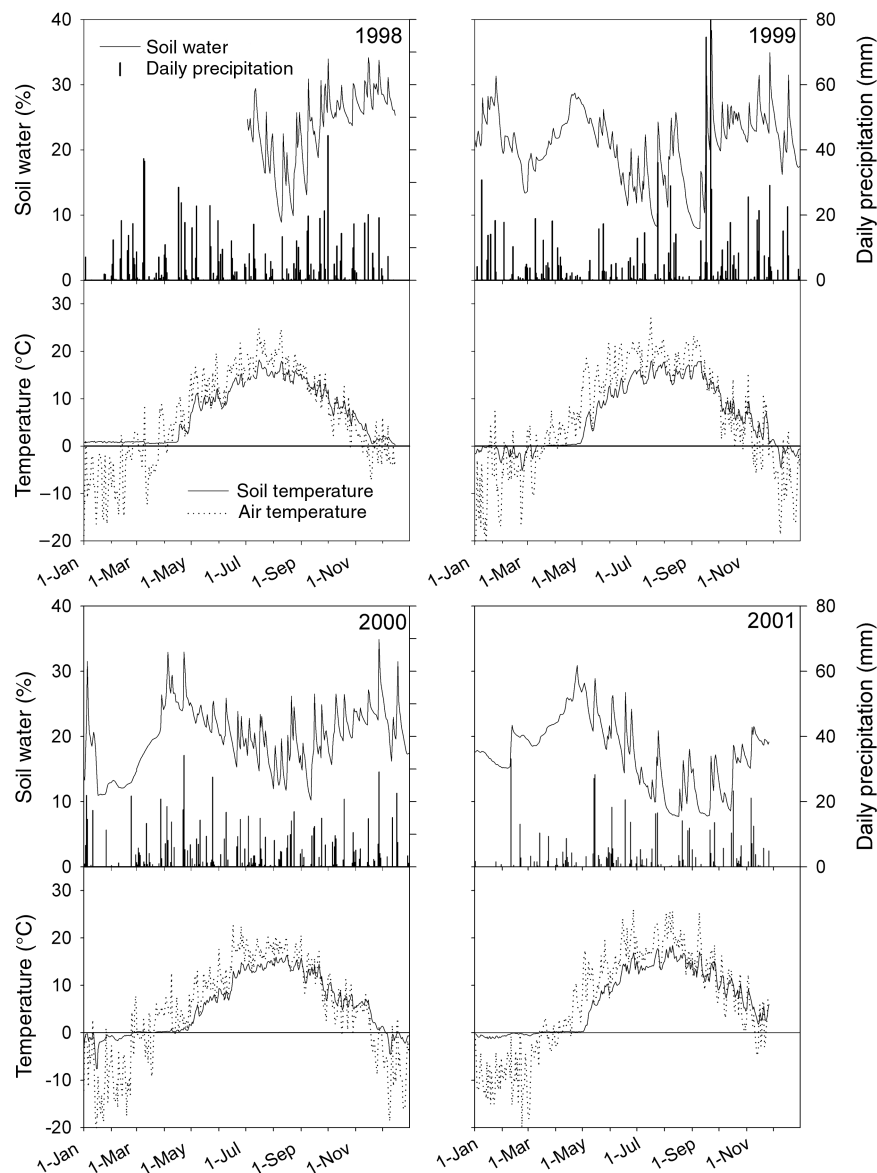


Figure 1. Soil and air temperatures, soil volumetric water content and daily precipitation in the studied balsam fir stand in central New Brunswick.

Table 1. Climate data recorded at a balsam fir stand in central New Brunswick. Growing season is defined as May 1 to October 31.

Year	Mean annual air temperature (°C)	Mean growing season air temperature (°C)	Mean annual soil temperature (°C)	Mean growing season soil temperature (°C)	Mean growing season soil water (%)	Growing season precipitation (mm)
1998	5.89	13.97	6.65	12.01	21.76 ¹	492.3
1999	6.22	14.98	6.14	12.05	19.00	528.3
2000	4.85	12.75	5.44	10.61	19.46	436.8
2001	5.42	14.71	6.09	11.73	15.31	355.9

¹ Data first recorded on July 3.

Table 2. Daily and weekly variability in soil temperature at 5 cm depth in a balsam fir stand in central New Brunswick

Year	Daily temperature range			Weekly temperature range		
	Mean	Max.	Min.	Mean	Max.	Min.
1998	1.18	3.55	0.11	3.13	8.10	0.53
1999	1.32	3.69	0.09	3.84	8.43	0.53
2000	1.16	3.56	0.07	3.26	8.93	0.37
2001	1.30	3.88	0.11	3.52	8.28	0.62

ters when snow cover was intact. Maximal diel and weekly variation of T_s occurred sporadically between May and November. Median weekly range of soil temperatures during the growing season of all years was approximately 4 °C.

Responses of r_s to T_s and Ψ_s based on survey data

We estimated coefficients of Equation 1 for each year based on the survey data (Figure 2). Results of the regression analyses are summarized in Table 3. Neither coefficient a ($P = 0.67$) nor

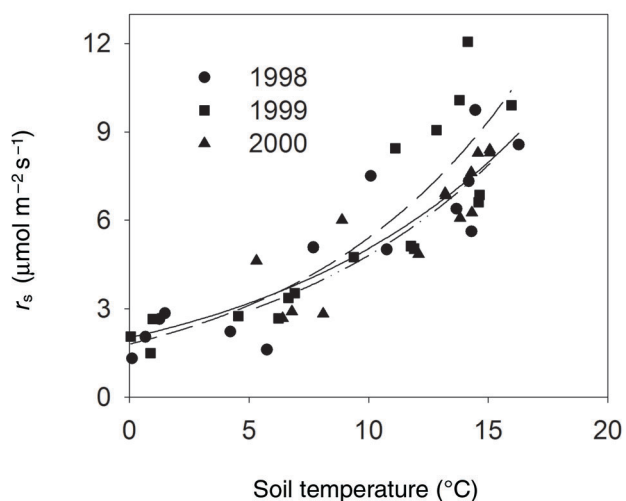


Figure 2. Relationship between soil respiration (r_s) and soil temperature at 5 cm depth (T_s) in a balsam fir stand in central New Brunswick over 3 years. Lines show fit to Equation 1 for each year. Regression statistics are provided in Table 3.

Table 3. The fit of Equation 1 to the relationship between soil respiration (r_s) and soil temperature (T_s) at 5 cm depth (\hat{r}_s) based on measurements taken as part of a survey repeated on different days during each growing season, where a and b are coefficients, r_{adjusted}^2 is the adjusted coefficient of determination, and Q_{10} is calculated from b ($Q_{10} = e^{10b}$) for a balsam fir stand in central New Brunswick. Standard errors of regression coefficients are shown in brackets.

Year	a ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	b ($^{\circ}\text{C}^{-1}$)	n	r_{adjusted}^2	Q_{10}
1998	5.04 (0.45)	0.092 (0.017)	14	0.78	2.50
1999	5.40 (0.51)	0.110 (0.021)	17	0.74	3.00
2000	4.81 (0.44)	0.098 (0.018)	14	0.76	2.67

b ($P = 0.79$) differed among years.

A relationship between r_{10} and Ψ_s existed in summer but not in spring or autumn (Figures 3a–c). Soil water was plentiful during spring and autumn in all years, and was unrelated to the wide range of observed r_{10} . Summertime variation in soil temperature was only 3–6 °C in the years 1998–2000, whereas Ψ_s ranged between –0.15 and –0.006 MPa in 1998, –0.62 and –0.009 MPa in 1999, and –0.28 and –0.017 MPa in 2000. Equation 4 adequately described the variation in r_s due to Ψ_s (Figure 3d, Table 4). Despite substantial differences among years in the apparent relationship between r_s and Ψ_s , values of d in Equation 4 were not statistically different, possibly because of the small sample sizes (Table 4).

In each year, the value of b estimated by Equation 4 (Table 4) was lower than the value estimated by Equation 1 (Table 3), but differences were not significant in any year.

Responses of r_s to drought and irrigation

Experiment 1 Soil water potential declined in D plots during the imposed drought in summer 2000 and rose to the value of I plots shortly after ending the drought. At the same time, Ψ_s rose with rainfall and irrigation, and declined between waterings in the I plots (data not shown). During the experimental period, T_s varied by less than 3 °C, so Equation 3 was used to assess the extent to which Ψ_s explained variation in r_s (Figure 4). Values of c and d were statistically similar to those observed in the survey data in 2000 (Table 4).

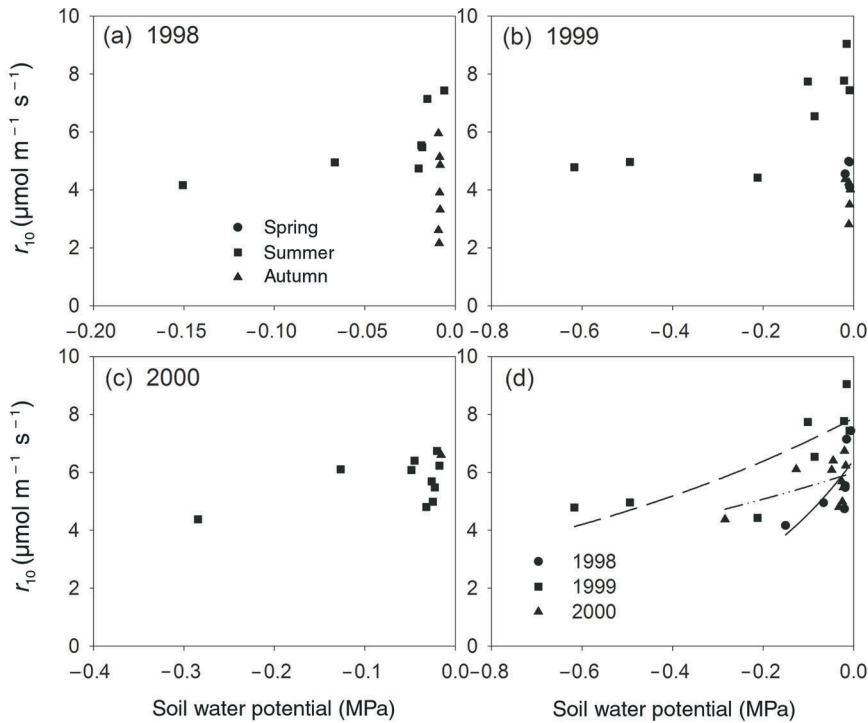


Figure 3. Relationship between soil respiration rate adjusted to 10 °C (r_{10}) and soil water potential in (a) 1998, (b) 1999 and (c) 2000 based on survey data collected in a balsam fir stand in central New Brunswick. The ranges of dates for which measurements were taken in each season during the years of this study were as follows. Year 1998: spring, no measurements; summer, July 8 to September 30; autumn, October 13 to December 9. Year 1999: spring, April 23 to May 31; summer, June 21 to October 1; autumn, October 15 to December 3. Year 2000: spring, May 16 to June 5; summer, June 23 to September 26; autumn, October 23. (d) Comparison of summer measurements among years. Lines depict fits to Equation 3 for each year (1998 = solid line; 1999 = dashed line; and 2000 = dash-dot-dot line).

Experiment 2 Imposed droughts in late spring and early autumn of 2001 reduced Ψ_s compared with the Ψ_s of I plots, although Ψ_s did not decline as much in TD plots as in D plots (data not shown). The main effect of the drought treatment was to extend the range of Ψ_s values during the experimental periods. Soil water potential was lower during the autumn 2001 experimental period than at any other time during the study (Figure 1) and, as a result, the widest range of Ψ_s values was observed in 2001 (Figures 5e and 5f). During the late spring experimental period, soil water was plentiful and the drought treatment induced only a modest range of Ψ_s values (Figures 4c and 4d).

The relationship between r_s and T_s appeared to be similar in spring and autumn for both trenched (Figure 5b) and untrenched plots (Figure 5a); however, values of b differed significantly between seasons (Table 5), but not between trenched and untrenched plots in either spring or autumn (Table 5).

The relationship between r_s and Ψ_s differed between seasons and between trenched and untrenched plots (Figures 5c–f). For trenched plots, values of c and d were similar in spring and autumn (Table 5), and it appears that one set of coefficients could be used in both seasons (Figure 5d). For untrenched plots, the value of d was higher in spring than in autumn (Table 5), and it appears that a different set of coefficients is required for each season (Figure 5c). In spring, the value of d was greater in untrenched plots than in trenched plots, but the opposite was found in autumn. In autumn, the range of Ψ_s values was much greater in untrenched plots than in trenched plots. When Equation 4 was fitted for untrenched plots in autumn based on measurements when Ψ_s was greater than -2 MPa, the resulting value of b (0.33 ± 0.087) did not differ significantly ($P = 0.79$) from that of trenched plots (Table 5). The value of c was higher in untrenched plots than in trenched plots (Table 5), because roots contributed normally to r_s in untrenched plots whereas roots made little contribution to r_s in trenched plots. However, the contribution of roots is not

Table 4. The application of Equation 4 to the relationship between summertime soil respiration (r_s), soil temperature (T_s) and soil water potential (Ψ_s) in the upper 30 cm, where b , c and d are coefficients, r_{adjusted}^2 is the adjusted coefficient of determination, and SEE is the standard error of estimate of the predicted values. Standard errors of regression coefficients are shown in brackets. One-way analysis of variance comparing coefficient values among years yielded P -values for b , c and d of 0.95, 0.43 and 0.21, respectively.

Year	b (°C ⁻¹)	c ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	d (MPa ⁻¹)	n	r_{adjusted}^2	SEE
1998	0.061 (0.033)	6.57 (0.96)	3.17 (1.75)	7	0.43	1.26
1999	0.075 (0.039)	7.53 (1.20)	1.02 (0.34)	8	0.60	1.44
2000	0.064 (0.027)	5.83 (0.69)	0.81 (0.61)	10	0.47	0.86

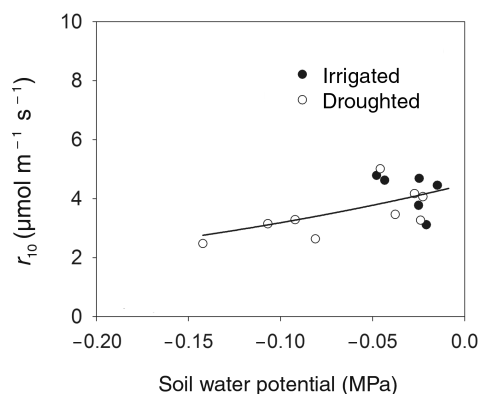


Figure 4. Relationship between soil respiration rate adjusted to 10 °C (r_{10}) and soil water potential in drought-treated and irrigated plots measured in summer of 2000 as part of Experiment 1. Data fitted by Equation 3, where the values of coefficients c and d are 4.47 and 3.41, respectively, and $r_{\text{adjusted}}^2 = 0.28$.

simply the difference in c between untilled and tilled plots, because there is additional heterotrophic activity in tilled plots as a result of decomposition of roots killed by tilling. Because of the small number of tilled plots in each treatment, we did not attempt to estimate the microbial and root contributions to r_s for this site.

Discussion

Our results support the view of Rayment and Jarvis (2000) and Widén (2002) that data collected in the field over a relatively short interval, such as a week, are unlikely to provide an accurate estimate of a temperature coefficient describing the response of r_s to T_s . First, our monitoring showed that T_s usually varied over a narrow range during the course of a week (Table 2), as has been found at other sites (Buchmann 2000, Morén and Lindroth 2000, Janssens et al. 2001, Drewitt et al.

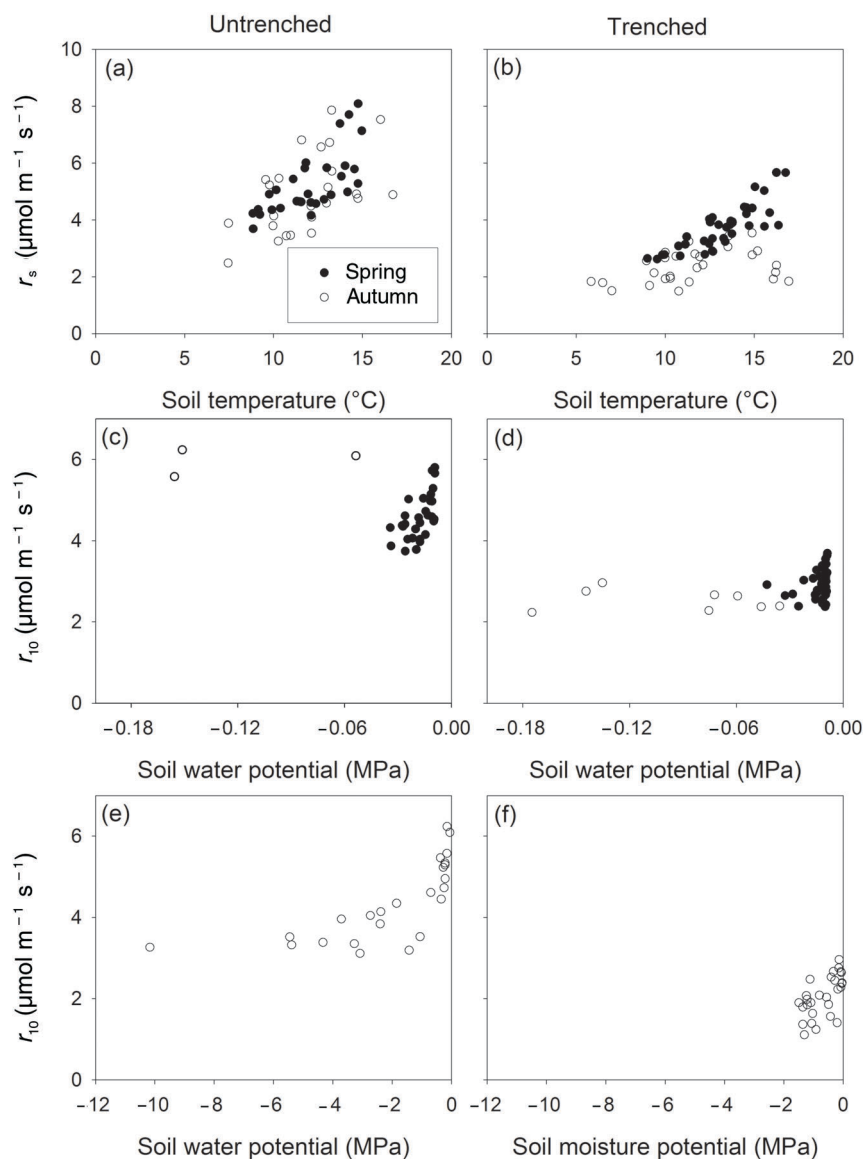


Figure 5. Results of Experiment 2 showing relationships between soil respiration rate (r_s) and soil temperature in (a) untilled plots and (b) tilled plots, and relationships between soil respiration rate adjusted to 10 °C (r_{10}) and soil water potential (Ψ_s) during the late-spring experimental period in (c) untilled plots and (d) tilled plots, and during the autumn experimental period in (e) untilled plots and (f) tilled plots. Autumn measurements with high Ψ_s are shown in (c) and (d) for comparative purposes.

Table 5. The fit of Equation 4 to the relationship between soil respiration (r_s), soil temperature (T_s) and soil water potential (Ψ_s) in the upper 30 cm, where b , c and d are coefficients, r^2_{adjusted} is the adjusted coefficient of determination, and SEE is the standard error of estimate of the predicted values. Standard errors of the regression coefficients are shown in brackets. Results of t -tests comparing coefficient values between spring and autumn and between trenched and untrenched plots are reported as P -values.

Treatment	Season	b (°C ⁻¹)	c	d	n	r^2_{adjusted}	SEE		
Untrenched	Spring	0.095 (0.010)	5.61 (0.28)	15.28 (2.57)	30	0.77	0.53		
Untrenched	Autumn	0.050 (0.012)	5.3 (0.26)	0.11 (0.020)	28	0.70	0.80		
Trenched	Spring	0.092 (0.010)	2.94 (0.17)	5.22 (2.83)	38	0.71	0.43		
Trenched	Autumn	0.028 (0.009)	2.69 (0.15)	0.30 (0.151)	28	0.49	0.41		
Comparison					t -test (P -values)				
Treatment	×	Season	Versus	Treatment	×	Season	b	c	d
Untrenched		Spring		Untrenched		Autumn	0.005	0.42	< 0.001
Trenched		Spring		Trenched		Autumn	< 0.001	0.29	0.14
Untrenched		Spring		Trenched		Spring	0.84	< 0.001	0.013
Untrenched		Autumn		Trenched		Autumn	0.15	< 0.001	0.012

2002, Widén 2002). Second, a wide range of Ψ_s values can be experienced over a 1-week period at this site (Figure 1), which can confound interpretation of the relationship between r_s and T_s (Kelliher et al. 1999, Law et al. 1999, 2001).

Collecting measurements over an entire growing season to estimate the temperature response of r_s yields observations over a wide range of T_s , but problems with interpreting the results arise because (1) there are seasonal variations in the quantity and activity of both roots and soil microorganisms (Hanson et al. 1993, Epron et al. 1999, Law et al. 1999, Morén and Lindroth 2000, Rayment and Jarvis 2000, Janssens and Pilegaard 2001, Drewitt et al. 2002, Widén 2002), and (2) soil water content often co-varies with T_s (Hanson et al. 1993, Davidson et al. 1998, Epron et al. 2001, Janssens et al. 2000 and Drewitt et al. 2002). We also observed that periods of low Ψ_s are more common during summer when T_s is high (Figure 1).

The temperature response of r_s can be overestimated if seasonal variation is not taken into account. For example, Janssens et al. (2001) found that diurnal variation in r_s was overestimated when responses to T_s were predicted with parameters calculated from data collected over the entire field season, and Epron et al. (2001) calculated a $Q_{10} = 3.9$ from r_s measurements collected over a growing season, but observed $Q_{10} = 2.2$ for root respiration measured over short intervals under controlled conditions. Similarly, at our balsam fir site, values of Q_{10} between 2.5 and 3.0 were estimated based on data collected over several growing seasons (Table 3), but this probably overestimates the short-term response of r_s to changes in T_s .

The relationship of r_s with Ψ_s is less well studied than the relationship with T_s and, as a result, many uncertainties exist. Several equations have been used to describe the r_s – Ψ_s relationship, with no consensus as to the best equation. This problem arises in part because both θ_s and Ψ_s have been used as the measure of soil water availability, and because of the tendency for T_s and soil water availability to co-vary. We followed the

most common approach and used an equation that includes both T_s and Ψ_s (Schlentner and Van Cleve 1985, Hanson et al. 1993, Davidson et al. 1998, 2000, Epron et al. 1999, Fang and Moncrieff 1999, Moncrieff and Fang 1999, Qi and Xu 2001, Janssens et al. 2001, Drewitt et al. 2002). However, the use of such an equation is based on the assumption that the effects of T_s and Ψ_s on r_s are multiplicative and independent. Moreover, in the past, seasonal variation has not been taken into account when using the combined equation. We made the common assumption about the independence of r_s and Ψ_s , but we did account for seasonal variation.

Modest water stress caused a substantial reduction in r_s at the study site. In most of our data sets, the lowest Ψ_s was greater than -1.0 MPa; however, r_s declined by 25–50% compared with when soil was at field capacity (Figures 3d, 4, 5c and 5d). This response could be because balsam fir grows only in moist cool climates on moist well-drained sites, and even modest water stress is known to affect its functioning. Severe soil drying was observed only in autumn 2001 (Figures 5e and 5f), and it caused only a small further decrease in r_s compared with r_s measured under conditions of modest water stress. It is possible that roots in this balsam fir ecosystem acclimated to water stress as soil water content declined from field capacity, so that the acclimated roots were much less sensitive to further declines in Ψ_s (Atkin et al. 2000).

The estimated value of d appeared to depend on the range of Ψ_s available for its determination. Low values of d were estimated in autumn 2001 when the range of Ψ_s was high (Table 5). In contrast, high values of d were estimated in spring 2001 (Table 5) and the summers of 1998–2000 (Table 4, Figure 4) when narrower ranges of Ψ_s and a modest degree of water stress were observed. The low values of d in autumn 2001 may reflect acclimation of the roots to water stress (Atkin et al. 2000), but it is also possible that d can only be estimated accurately when there is a wide range of Ψ_s .

Summer measurements from the survey data were suitable for assessing the role of Ψ_s on r_s at this site. This is because T_s varies little during summer, whereas Ψ_s varies episodically over the summer. Also, there is much less seasonal variation in r_s to confound interpretation of the relationship between r_s and Ψ_s during summer than during spring or autumn (Lavigne et al. 2003). Based on summer measurements only, we found that Ψ_s explained a significant amount of the variation in r_s (Figure 3d, Table 4). The survey data collected in spring and autumn could not be used to assess the relationship between r_s and Ψ_s at this site, because seasonal variations confounded the relationships of r_s with both T_s and Ψ_s (Figure 3a–c), and T_s and Ψ_s co-varied.

Seasonal variation occurs because the respiratory activities of roots and soil microorganisms vary during the year. The r_s of roots and microorganisms might also respond differently to T_s and Ψ during the year. Our results suggest that root respiration is greater in autumn than in spring and consequently plays a larger role in determining the response of r_s to T_s and Ψ_s during that season. We observed that r_s and its responses to abiotic factors clearly differed between spring and autumn in untilled plots (Table 5, Figures 5a, c and e), but r_s and responses to abiotic factors were similar during spring and autumn in tilled plots (Table 5, Figures 5b, d and f).

The modest response of r_s to soil drying in the tilled plots (Figures 5d and 5f) is similar to the r_s response observed in soil monoliths collected from a Sitka spruce ecosystem (Fang and Moncrieff 2001), and in incubated soil samples collected mostly from conifer ecosystems (Howard and Howard 1993, Bowden et al. 1998, Lomander et al. 1998, Leirós et al. 1999). Fungi dominate the decomposer community in acidic soils such as the one at this balsam fir ecosystem and are only moderately affected under conditions of modest water stress (Orchard and Cook 1983, Davidson et al. 1998). The role of fungi may, therefore, explain the modest response of r_s to soil drying in the tilled plots.

In contrast to studies in soil that lacks or has reduced root activity, field studies in undisturbed locations usually measure large r_s responses to variation in soil water content (Hanson et al. 1993, Davidson et al. 1998, 2000, Epron et al. 1999, Qi and Xu 2001, Drewitt et al. 2002). In addition, Burton et al. (1998) found that root respiration was sensitive to soil water content. This seasonal variation in root respiration might occur because the relative contribution of root respiration to r_s fluctuates during the year (Lavigne et al. 2003), or because sensitivity of roots to temperature and water stress changes during the year as rates of root production and standing crop of fine roots rise and fall (Atkin et al. 2000, Pregitzer et al. 2000).

We conclude that interannual differences in r_s make it inappropriate to combine data collected over several years to establish relationships between r_s and abiotic factors. The wide variation in r_s shown in Figure 3d argues against combining years to establish a relationship between r_s and Ψ_s . Interannual differences in the relationship between r_s and Ψ_s were greater than differences in the relationship between r_s and T_s (Figure 2), although the interannual differences were not statisti-

cally significant (Table 4). The lack of statistical significance may be associated with the small number of observations available to estimate the coefficients for each year.

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