Soil-surface carbon dioxide efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem

CREIGHTON M. LITTON*, MICHAEL G. RYAN†, DENNIS H. KNIGHT* and PETER D. STAHL‡

*Department of Botany, University of Wyoming, PO Box 3165, Laramie, WY 82071, USA, †US Department of Agriculture-Forest Service, Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, CO 80526, USA and Department of Forest Sciences and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA, ‡Department of Renewable Resources, University of Wyoming, PO Box 3354, Laramie, WY 82071, USA

Abstract

The effects of fire on soil-surface carbon dioxide (CO_2) efflux, F_S, and microbial biomass carbon, C_{mic}, were studied in a wildland setting by examining 13-year-old postfire stands of lodgepole pine differing in tree density (< 500 to $> 500\,000$ trees ha^{-1}) in Yellowstone National Park (YNP). In addition, young stands were compared to mature lodgepole pine stands ($\sim$110-year-old) in order to estimate ecosystem recovery 13 years after a stand replacing fire. Growing season F_S increased with tree density in young stands (1.0 μmol CO_2 m^{-2} s^{-1} in low-density stands, 1.8 μmol CO_2 m^{-2} s^{-1} in moderate-density stands and 2.1 μmol CO_2 m^{-2} s^{-1} in high-density stands) and with stand age (2.7 μmol CO_2 m^{-2} s^{-1} in mature stands). Microbial biomass carbon in young stands did not differ with tree density and ranged from 0.2 to 0.5 mg C g^{-1} dry soil over the growing season; C_{mic} was significantly greater in mature stands (0.5–0.8 mg C g^{-1} dry soil). Soil-surface CO_2 efflux in young stands was correlated with biotic variables (above-ground, below-ground and microbial biomass), but not with abiotic variables (litter and mineral soil C and N content, bulk density and soil texture). Microbial biomass carbon was correlated with below-ground plant biomass and not with soil carbon and nitrogen, indicating that plant activity controls not only root respiration, but C_{mic} pools and overall F_S rates as well. These findings support recent studies that have demonstrated the prevailing importance of plants in controlling rates of F_S and suggest that decomposition of older, recalcitrant soil C pools in this ecosystem is relatively unimportant 13 years after a stand replacing fire. Our results also indicate that realistic predictions and modeling of terrestrial C cycling must account for the variability in tree density and stand age that exists across the landscape as a result of natural disturbances.

Keywords: carbon pools and fluxes, disturbance, fire, lodgepole pine (*Pinus contorta* var. *latifolia*), microbial biomass carbon, soil respiration, soil-surface CO_2 efflux, stand age, tree density, Yellowstone National Park

Received 22 July 2002; revised version received 3 December 2002 and accepted 22 January 2003

Introduction

Globally, forests are the most important carbon (C) pool in terrestrial ecosystems (Dixon *et al.*, 1994), containing 66–80% of all C stored in above-ground biomass and $\sim$45% of that found in below-ground terrestrial pools (Dixon & Turner, 1991; Smith *et al.*, 1993; Waring & Running, 1998). Moreover, forests account for as much as 75% of terrestrial net primary productivity (NPP) (Melillo *et al.*, 1993). An average of 69% of ecosystem C in forests is below-ground in living biomass and soil organic matter pools (Dixon *et al.*, 1994), although this

number can reach 75% or higher in some systems (Keith *et al.*, 1997). In all, soils represent one of the largest near-surface pools in the global C cycle (Schlesinger *et al.*, 2000), containing more than twice as much C as is currently found in the atmosphere and almost three times more C than is contained in terrestrial vegetation (Schimel *et al.*, 2000).

Soil-surface CO$_2$ efflux, F_S, or 'soil respiration' is the sum of all carbon dioxide (CO$_2$) produced by below-ground processes and includes root respiration and respiration by soil organisms. Soil-surface CO$_2$ efflux accounts for 67–76% of total ecosystem respiration (TER) in forests (Law *et al.*, 1999; Janssens *et al.*, 2001; Xu *et al.*, 2001). If TER is the main determinant of the C balance in forest ecosystems (Valentini *et al.*, 2000), then soil C flux plays a critical role in determining the net exchange of C between forests and the atmosphere. Globally, F_S exceeds NPP by 25–60% (Raich & Schlesinger, 1992; Raich & Potter, 1995) and in forests it releases more than half of the C fixed in gross primary productivity (GPP) back to the atmosphere (Law *et al.*, 1999; Janssens *et al.*, 2001).

Disturbances – both natural and anthropogenic – are an important aspect of the interface between global change biology and C cycle science. Any changes in major C fluxes during ecosystem recovery from disturbance could have large implications for the net exchange of C between terrestrial ecosystems and the atmosphere. Wildfires in temperate and boreal forests are estimated to account for as much as two-fifth of the total biogenic flux of CO$_2$ to the atmosphere through direct and postfire emissions (Auclair & Carter, 1993). During fires in coniferous forests, approximately 25% of the C stored in above-ground pools is released to the atmosphere through direct combustion (Stocks, 1991). Following fire, however, changes in productivity, quantity and quality of C pools, and environmental site conditions can directly influence the flux of C from soils (Burke *et al.*, 1997). Consequently, the amount of C released to the atmosphere via postfire CO$_2$ emissions can be two to six times greater than during the initial combustion of biomass (Auclair & Carter, 1993; Dixon & Krankina, 1993).

Natural disturbances lead to patchy landscapes characterized by a mosaic of stands differing in age and stand structural characteristics – for example, tree density – (Turner *et al.*, 1994; Turner *et al.*, 1997; Foster *et al.*, 1998). This landscape mosaic, in turn, influences regional patterns of energy flow, nutrient cycling and susceptibility to future disturbances (Turner & Dale, 1998). The frequency, size and intensity of disturbances are contingent upon weather and climate as well as forest structure and composition (Dale *et al.*, 2001) and thus projected climate change is expected to result in modifications to natural disturbance regimes (Overpeck *et al.*, 1990; Baker, 1995; Turner *et al.*, 1998; He *et al.*, 1999). Altered disturbance regimes, whether caused by management activities or climate, may have large impacts on forest dynamics and C cycling through changes in the distribution of stand age classes and composition across the landscape. Extensive fires and insect outbreaks, for example, during the 1970s and 1980s are thought to have switched the Canadian forest sector from a net C sink to a source (Kurz & Apps, 1999).

The overall goal of our study was to investigate ecosystem recovery from a natural disturbance by examining soil C pools and fluxes in postfire lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) stands differing in tree density and stand age. Yellowstone National Park (YNP) provides an ideal natural laboratory for studies of this kind as a result of the great spatial variability in postfire tree establishment following the 1988 fires and the landscape mosaic of stand ages existing from centuries of a relatively natural fire regime.

Our first objective was to examine temporal patterns of F_S, microbial biomass C, C_{mic}, and soil temperature and moisture over the growing season. We hypothesized that F_S and C_{mic} would follow shifts in soil temperature and exhibit similar temporal patterns. Soil moisture is important in controlling F_S and C_{mic}, but we hypothesized that it would be of minor importance in a lodgepole pine ecosystem characterized by rapid soil drying following snowmelt and a very dry growing season. We also hypothesized that soil temperature and moisture would be higher in young stands because of canopy removal, surface albedo changes and a reduction in evapotranspiration rates following disturbance (Aber & Melillo, 1991).

Our second objective was to estimate and compare yearly rates of C flux from soils in order to gain a better understanding of ecosystem recovery of F_S, the major flux of TER, 13 years after a stand replacing fire. We hypothesized that the yearly flux of C from soils would be similar between young and mature stands as postfire changes in the soil environment – for example, increased soil temperature and moisture – can lead to increased decomposition rates (Burke *et al.*, 1997) that may offset decreases in root respiration.

The last objective was to determine whether stand level F_S and C_{mic} were correlated with one another and with various biotic (above- and below-ground plant biomass) and abiotic variables (soil C and N content, bulk density and soil texture). We hypothesized that F_S and C_{mic} would be correlated because they would respond to similar environmental variables – for example, soil temperature and moisture. However, we hypothesized that F_S would be controlled primarily by biotic variables (Högberg *et al.*, 2001) and C_{mic} by abiotic variables (Xu & Qi, 2001).

Materials and methods

We used a full factorial design with four replicates of four forest types – low (< 1000 trees ha^{-1}), moderate ($7\,000$–$40\,000$ trees ha^{-1}) and high ($> 50\,000$ trees ha^{-1}) densities in 13-year-old stands and mature stands (100–120-year-old) with a mean density of 2250 trees ha^{-1} – in YNP in order to investigate the effects of stand density and age on F_S and C_{mic} in postfire lodgepole pine ecosystems (Table 1). Soil-surface CO_2 efflux, soil temperature and soil moisture were measured five times and C_{mic} was sampled three times during the growing season in each stand. In addition, we sampled biotic (above- and below-ground plant biomass) and abiotic variables (soil physical and chemical properties). Measurements of F_S from each stand were used to estimate yearly C flux from soils by linear interpolation between measurement periods. For comparison, we also estimated yearly F_S with temperature response equations and continuous measurements of soil temperature.

Study area

Yellowstone National Park is located primarily in northwest Wyoming and covers about 9000 km^2, the majority of which occurs on several high-elevation, relatively flat, forested plateaus (Turner *et al.*, 1994; Turner *et al.*, 1997). As a result of recurring fire and insect epidemics,

lodgepole pine forests currently cover some 80% of the park, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is thought to be the primary climax species on the plateaus (Despain, 1990; Whitlock, 1993). Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and whitebark pine (*Pinus albicaulis* Engelm.) can be locally abundant as well (Despain, 1990).

Our stands were located on sites similar in environmental and topographic characteristics throughout the subalpine plateaus of YNP at elevations between 2000 and 2500 m (Table 1). Plots were randomly selected in stands located within ∼1 km of the existing road network in areas representative of the surrounding landscape (Litton, 2002). Young stands used in this study established following the 1988 Yellowstone fires (13-year-old) and span the natural range of variability in stand density that is present across the landscape (< 500 to $> 500\,000$ trees ha^{-1}). Mature postfire stands were 100–120-year-old, with densities ranging from 1320 to 3360 trees ha^{-1}. Sampling was performed on 0.25 ha plots that were located within larger (> 2 ha), homogeneous, monotypic stands of lodgepole pine. Data on F_S were collected from three 20-m permanent transects spaced at 20-m intervals and temporary transects (20–50 m) were located between the permanent transects for measuring other variables.

All stands were located on rhyolitic soils, the dominant soil type on the subalpine plateaus, resulting from major

Table 1 Site characteristics for study areas in Yellowstone National Park, Wyoming

Stand name	Density class*	Age class[†]	Density (trees ha^{-1})	Mean basal area (cm^2)[‡]	Mean tree height (m)	Elevation (m)	Soil C Content (g C m^{-2})[§]
Cascade Meadows	Low	Young	425	6.6 (1.3)	0.62 (0.06)	2486	2797
Lewis Canyon North	Low	Young	533	8.8 (1.6)	0.67 (0.07)	2372	4348
Cygnet Lakes	Low	Young	742	10.6 (1.3)	0.79 (0.06)	2508	2975
Pitchstone Plateau	Low	Young	758	12.3 (1.4)	0.82 (0.06)	2368	4535
Riddle Lake TH	Moderate	Young	7000	7.2 (0.5)	1.00 (0.04)	2429	3298
Lewis Canyon South	Moderate	Young	8700	9.9 (0.9)	1.13 (0.05)	2363	3612
Biscuit Basin	Moderate	Young	25 250	6.7 (0.5)	1.21 (0.04)	2223	2100
Howard Eaton	Moderate	Young	39 167	3.5 (0.2)	0.94 (0.03)	2370	2501
Riddle High	High	Young	50 167	4.3 (0.2)	0.96 (0.02)	2417	2864
Firehole Loop	High	Young	73 455	2.2 (0.2)	0.76 (0.03)	2166	1722
Gibbon Falls	High	Young	75 500	2.8 (0.2)	0.85 (0.02)	2131	3351
7-Mile Bridge	High	Young	598 462	0.7 (0.0)	0.60 (0.01)	2076	2868
Crawfish Creek	–	Mature	1920	206.4 (12.3)	15.1 (0.43)	2278	4308
Firehole River	–	Mature	3360	113.8 (6.1)	11.6 (0.30)	2195	3184
Midway Geyser	–	Mature	2400	175.3 (8.0)	13.4 (0.28)	2213	4868
West Thumb	–	Mature	1320	397.6 (27.3)	17.5 (0.30)	2347	4617

Soils for all sites were sandy loams with low clay content (2–7%). Numbers in parentheses are 1 SE of the mean.
*For young stands: low density is < 1000 trees ha^{-1}, moderate density is 7000–40 000 trees ha^{-1} and high density is $> 50\,000$ trees ha^{-1}.
[†]All young stands were 13-year-old and mature stands were 100–120-year-old.
[‡]From basal diameter for young stands and diameter at 1.3 m for mature stands.
[§]Carbon content in the litter layer and top 30 cm of mineral soil.

volcanic activity in the Quaternary Era (Despain, 1990; Whitlock, 1993). Rhyolitic soils are relatively infertile – for example, mean values of 1.1% organic C and 0.05 meq 100 g^{-1} total N – and are classified in the Cryochrept or Cryumbrept families (Trettin, 1986). The soils in our stands were sandy loams with low clay content (2–7%). The litter layer and most fine fuels in the canopy were completely consumed in young stands during the 1988 fires. Development of a well-defined surface organic horizon has still not occurred after 13 years in these stands, primarily because of high needle retention by young trees and a lack of other fine litter inputs. On average, litter C was only 6% of total soil C in our young stands, whereas it accounted for 25% of soil C in mature stands.

Yellowstone National Park has cool temperatures throughout the year and a dry growing season. At Yellowstone Lake (2360 m) the mean January temperature is −11.8 °C and the mean July temperature is 12.9 °C; mean annual precipitation is 465 mm (Dirks & Martner, 1982). Approximately 65–85% of the annual precipitation comes as snow and snow cover usually exists from mid-October to late May (Despain, 1990).

Soil-surface CO₂ efflux

Soil-surface CO₂ efflux originating from the litter layer and mineral soil was measured in each stand five times during the growing season, four times in 2000 and once in the early summer of 2001. Previous year's snowpack, snowmelt dates and overall climatic conditions for the two growing seasons were very similar. Soil-surface CO₂ efflux was measured with a dynamic closed chamber portable infrared gas analyzer (IRGA) coupled to a soil respiration chamber (PP-Systems EGM-2 IRGA and SRC-1 soil respiration chamber; PP-Systems, Herts, UK). The respiration chamber was inserted directly through the litter layer and into the mineral soil ($\approx$1 cm) immediately prior to the measurements and flux was measured over a period of 90–120 s. For each measurement period, efflux was measured every 2 m along three 20 m permanent transects in each stand (30 measurements/stand).

The PP-Systems SRC-1 soil respiration chamber may yield 30–50% higher estimates of F_S compared to other chamber systems (Le Dantec et al., 1999; Janssens et al., 2000). In order to address this concern we compared mean F_S rates measured with the SRC-1 soil respiration chamber (30 points/stand) with simultaneous measurements taken with a LI-COR dynamic closed chamber IRGA system (10 points/stand, two measurements/point) (LI-COR 6400 portable photosynthesis system and LI-COR 6400-09 soil respiration chamber; LI-COR, Lincoln, NE) in each of the 16 stands in June 2001. For the LI-COR measurements we used PVC collars inserted

2–3 cm through the litter layer and directly into the mineral soil at least 48 h prior to sampling. Measurements were made by drawing down the CO₂ concentration inside of the LI-COR chamber below ambient concentrations at the soil surface and measuring through ambient. Carbon dioxide efflux from snowpack was measured in 12 stands (three mature stands and three young stands in each density class) during March 2001 with the LI-COR 6400-09 chamber adapted for snow measurements (McDowell et al., 2000).

Percent volumetric water content in the top 12 cm of soil and soil temperature at 10 cm were sampled next to each efflux measurement with a Hydrosense soil water content measurement system (Campbell Scientific, Inc., Logan, UT) and a digital soil thermometer. Continuous measurements of soil temperature were also made in one stand from each density/age class from June 2000 to August 2001 using Campbell 21x dataloggers (Campbell Scientific, Inc., Logan, UT) and eight thermocouple sensors buried 10 cm under the soil. Soil temperature was recorded every 15 min and was averaged over 3-h time periods for each sensor. Data from the eight sensors were then averaged in order to determine mean soil temperature at 3-h intervals, mean daily soil temperature and the daily amplitude in soil temperature for each treatment.

Annual estimates of soil C flux

Yearly C flux from soils was estimated by linear interpolation of mean daily F_S between measurement periods during the growing season and by applying measured CO₂ efflux from snowpack across the entire snowpack season. The temperature response of F_S was estimated from two diurnal measurements of F_S (μmol CO₂ m^{-2} s^{-1}) and soil temperature (°C) at 10 cm (T) in June and August in one young and one mature stand. Soil-surface CO₂ efflux and T were measured every 2 h for 24 h on 10 points in each stand with the LI-COR chamber and a digital soil thermometer. Soil-surface CO₂ efflux was then fit to an exponential model by stand age and measurement period:

$$F_S = \alpha * e^{\beta T} \qquad (1)$$

where α and β are constants fitted with non-linear regression techniques. Q_{10} values were calculated as:

$$Q_{10} = e^{10 * \beta} \qquad (2)$$

where the Q_{10} value is the factor by which F_S increases for every 10 °C increase in T.

Mean daily F_S (μmol CO₂ m^{-2} s^{-1}) was then determined for each site by first adjusting mean measured F_S rates to mean daily T:

$$\overline{F}_S = F_S * e^{\beta(\overline{T}-T)} \tag{3}$$

where $\overline{F}_S$ is measured CO_2 efflux adjusted to mean daily soil temperature and $\overline{T}$ is mean daily soil temperature (°C) at 10 cm taken from continuous recordings (individual datalogger measurements were applied to all stands in that treatment). The non-linear relationship between respiration and temperature can bias respiration estimates if daily temperature amplitudes are ignored (Ryan, 1991). Therefore, we adjusted estimates of $\overline{F}_S$ for the effect of daily amplitude, A, in T with a sine function, I_0, for all days during the snow-free period (Ågren & Axelsson, 1980):

$$\overline{F}_S = \overline{F}_S * I_0(\beta * A) \tag{4}$$

where A is derived from continuous measurements of T (as before, individual datalogger measurements were applied to all stands in that treatment). Finally, we estimated the yearly flux of C from soils during the growing season for each stand by interpolating F_S between measurement periods.

Daily mean efflux of C from soils during the winter was estimated from measured values of CO_2 efflux from snowpack applied across the entire snowpack period. For stands that were not sampled for CO_2 efflux during winter, values were estimated as the mean of measured efflux from the three stands in that treatment group. Snowpack duration was determined for each treatment by examining the diurnal amplitudes in T and air temperature (3 m) for a given treatment's datalogger and snowpack was considered present for that period in which the diurnal amplitude in soil temperature was minimal ($<1–2$ °C) compared to the diurnal amplitude in air temperature. Finally, corrected and adjusted mean daily F_S (µmol $CO_2\,m^{-2}\,s^{-1}$) estimates for the entire year were converted to daily C flux from soils ($g\,C\,m^{-2}\,day^{-1}$) and summed over 365 days to yield yearly soil C flux estimates ($g\,C\,m^{-2}\,yr^{-1}$).

For comparison, we also estimated yearly C flux from soils using stand specific temperature response equations and continuous measurements of soil temperature. Stand temperature response equations were calculated from Eqns (1) and (2) using stand mean values of F_S and T from the five growing season measurement periods. Temperature response functions were then applied to continuous 3-h measurements of T during the growing season (measurements of soil temperature from each of the four dataloggers were applied to all stands within that treatment). Carbon dioxide efflux from snowpack was estimated as above.

Microbial biomass C

Mineral soil C_{mic} was sampled in 12 stands (three from each density class in young stands and three mature stands) three times during the 2000 growing season (6/27–7/1, 8/12–8/1, and 9/20–9/26). For each measurement period, 15 soil samples were taken throughout each stand from the mineral soil to a depth of 10 cm with a soil auger (5-cm diameter) and composited. Composite samples were sieved through a 2-mm mesh, mixed thoroughly and stored at 2 °C until early October 2000 when all samples could be analyzed simultaneously. Some microbial activity may continue during storage at 2 °C, particularly for soils characterized by cryophilic organisms. However, this should not influence our results and conclusions as storage should have affected all samples equally and our focus was on trends in C_{mic} with stand age and tree density in YNP, and not a comparison of our values with other studies.

Microbial biomass C was estimated with the chloroform fumigation extraction method modified from Vance *et al.* (1987), where C_{mic} is calculated as the difference in organic C between fumigated and unfumigated (control) samples. For all composite samples, a small subsample (10–12 g) was weighed and dried to a constant weight at 60 °C in order to determine percent soil moisture and three subsamples were analyzed for C_{mic}. For each subsample, two 25 g field moist samples were weighed and one was fumigated with alcohol-free $CHCl_3$ in a sealed desiccator for 24 h at 25 °C, whereas the other was stored at 4 °C. Both samples were then placed on a shaker for 30 min and extracted with 125 mL of 0.5 M K_2SO_4. Extracts were filtered through Whatman No. 42 filter paper and frozen for storage. All extracts were analyzed for organic C content on a Shimadzu 5000 Total Organic Carbon Analyzer (Shimadzu Scientific Instruments, Columbia, MD) and C_{mic} was determined as:

$$C_{mic} = EC/k_{EC} * \%H_2O \tag{5}$$

where EC is the difference in C extracted from the fumigated and unfumigated samples, k_{EC} is the correction factor (0.35) and $\%H_2O$ is percent soil moisture. Mean C_{mic} values from the three subsamples for a given stand and measurement period were used for data analysis.

Above- and below-ground plant biomass

Above- and below-ground biomass estimates for lodgepole pine trees in our young stands in YNP were reported by Litton *et al.* (2003). Biomass was estimated using measurements of basal diameter from trees in three belt transects in each stand applied to allometric equations developed in YNP for predicting coarse root (>2 mm) and above-ground biomass in 13-year-old lodgepole pine trees. Fine root biomass was estimated in each stand during a 2-week period in July 2000. Fine roots were collected from the litter layer and mineral soil with 15 cores (6.35-cm diameter) taken to a depth of 30 cm.

Above-ground biomass for herbaceous and shrub species was estimated using allometric equations developed in YNP for predicting biomass from percent cover (Tinker *et al.*, submitted). In each stand, we measured percent cover of all herbaceous and shrub species at approximate peak biomass in twenty $0.25\,m^2$ quadrats. Below-ground biomass – that is, fine roots – for herbaceous and shrub species was estimated using root cores (fifteen 6.35-diameter cores in each stand). Above- and below-ground biomass for herbaceous and shrub species were added to estimates of tree biomass in young stands.

Soil physical and chemical properties

Soil C and nitrogen (N) contents were calculated as the sum of the litter layer and the top 30 cm of mineral soil. Carbon and N pools in the litter layer were calculated for each stand by multiplying estimates of litter mass by values of percent C and N in litter. Litter mass (needles, bark, cones and branches $<7.5\,cm$ diameter) was estimated by sampling the forest floor with fifteen $300\,cm^2$ frames. Samples were composited within a stand, dried to a constant weight at $70\,°C$ and final estimates of litter mass were corrected for ash-free weight by processing a subsample in a muffle furnace. Carbon and N pools in the top 30 cm of mineral soil were estimated by multiplying values of percent C and N in the mineral soil by soil-bulk density measurements from each stand. Percent C and N in the mineral soil was estimated from composite soil samples from 15 cores (6.35 cm diameter) taken to a depth of 30 cm. Composite samples were passed through a 2-mm sieve, mixed thoroughly and dried to a constant weight at $70\,°C$. Subsamples of litter and mineral soil were isolated and processed overnight on a roller mill in order to determine %C and %N on a LECO-100 CHN analyzer (LECO Corporation, St Joseph, MI).

Soil-bulk density was determined on five separate 6.35-cm-diameter cores taken to a depth of 30 cm throughout each stand using a standard core method (Culley, 1993). Soil texture was determined on a composite sample from the bulk density cores using the hydrometer method (Sheldrick & Wang, 1993).

Statistical analyses

The sample unit for this study was the stand and, thus, all variable measurements represent mean stand values or single values taken from a composite. All statistical analyses were performed in SPSS 10.0 for Windows (SPSS Inc., Chicago, IL) at an $\alpha = 0.05$. Stands were grouped into age and density classes for analyses (Table 1) and all data were tested for assumptions of normality and equality of variance. The effect of age on measured variables was assessed with a contrast model and density effects were assessed by constraining the analyses to young stands. Differences between individual treatment groups were analyzed with post hoc tests using Tukey's honestly significant difference (HSD) method or with Dunnett's C method in the case of unequal variances. Treatment and time effects for F_S, C_{mic}, soil temperature and soil moisture were analyzed with a Repeated Measures General Linear Model (GLM). A One-way Analysis of Variance (ANOVA) was used in order to test for effects of stand age and tree density on the flux of CO_2 from snowpack and the yearly flux of C from soils. A bivariate correlation analysis was performed using a two-tailed test of significance in order to identify correlations between mean daily F_S, C_{mic}, and various biotic and abiotic variables in young stands. Mature stands were eliminated from this analysis because their inclusion resulted in nonlinear relationships and the sample size ($n = 4$) was too small to detect reliable correlations when analyzed separately.
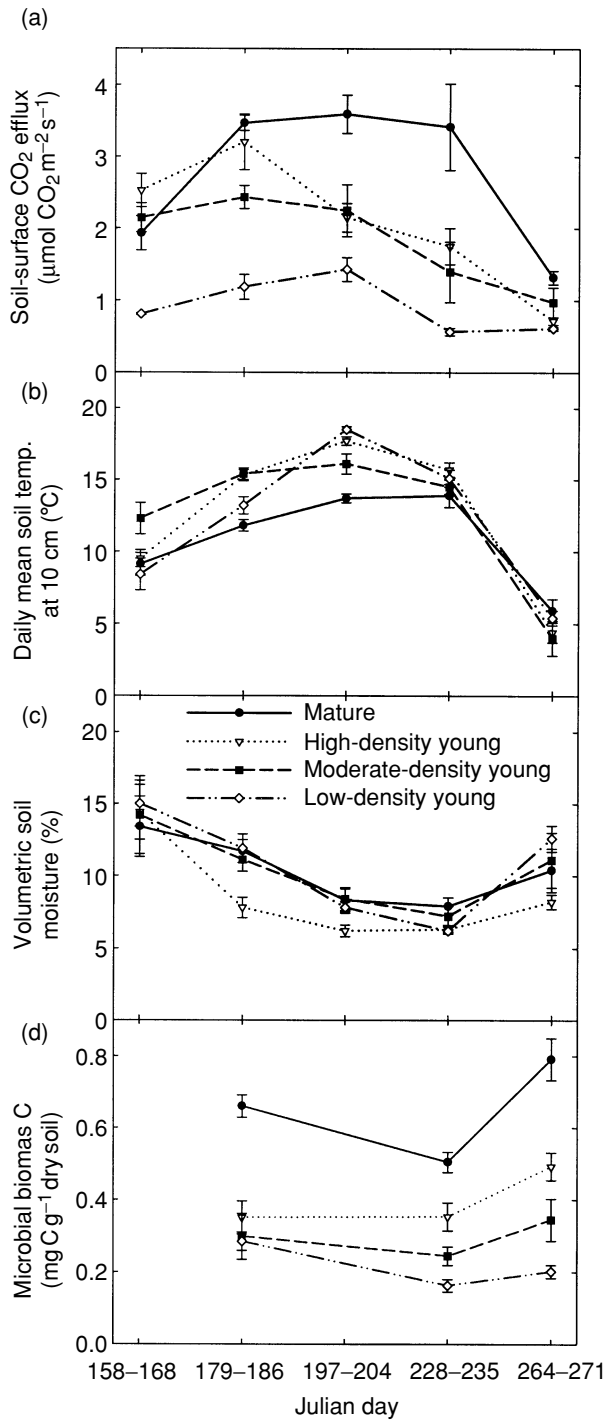
Results

Soil-surface CO$_2$ efflux

Both tree density and stand age had significant effects on F_S ($P < 0.01$). Within young stands, efflux in the low-density class was lower than in the moderate- and high-density classes ($P = 0.01$); moderate- and high-density classes did not differ ($P = 0.58$). Mature stands exhibited higher F_S than low ($P < 0.01$), moderate ($P = 0.01$), or high-density young stands ($P = 0.04$). Results of repeated measures analysis on F_S show strong treatment ($P < 0.01$) and time effects ($P < 0.01$), and the interaction between time and treatment ($P = 0.02$) indicates that treatments responded differently over time (Fig. 1a).

Temporal patterns of F_S followed patterns of soil temperature only for mature stands (Fig. 1a, b). The overall pattern in F_S from young stands was of increasing efflux in the early part of the growing season and decreasing efflux beginning in early to mid-July (Fig. 1a). During the growing season, treatment means of F_S ranged from 0.6 to $1.4\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for low-density young stands, $1.0–2.4\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for moderate-density young stands and $0.7–3.2\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for high-density young stands. In mature stands, F_S increased during the early part of the growing season, remained relatively stable from early July through the end of August with a maximum of $3.6\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ and decreased to a minimum of $1.3\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ in late September (Fig. 1a). Growing season mean values of F_S were $1.0\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for low-density young stands, $1.8\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for moderate-density young stands $2.1\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for high-density young stands and $2.7\,\mu mol\ CO_2\,m^{-2}\,s^{-1}$ for mature stands.

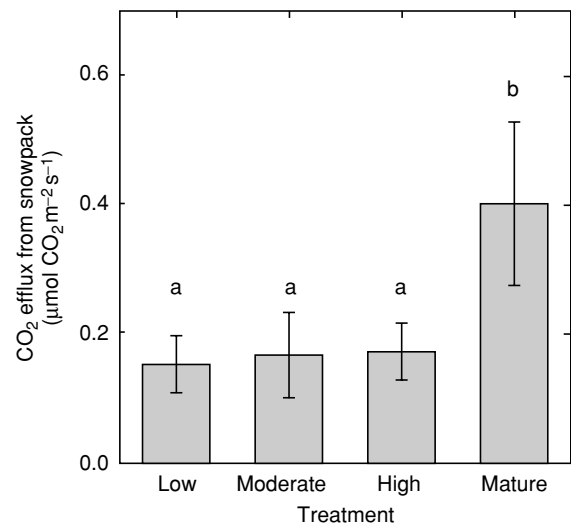Tree density did not affect CO_2 efflux from snowpack in young stands ($P = 0.38$), but age did have a significant effect on winter-time efflux rates ($P < 0.01$) (Fig. 2). Carbon dioxide efflux rates from snowpack were much lower than growing season values, ranging from 0.1–0.2 μmol CO_2 m^{-2} s^{-1} in young stands to 0.4 μmol CO_2 m^{-2} s^{-1} in mature stands.

Considerable spatial variation in measured F_S rates existed within individual sites. Coefficients of variation (CV) throughout the growing season ranged from 23–81% within low-density young stands, 24–78% within moderate-density young stands, 29–66% within high-density young stands and 9–57% within mature stands. Coefficients of variation of F_S (mean stand values) within a given treatment group were much lower across measurement periods (3–29% for low-density young stands, 13–32% for moderate-density young stands, 14–29% for high-density young stands and 6–35% for mature stands). In addition, much less spatial variability was present during wintertime measurements of CO_2 efflux from snowpack (mean CV for all stands = 29%).

We found no difference in stand mean F_S measured with the PP-Systems SRC-1 and LI-COR 6400-09 soil respiration chambers ($P = 0.91$, paired samples t-test) (Fig. 3). Stand mean F_S measured with the PP-Systems and LI-COR chambers in early June ranged from 0.7–3.9 to 0.6–3.1 μmol CO_2 m^{-2} s^{-1}, respectively. Measurements taken with the two systems were highly correlated ($R^2 = 0.83$) and did not differ from a 1:1 relationship, with an intercept of 0.09 (95% C.I. of −0.4 to 0.6) and a slope of 0.95 (95% C.I. of 0.7 to 1.2). Therefore, we did not adjust our measurements of F_S.

Fig. 1 Treatment means ($\pm$ 1 SE) in lodgepole pine stands of (a) soil-surface CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) adjusted to daily mean soil temperature (°C) at 10 cm, (b) daily mean soil temperature (°C) at 10 cm, (c) volumetric soil moisture (%) in the top 12 cm of soil and (d) microbial biomass C (mg C g^{-1} dry soil) in the top 10 cm of mineral soil.

Fig. 2 Carbon dioxide (CO_2) efflux from snowpack (μmol CO_2 m^{-2} s^{-1}; mean $\pm$ 1SE) for different treatment groups measured in early March 2001.
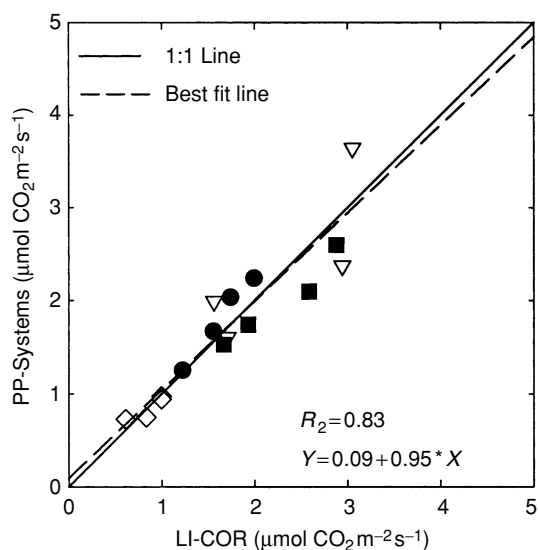
Fig. 3 Comparison of soil-surface CO$_2$ efflux (μmol CO$_2$ m^{-2}s^{-1}) measured simultaneously with two dynamic closed chamber portable IRGAs (PP-Systems EGM-2 and LI-COR 6400) and their respective soil respiration chambers (PP-Systems SRC-1 and LI-COR 6400-09). Points are means of 30 measurements for the PP-Systems and 10 independent measurements for the LI-COR. Open diamonds represent low-density young stands, solid boxes moderate-density young stands, open triangles high-density young stands and solid circles mature stands.

Soil temperature and moisture

Soil temperature varied with treatment ($P = 0.02$), time ($P < 0.01$) and treatment over time ($P < 0.01$) (Fig. 1b). There was a significant stand age effect ($P < 0.01$), with mature stands exhibiting lower soil temperatures than either the moderate- or high-density young stands ($P = 0.03$). There was no tree density effect within young stands ($P = 0.67$). For all treatments, growing season soil temperature rose to a maximum in late July and dropped to a minimum in late September. For the four datalogger sites, mean yearly soil temperature and mean soil temperature for the snow-free period at 10-cm depth were 6.3 and 10.4 °C for the low-density young stand, 5.9 and 9.9 °C for the moderate-density young stand, 5.7 and 9.9 °C for the high-density young stand and 5.4 and 9.0 °C for the mature stand. The average soil temperature at 10 cm for all sites during the snowpack period was −0.9 °C.

Soil moisture (percentage volumetric) differed over time ($P < 0.01$) and with treatment ($P = 0.05$) (Fig. 1c), but the different treatments exhibited similar temporal patterns ($P = 0.55$). There was no effect of stand age on soil moisture ($P = 0.49$), but soil moisture did differ with tree density in the young stands ($P = 0.05$) with higher levels of soil moisture in low-density stands than in high-density stands. During the growing season, soil moisture ranged from 6 to 15% in young stands and 8–13% in mature stands. Soil moisture was highest in the early growing season, declined steadily through late August and began to rise again in September.

Annual estimates of soil C flux

The Q_{10} values determined from diurnal measurements were higher in young stands than in mature stands, but were remarkably similar within a given stand age across the growing season (Fig. 4). The Q_{10} values in the young stand were 1.85 in late June and 1.89 in late August. For the same measurement periods in the mature stand, Q_{10} values were 1.42 and 1.46. The 0 °C respiration value (α coefficient in Eqn. (1)) was lower in the young stand than in the mature stand. It also differed with time within a given stand type, with lower values later in the growing season (Fig. 4).

Mean daily flux of C from soils ranged throughout the year from 0.2 to 1.5 g C m^{-2} day^{-1} in low-density young stands, 0.2 to 2.5 g C m^{-2} day^{-1} in moderate-density young stands, 0.2 to 3.3 g C m^{-2} day^{-1} in high-density young stands and 0.3 to 3.7 g C m^{-2} day^{-1} in mature stands (Fig. 5). Growing season mean values of soil C flux were 0.8, 1.5, 1.7 and 2.5 g C m^{-2} day^{-1} for low-density young, moderate-density young, high-density young and mature stands, respectively. The percentage of yearly flux of C from soils occurring during the snowpack period was 22% for low-density young stands, 10% for moderate-density young stands, 9% for high-density young stands and 20% for mature stands.

Yearly flux of C from soils (g C m^{-2} yr^{-1}) varied with tree density in young stands ($P < 0.01$) and with stand age ($P < 0.01$) (Fig. 5). Within young stands, significant differences were confined to low-density stands ($P < 0.01$); moderate- and high-density stands did not differ ($P = 0.60$). Treatment mean rates of C flux from soils were 156 g C m^{-2} yr^{-1} for low-density young stands, 303 g C m^{-2} yr^{-1} for moderate-density young stands, 351 g C m^{-2} yr^{-1} for high-density young stands and 460 g C m^{-2} yr^{-1} for mature stands, with CVs of 3, 27, 13 and 11%, respectively.

Yearly C flux from soils estimated with temperature response equations from individual stands always exceeded estimates from linear interpolation. Differences were primarily because of overestimates of F_S in mid to late summer in both young and mature stands (Fig. 6). On average, the temperature response equations resulted in 14% higher estimates of yearly C flux. Best agreement between linear interpolation and temperature response equation estimates occurred in low-density young stands (6–12% difference); largest differences were associated
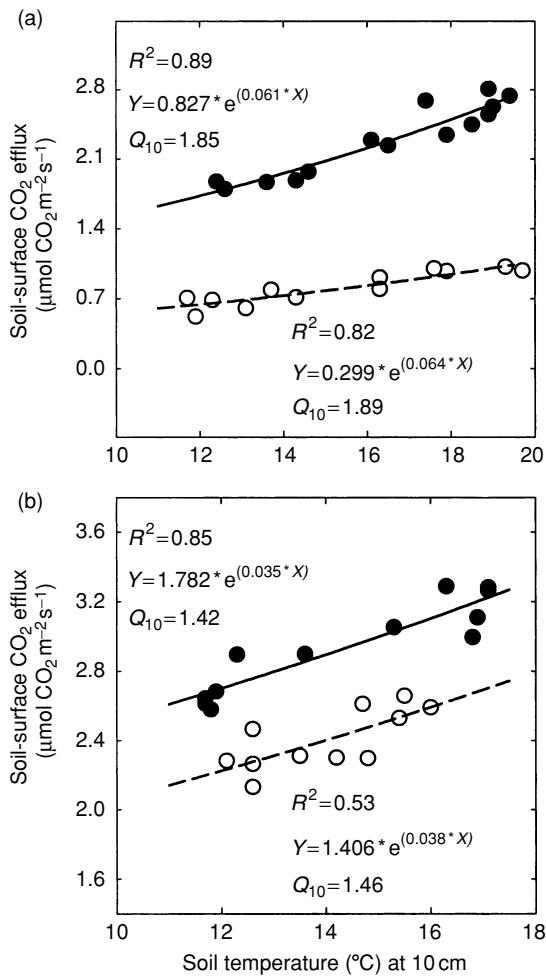
Fig. 4 Temperature response equations and Q_{10} values for soil-surface CO_2 efflux in (a) young and (b) mature lodgepole pine stands. Equations were fitted with non-linear regression techniques using data from diurnal measurements of soil-surface CO_2 efflux and soil temperature (°C) at 10-cm depth for late June (solid lines and circles) and late August (dashed lines and open circles). Points are means of 10 independent measurements for soil-surface CO_2 efflux (LI-COR 6400 IRGA and 6400-09 soil respiration chamber) and soil temperature.

with mature stands (15–28%). Individual site temperature response equations did a reasonable job of explaining the variation in F_S from T on most sites (R^2 values ranging from 0.33 to 0.78 (mean of 0.59) in young stands and 0.87–0.91 in mature stands). The Q_{10} values ranged from 1.6 to 2.6 in young stands and 3.4–4.6 in mature stands.

Microbial biomass and soil C

Microbial biomass carbon (mg C g^{-1} dry soil) varied across treatments ($P < 0.01$) and with time ($P < 0.01$), but
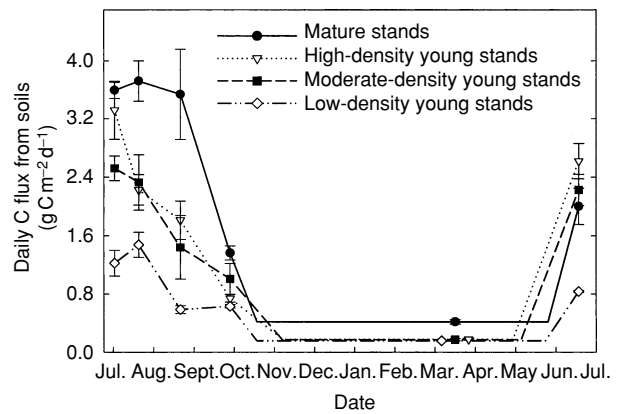
Fig. 5 Daily C flux from soils (g C m^{-2} day^{-1}) for different tree density and stand age treatments in lodgepole pine forests. Values are adjusted to mean daily soil temperature (°C) at 10 cm and corrected for the diurnal amplitude in soil temperature. Points represent mean treatment flux rates ($\pm$ 1 SE) based on four stands/treatment and lines represent a linear interpolation between measurement periods.
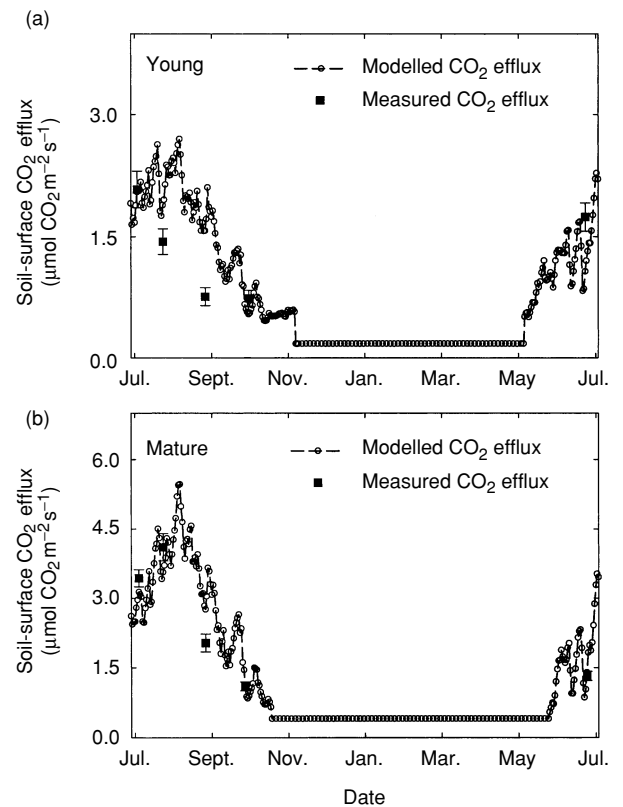
Fig. 6 Modelled (dashed lines and open circles) and measured (solid boxes; mean $\pm$ 1 SE) mean daily soil-surface CO_2 efflux (μmol CO_2 m^{-2} s^{-1}; adjusted to daily mean soil temperature (°C) at 10 cm and corrected for the diurnal amplitude in soil temperature) for representative (a) young and (b) mature stands of lodgepole pine.

Table 2 Pearson product-moment correlation coefficients between various biotic and abiotic variables and microbial biomass (C_{mic}) and stand daily mean soil-surface CO_2 efflux (F_S; $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) at five measurement periods and for the entire growing season in young postfire stands of lodgepole pine

	$C_{mic}(mg\ C\ g^{-1}$ dry soil)*	Above-ground biomass (kg dry wt. ha^{-1})†	Below-ground biomass (kg dry wt. ha^{-1})‡	Soil C content (g C m^{-2})§	Soil N content (g N m^{-2})§	Soil bulk density (g cm^{-3})¶	Soil texture (% clay)¶
C_{mic}	–	0.44	**0.83**	−0.47	−0.42	0.20	0.30
F_S (06/06–06/16)	**0.71**	**0.90**	**0.78**	−0.47	−0.34	0.50	−0.18
F_S (06/27–07/08)	**0.81**	**0.81**	**0.88**	−0.33	−0.24	0.28	−0.17
F_S (07/15–07/29)	**0.80**	**0.61**	**0.59**	−0.13	−0.03	0.06	−0.45
F_S (08/10–08/22)	0.25	**0.80**	0.43	−0.12	−0.02	0.57	−0.40
F_S (09/20–09/28)	0.07	**0.58**	0.07	0.06	0.14	0.21	−0.35
F_S Growing Season**	**0.66**	**0.88**	**0.68**	−0.27	−0.16	0.47	−0.39

Bold numbers indicate a significant correlation at $\alpha = 0.05$.
*Mean growing season microbial biomass C in the top 10 cm of mineral soil.
†Includes tree, herbaceous and shrub above-ground biomass.
‡Includes tree, herbaceous and shrub fine root biomass and tree coarse root biomass.
§Includes soil C and N in the litter layer and top 30 cm of the mineral soil.
¶Values are for the top 30 cm of the mineral soil.
**Growing season refers to the period during which snowpack is absent (beginning April 22–May 18 and lasting through October 13–November 1, depending on the site).

treatments behaved similarly over time ($P = 0.12$) (Fig. 1d). There was an effect of stand age ($P < 0.01$), but no effect of tree density in young stands ($P = 0.16$). However, a pattern of increasing C_{mic} with increasing tree density in young stands was apparent (Fig. 1d). Through the growing season, C_{mic} ranged from 0.2 to 0.3 mg C g^{-1} dry soil in low-density young stands, 0.3–0.4 mg C g^{-1} dry soil in moderate-density young stands, 0.4–0.5 mg C g^{-1} dry soil in high-density young stands and 0.5–0.8 mg C g^{-1} dry soil in mature stands. Temporal patterns of C_{mic} did not follow changes in soil temperature (Fig. 1b, d), but instead appeared to be correlated with soil moisture, declining through August and rising again at the end of the growing season (Fig. 1c, d).

Soil C content in the litter layer and top 30 cm of mineral soil did not vary with stand age ($P = 0.30$), or with tree density in young stands ($P = 0.11$) (Table 1). Bulk density of the mineral soil did not differ across treatment groups either ($P = 0.67$).

Correlation analysis

Stand mean values of F_S in young stands during the five growing season measurement periods were correlated with microbial biomass ($R = 0.65$–0.86), above-ground plant biomass ($R = 0.58$–0.90) and below-ground plant biomass ($R = 0.59$–0.88) (Table 2). Soil-surface CO_2 efflux was correlated throughout the entire growing season in young stands with above-ground biomass, but the strong correlations observed between F_S and both microbial biomass and below-ground plant biomass that existed

during the first half of the growing season were not present for later measurement periods. No significant correlations were found between F_S and measured abiotic variables (Table 2). Mean growing season F_S was correlated with biotic variables, including below-ground plant biomass (Table 2; Fig. 7a). Importantly, C_{mic} was highly correlated with below-ground plant biomass ($R = 0.83$), but not with any of the other measured biotic or abiotic variables (Table 2; Fig. 7b).

Discussion

Changes that occur in ecosystem properties following fire, both biotic and abiotic, may strongly affect soil C pools and fluxes (Burke *et al.*, 1997) and these changes could potentially influence the net exchange of C with the atmosphere more than the direct emission of CO_2 during biomass combustion (Auclair & Carter, 1993; Dixon & Krankina, 1993). In general, soil temperature can increase after fire with overstory removal and changes in surface albedo; soil moisture can increase with a reduction in transpiration rates; and soil pH levels can increase with a large input of cations in ash deposits (Aber & Melillo, 1991). Detrital inputs can also be greatly altered, with a decline in fine litter inputs, loss of rhizosphere exudation and a large initial increase in inputs of coarse woody debris (CWD). Increased inputs of below-ground litter can be particularly important in coniferous forests as a large pool of C that was previously found in live root biomass suddenly becomes available for decomposition. All of these changes are hypothesized to lead to increased
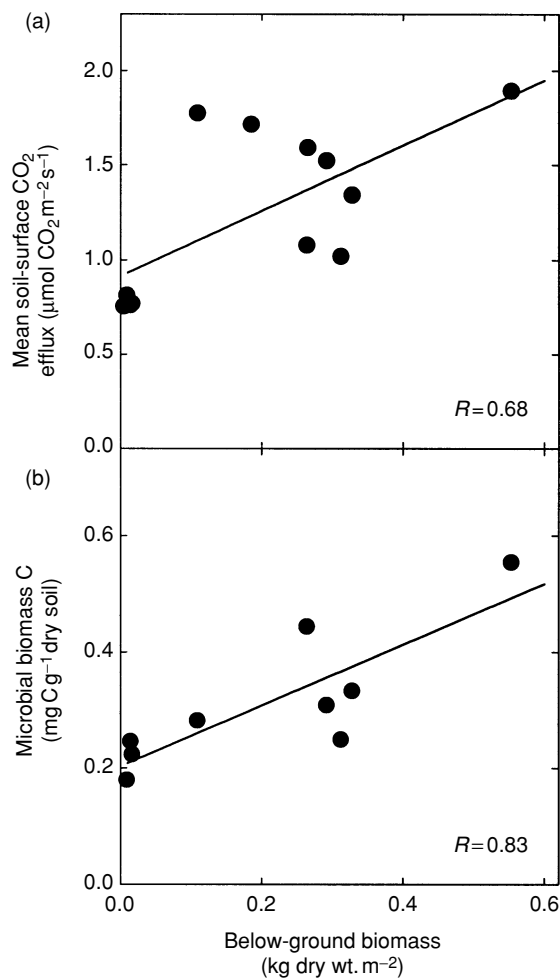
Fig. 7 Relationship between below-ground plant biomass (kg dry wt. m^{-2}) and (a) growing season mean soil-surface CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) and (b) microbial biomass (mg C g^{-1} dry soil) for young stands of lodgepole pine. The regression equation for soil-surface CO_2 efflux, F_S, is: $F_S = 0.92 + 1.72 *$ Below-ground Biomass ($R^2 = 0.46$; $P = 0.02$) and the regression equation for microbial biomass, C_{mic}, is: $C_{mic} = 0.20 + 0.52 *$ Below-ground Biomass ($R^2 = 0.69$; $P < 0.01$).

microbial activity in disturbed stands (Burke *et al.*, 1997), which could potentially release large amounts of CO_2 as F_S recovers rapidly to prefire levels with increased decomposition of bulk soil organic matter.

Our results for 13-year-old postfire stands do not follow the generalized model for changes in F_S following fire described above. Soil-surface CO_2 efflux rates did not increase in young postfire stands in our study area, even though there was a considerable input of C into soils from formerly live roots and soil temperature increased after fire. Our results are for 13-year-old stands and it is possible that higher levels of F_S occurred sometime in the

previous 12 years (Burke *et al.*, 1997). However, our correlation analysis (see *Correlation Analysis*, below) indicates that overall F_S rates are controlled principally by plant activity (Table 2; Fig. 7), suggesting that this was not likely the case. Canopy and surface fine fuels were entirely eliminated during the fire and the production of rhizosphere exudates would cease with the death of roots. Currently, litter C is a much smaller pool in young postfire stands in our study area (Litton, 2002) and F_S rates are not likely to recover to prefire levels until there is a sufficient buildup of litter C and a greater contribution from litter decomposition and rhizosphere respiration.

Soil-surface CO_2 efflux

Tree density strongly affected the flux of C from soils in young stands, with higher density stands characterized by higher flux rates. Similar results were observed for young, fast growing *Eucalyptus* plantations in Hawaii established on former sugarcane plantations (Giardina & Ryan, 2002). However, no studies that we know of have examined the effect of tree density on F_S in ecosystems recovering from natural disturbance. We attribute increased flux of C from soils in high-density stands to larger pools of C in both C_{mic} (Fig. 1d; although results not significant) and below-ground plant biomass (Litton *et al.*, 2003). Increased flux of CO_2 from decomposition of the litter layer is another possible explanation for higher F_S in high-density young stands, as litter C in high-density stands was approximately $4 \times$ that in low-density stands (Litton, 2002). However, this is not likely as the litter layer in young postfire stands displays no visible signs of advanced decomposition, more than likely because litter dries out very quickly in the spring following snowmelt. Flux measurements taken of the litter layer (data not shown) indicated virtually no decomposition of litter once it has dried out. In addition, we found no correlation between F_S and soil C, which includes litter and mineral soil C, in our young stands.

Compared to our mature stands, we observed lower fluxes of F_S in young stands. Using our mature stands as a frame of reference for prefire conditions, the 13-year-old postfire stands have not recovered to prefire emission levels, even in very-high-density stands (> 50 000 trees ha^{-1}). No consistent pattern emerges from the work that has been performed to date in other areas on the effect of stand age on C flux from soils. Working in clearcuts in Oregon, Law *et al.* (2001) found a pattern similar to ours in ponderosa pine (*Pinus ponderosa* Laws. & Laws.) stands, with lower rates in a 15-year-old stand than a 250-year-old stand. In lodgepole pine stands in south-central Wyoming, F_S was also significantly lower in 15-year-old stands than in 100-year-old forests (Smith &

Resh, 1999). However, F_S in jack pine (*Pinus banksiana* Lamb.) stands in central Saskatchewan was lowest in a 1-year-old clearcut stand, highest in an 8-year-old stand, and decreased with age thereafter (Striegl & Wickland, 2001). Moreover, F_S in postfire upland Canadian boreal forests was found to be similar in 1-year and >7-year postburn forests, and significantly lower in stands of intermediate age (2–5-year postburn) (Burke *et al.*, 1997). Other studies have documented increases (Ewel *et al.*, 1987; Gordon *et al.*, 1987), decreases (Weber, 1990; Joshi *et al.*, 1991), and no significant differences (Fernández *et al.*, 1993; Toland & Zak, 1994; Marra & Edmonds, 1996) in F_S rates following natural and anthropogenic disturbances. One possible reason for the absence of a general consensus on the effect of stand age on F_S may be the pervasive lack of replication that is common in these studies. Also, studies are often performed in stands that represent a wide range of time periods following the initial disturbance and the disturbances themselves often vary greatly in type and intensity.

Growing season rates of F_S in our stands of lodgepole pine (0.6–3.2 μmol CO_2 m^{-2} s^{-1} for young stands and 1.3–3.6 μmol CO_2 m^{-2} s^{-1} for mature stands) agree with rates reported for 15–260-year-old lodgepole pine stands in southcentral Wyoming (1.4–4.2 μmol CO_2 m^{-2} s^{-1}) (Smith & Resh, 1999). Lodgepole pine forests, however, are on the low end of estimates from studies performed in other forests dominated by *Pinus* in the Rocky Mountains. Measured rates of CO_2 efflux from soils in ponderosa pine stands in Oregon and California are 1.0–6.5 μmol CO_2 m^{-2} s^{-1} (Law *et al.*, 1999; Xu & Qi, 2001), whereas rates in jack pine in Saskatchewan have been measured at 0.3–7.2 μmol CO_2 m^{-2} s^{-1} (Burke *et al.*, 1997; Striegl & Wickland, 2001).

Our estimates of CO_2 efflux from snowpack (0.1–0.2 μmol CO_2 m^{-2} s^{-1} in young stands and 0.4 μmol CO_2 m^{-2} s^{-1} in mature stands) are also on the low end of estimates for some coniferous forests in the Rocky Mountains (0.3–0.8 μmol CO_2 m^{-2} s^{-1}) (Sommerfeld *et al.*, 1996; McDowell *et al.*, 2000). Carbon dioxide efflux from snow in jack pine stands (1–70-year-old) ranged from 0.1 to 0.22 μmol CO_2 m^{-2} s^{-1} (Striegl & Wickland, 2001), which is similar to flux rates in our young stands. These investigators, however, found no difference in CO_2 efflux rates from snow in stands of different ages, contradicting the strong age effect that we observed.

We found no difference between flux rates measured with the SRC-1 chamber and the LI-COR 6400-09 and our results agree with those of other investigators (Arneth *et al.*, 1998; Giardina & Ryan, 2002), although it has been shown in previous studies that F_S measured with the PP-Systems chamber can overestimate flux by as much as 30–50% compared to other chamber systems (Le Dantec *et al.*, 1999; Janssens *et al.*, 2000). Owing to the lack of

reference data for F_S, it is impossible to say which method is the most accurate (Janssens *et al.*, 2000), although the LI-COR 6400-09 seems to be the preferred method because it contains a pressure equilibration tube and it measures F_S through ambient concentrations. We recommend that an *in situ* comparison, like that used in our study, be made when using the PP-Systems SRC-1 chamber to measure F_S to allow for intersite comparisons of data collected with different measurement systems.

Annual estimates of soil C flux

The yearly flux of C from soils in our young stands was significantly lower than mature stands. This is contrary to our initial hypothesis, as we expected that F_S in young stands would be similar to that from mature stands as a result of increased decomposition rates in young postfire stands. Recovery of the major component of ecosystem respiration has not occurred after 13 years and lower rates in young stands suggest that little or no increase in decomposition of soil organic matter pools has occurred as a result of fire (see *Correlation analysis* below). This was true despite increased soil temperature in all young stands and increased soil moisture in low-density young stands.

Comparison of our estimates of the annual flux of C from soils with other studies yields a similar pattern as outlined for growing season F_S. Our values from linear interpolation (156–460 g C m^{-2} yr^{-1}) are on the low end of published values for Rocky Mountain coniferous forests, and well below a mean value of 681 ± 95 g C m^{-2} yr^{-1} reported for temperate coniferous forests (Raich & Schlesinger, 1992). Other investigators have estimated annual soil C fluxes of 145–415 g C m^{-2} yr^{-1} in jack pine (Striegl & Wickland, 2001), 654–780 g C m^{-2} yr^{-1} in ponderosa pine (Law *et al.*, 1999; Law *et al.*, 2001), 764 g C m^{-2} yr^{-1} in mixed coniferous forest (McDowell *et al.*, 2000) and 883–1367 g C m^{-2} y^{-1} in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Klopatek, 2002). Our estimates of the contribution of CO_2 efflux from snowpack to the yearly flux of C from soils (9–22%, mean of 15%) compare well with the value of 17% reported for a mixed conifer site in northern Idaho (McDowell *et al.*, 2000).

Linear interpolation of measured flux rates from only five measurement periods during the growing season has the potential to bias yearly flux estimates, particularly if one or more of the measurement periods fall during atypical conditions – for example, right after a rain event – (Irvine & Law, 2002). However, our linear interpolation should provide a relatively unbiased estimate of yearly flux rates because (i) the five measurement periods were spread out over a very short growing season (~4 months), (ii) corrections that were made to adjust flux rates to mean daily soil temperature incorporate

seasonal Q_{10} values, (Eqn (3)) which would at least partially account for any seasonal moisture effects, (iii) the summer of 2000 in YNP was very dry and characterized by an absence of summer precipitation events and (iv) our annual estimates of F_S agree relatively well with annual flux estimates from temperature response curves and continuous recording of soil temperature. However, in order to bound our estimates of annual soil C flux and provide some estimate of error, we estimated 95% C.I.s for each stand during each measurement period. We then reanalyzed our linear interpolation by using only the upper bounds of the 95% C.I. and then again using the lower bounds. These results suggest that our estimates of annual soil C flux are within $\pm 25\,g\,C\,m^{-2}\,yr^{-1}$ for low-density young stands, $\pm 51\,g\,C\,m^{-2}\,yr^{-1}$ for moderate-density young stands, $\pm 53\,g\,C\,m^{-2}\,yr^{-1}$ for high-density young stands and $\pm 58\,g\,C\,m^{-2}\,yr^{-1}$ for mature stands. These values represent 16, 17, 15 and 13%, respectively, of total annual treatment fluxes estimated with linear interpolation based on measured and adjusted mean F_S rates.

Annual F_S estimates determined with temperature response equations exceeded estimates from linear interpolation by an average of 14%, primarily because of high flux predictions in mid- to late summer (Fig. 6). This is more than likely because the temperature response equations do not fully take into account the importance of phenology and soil moisture, the latter of which decreased during that time period while soil temperatures were relatively stable (Fig. 1b, c). Soil moisture effects would be at least partially accounted for in that soil moisture would affect the diurnal responses to temperature that were used in calculating annual estimates (Eqn (1)). Diurnal temperature responses were estimated from two separate periods in the growing season (Fig. 4) that represented different periods of moisture availability (Fig. 1c). The temperature response, or Q_{10}, of these measurement periods did not differ over the growing season within a given stand type (Fig. 4), indicating no substantial effect of soil moisture on F_S during the dry 2000 growing season. Soils dried out rapidly following spring snowmelt and received no substantial inputs of moisture until the following autumn (Fig. 1c). Even in a *P. ponderosa* system, where rain events during the growing season resulted in brief periods of high F_S, the influence of these precipitation events on annual efflux was insignificant (Irvine & Law, 2002).

Microbial biomass and soil C

While C_{mic} comprises a small portion of the C content in soils (0.7–2.3% in our stands), the microbial population is known to play key roles in numerous fundamental ecosystem processes – for example, decomposition of

organic matter, nutrient cycling and plant nutrient acquisition. Results from our study indicate that C_{mic} in soils of young, postfire lodgepole pine stands remains significantly lower than mature stands for a period of ≥ 13 years. No significant tree density effects on C_{mic} were found in our young stands, even though belowground plant biomass varied significantly with density (Litton *et al.*, 2003). This is probably due to the small sample size ($n = 3$), as a general pattern of increasing C_{mic} with increasing tree density was apparent (Fig. 1d).

Decreases in microbial populations have been widely reported immediately following fire (e.g. Ahlgren & Ahlgren, 1965; Fritze *et al.*, 1994; Pietikäinen & Fritze, 1995; Prieto-Fernández *et al.*, 1998), apparently because of concomitant changes in environmental conditions rather than the direct effects of heating (Ahlgren, 1974; Fritze *et al.*, 1994). Reports of long-term fire effects on microbial biomass vary. Bissett & Parkinson (1980) found no effect of fire on total microbial biomass after 6 years in a subalpine coniferous forest in Canada. Hossain *et al.* (1995) found that the effects of fire on microbial biomass disappeared within 4 years in subalpine *Eucalyptus* forests in Australia. Other investigators, in turn, have demonstrated that microbial biomass levels in forest soils under *Pinus* spp. can remain significantly lower in burned stands for 11–13 years after a fire (Dumontet *et al.*, 1996; Prieto-Fernández *et al.*, 1998), supporting the results of our study.

Seasonal trends in C_{mic} in our stands followed patterns of soil moisture, not soil temperature, through the growing season (Fig. 1b, c, d). Similarly, F_S did not always track changes in soil temperature in our stands, as initially hypothesized, further highlighting the importance of soil moisture in determining C_{mic} and rates of C flux from soils (e.g. Maier & Kress, 2000; Qi & Xu, 2001; Xu & Qi, 2001). Our results agree with previous work suggesting that temperature is not as universally important as previously believed in controlling rates of mineral soil decomposition (Giardina & Ryan, 2000).

Correlation analysis

Immediately following fire, F_S rates should be the result of microbial activity and decomposition of labile soil C pools. As labile pools become depleted and plant regrowth occurs, F_S will be the result of root respiration and microbial decomposition of new inputs of labile C – for example, root exudates – as well as any decomposition of older, recalcitrant pools of soil C. If the decomposition of older pools with slow turnover rates increases, then the potential exists for the loss of a relatively long-term terrestrial C pool following fire.

The fact that F_S in young stands has not recovered to prefire levels suggests that little or no increase in

decomposition of soil organic matter pools has occurred. However, because the decomposition of old, passive soil organic matter pools accounts for only ∼10% of total F_S in some forests (Thierron & Laudelout, 1996), conclusions regarding changes in decomposition of this recalcitrant pool of C should not be made on total flux estimates alone. The results of our correlation analysis clearly show that F_S in young stands is correlated with biotic (plant and microbial biomass) and not abiotic variables (Table 2; Fig. 7a). Moreover, C_{mic} is dependent on below-ground plant biomass and not the amount or quality of soil C (Table 2; Fig. 7b), suggesting that labile C inputs in the rhizosphere are more important than bulk soil decomposition processes in controlling overall microbial biomass and activity. Taken together, our results indicate that plant activity controls F_S in forests recovering from stand replacing fire.

Additional support for this conclusion is evident when examining soil C contents. Overall differences in soil C content with density and stand age are likely a result of prefire stand characteristics and stand history (Litton, 2002). In our stands there was a trend of decreasing soil C with increasing tree density in young stands (Table 1) ($P = 0.11$), yet F_S and C_{mic} increased with tree density ($P < 0.01$ and $P = 0.16$, respectively). In addition, F_S and C_{mic} in high-density young stands did not differ significantly from mature stands, despite lower soil C content in the high-density young stands (Table 1). Moreover, highest soil C contents were associated with mature and low-density young stands, yet F_S and C_{mic} were considerably higher in mature stands (Fig. 1a, d). Taken together, these trends suggest that the overriding influence of recent plant assimilates on F_S negates any differences in initial site conditions.

Our findings on the importance of plant activity to the flux of C from soils agree with recent work that has shown that NPP and the flux of C assimilates to roots are the main determinants of F_S (Fitter et al., 1998; Fitter et al., 1999; Ekblad & Högberg, 2001; Högberg et al., 2001; Janssens et al., 2001). The apparent lack of increased decomposition of older, recalcitrant soil C means that fire does not necessarily affect this relatively long-term pool of C in forest ecosystems.

Conclusions

Fire, through effects on tree density and stand age, plays an important role in the flux of C from soils in lodgepole pine ecosystems. Within young stands, higher tree densities result in significantly higher F_S rates, the major component of ecosystem respiration. Recovery of F_S, yet, has still not occurred 13 years after a stand replacing fire, even in very-high-density stands (> 50 000 trees ha^{-1}).

Soil-surface CO$_2$ efflux in our study area is correlated with biotic variables – that is, above- and below-ground plant biomass and microbial biomass – and not soil physical and chemical properties, which are the legacy of decades to centuries of soil formation. Importantly, plant activity drives the flux of C from soils through root respiration and controls over microbial biomass. The apparent lack of increased decomposition of older, more recalcitrant pools of soil organic matter in recently burned stands indicates that mineralization of these pools is limited by factors that are not influenced by postfire changes in the soil environment – for example, microbial enzymatic capabilities, protection within soil aggregates, etc.

A better understanding of how disturbance affects C cycling is crucial for predicting how changes in climate and disturbance regimes will affect the exchange of C between forest ecosystems and the atmosphere. Natural disturbances such as fire lead to a heterogeneous landscape characterized by a mosaic of stands differing in age and structure. The differences in soil C pools and fluxes that we have shown for gradients in tree density and stand age likely represent important contrasts in C cycling over the landscape. Increased understanding of the effects of natural disturbance on the net exchange of C in forests via changes in stand structure and age will enable more accurate modeling of global C dynamics and better predictions of the effects of global change biology on terrestrial C cycling. This is particularly important in light of predictions that disturbances may increase in frequency and intensity with projected changes in climate.

References

Aber JD, Melillo JM (1991) *Terrestrial Ecosystems*. Saunders College Publishing, Philadelphia.

Ågren GI, Axelsson B (1980) Population respiration – a theoretical approach. *Ecological Modelling*, **11**, 39–54.

Ahlgren IF (1974) The effect of fire on soil organisms. In: *Fire and Ecosystems* (eds Kozlowski TT, Ahlgren CE), pp. 46–72. Academic Press, New York.

Ahlgren IF, Ahlgren CE (1965) Effects of prescribed burning on soil-microorganisms in a Minnesota jack pine forest. *Ecology*, **46**, 304–310.

Arneth A, Kelliher FM, McSeveny TM *et al.* (1998) Fluxes of carbon and water in a *Pinus radiata* forest subject to soil water deficit. *Australian Journal of Plant Physiology*, **25**, 557–570.

Auclair AND, Carter TB (1993) Forest wildfires as a recent source of CO_2 at northern latitudes. *Canadian Journal of Forest Research*, **23**, 1528–1536.

Baker WL (1995) Long-term response of disturbance landscapes to human intervention and global change. *Landscape Ecology*, **10**, 143–159.

Bissett J, Parkinson D (1980) Long-term effects of fire on the composition and activity of the soil microflora of a subalpine, coniferous forest. *Canadian Journal of Botany*, **58**, 1704–1721.

Burke RA, Zepp RG, Tarr MA *et al.* (1997) Effect of fire on soil-atmosphere exchange of methane and carbon dioxide in Canadian boreal forest sites. *Journal of Geophysical Research-Atmospheres*, **102**, 29289–29300.

Culley JLB (1993) Density and compressibility. In: *Soil Sampling and Methods of Analysis* (ed. Carter MR), pp. 529–539. Lewis Publishers, Boca Raton.

Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbances. *Bioscience*, **51**, 723–734.

Despain DG (1990) *Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting*. Roberts Rinehart, Inc. Publishers, Boulder.

Dirks RA, Martner BE (1982) The climate of Yellowstone and Grand Teton National Parks. *National Park Service Occasional Paper*, **6**, p. 27.

Dixon RK, Brown S, Houghton RA *et al.* (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.

Dixon RK, Krankina ON (1993) Forest fires in Russia: carbon dioxide emissions to the atmosphere. *Canadian Journal of Forest Research*, **23**, 700–705.

Dixon RK, Turner DP (1991) The global carbon cycle and climate change – responses and feedbacks from belowground systems. *Environmental Pollution*, **73**, 245–262.

Dumontet S, Dinel H, Scopa A *et al.* (1996) Post-fire soil microbial biomass and nutrient content of a pine forest soil from a dunal Mediterranean environment. *Soil Biology and Biochemistry*, **28**, 1467–1475.

Ekblad A, Högberg P (2001) Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia*, **127**, 305–308.

Ewel KC, Cropper WP, Gholz HL (1987) Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. *Canadian Journal of Forest Research*, **17**, 325–329.

Fernández IJ, Son YW, Kraske CR *et al.* (1993) Soil carbon dioxide characteristics under different forest types and after harvest. *Soil Science Society of America Journal*, **57**, 1115–1121.

Fitter AH, Graves JD, Self GK *et al.* (1998) Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. *Oecologia*, **114**, 20–30.

Fitter AH, Self GK, Brown TK *et al.* (1999) Root production and turnover in an upland grassland subjected to artificial soil warming respond to radiation flux and nutrients, not temperature. *Oecologia*, **120**, 575–581.

Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems*, **1**, 497–510.

Fritze H, Smolander A, Levula T *et al.* (1994) Wood-ash fertilization and fire treatments in a scots pine forest stand: effects on the organic layer, microbial biomass, and microbial activity. *Biology and Fertility of Soils*, **17**, 57–63.

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.

Giardina CP, Ryan MG (2002) Total belowground carbon allocation in a fast growing *Eucalyptus* plantation estimated using a carbon balance approach. *Ecosystems*, **5**, 487–499.

Gordon AM, Schlentner RE, Vancleve K (1987) Seasonal patterns of soil respiration and CO_2 evolution following harvesting in the white spruce forests of interior Alaska. *Canadian Journal of Forest Research*, **17**, 304–310.

He HS, Mladenoff DJ, Crow TR (1999) Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecological Modelling*, **114**, 213–233.

Högberg P, Nordgren A, Buchmann N *et al.* (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**, 789–792.

Hossain A, Raison RJ, Khanna PK (1995) Effects of fertilizer application and fire regime on soil microbial biomass carbon and nitrogen, and nitrogen mineralization in an Australian sub-alpine eucalypt forest. *Biology and Fertility of Soils*, **19**, 246–252.

Irvine J, Law BE (2002) Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biology*, **8**, 1183–1194.

Janssens IA, Kowalski AS, Longdoz B *et al.* (2000) Assessing forest soil CO_2 efflux: an *in situ* comparison of four techniques. *Tree Physiology*, **20**, 23–32.

Janssens IA, Lankreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.

Joshi M, Mer GS, Singh SP *et al.* (1991) Seasonal pattern of total soil respiration in undisturbed and disturbed ecosystems of central Himalaya. *Biology and Fertility of Soils*, **11**, 267–272.

Keith H, Raison RJ, Jacobsen KL (1997) Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. *Plant and Soil*, **196**, 81–99.

Klopatek JM (2002) Belowground carbon pools and processes in different age stands of Douglas-fir. *Tree Physiology*, **22**, 197–204.

Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, **9**, 526–547.

Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.

Law BE, Thornton PE, Irvine J *et al.* (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology*, **7**, 755–777.

Le Dantec V, Epron D, Dufrene E (1999) Soil CO₂ efflux in a beech forest: comparison of two closed dynamic systems. *Plant and Soil*, **214**, 125–132.

Litton CM (2002) Above- and belowground carbon allocation in post-fire lodgepole pine forests: effects of tree density and stand age. PhD Thesis, University of Wyoming, Laramie, WY.

Litton CM, Ryan MG, Tinker DB *et al.* (2003) Below- and above-ground biomass in young post-fire lodgepole pine forests of contrasting tree density. *Canadian Journal of Forest Research*, **33**, 351–363.

Maier CA, Kress LW (2000) Soil CO₂ evolution and root respiration in 11-year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Canadian Journal of Forest Research*, **30**, 347–359.

Marra JL, Edmonds RL (1996) Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, USA. *Canadian Journal of Forest Research*, **26**, 1337–1345.

McDowell NG, Marshall JD, Hooker TD *et al.* (2000) Estimating CO₂ flux from snowpacks at three sites in the Rocky Mountains. *Tree Physiology*, **20**, 745–753.

Melillo JM, McGuire AD, Kicklighter DW *et al.* (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.

Overpeck JT, Rind D, Goldberg R (1990) Climate-induced changes in forest disturbance and vegetation. *Nature*, **343**, 51–53.

Pietikäinen J, Fritze H (1995) Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. *Soil Biology and Biochemistry*, **27**, 101–109.

Prieto-Fernández A, Acea MJ, Carballas T (1998) Soil microbial and extractable C and N after wildfire. *Biology and Fertility of Soils*, **27**, 132–142.

Qi Y, Xu M (2001) Separating the effects of moisture and temperature on soil CO₂ efflux in a coniferous forest in the Sierra Nevada mountains. *Plant and Soil*, **237**, 15–23.

Raich JW, Potter CS (1995) Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles*, **9**, 23–36.

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B-Chemical and Physical Meteorology*, **44**, 81–99.

Ryan MG (1991) A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiology*, **9**, 255–266.

Schimel DS, Enting IG, Heimann M *et al.* (2000) CO₂ and the carbon cycle (extracted from the Intergovernmental Panel on Climate Change (IPCC) Report, 'Climate Change, 1994').

In: *The Carbon Cycle* (eds Wigley TML, Schimel DS), pp. 7–36. Cambridge University Press, Cambridge, UK.

Schlesinger WH, Winkler JP, Megonigal JP (2000) Soils and the global carbon cycle. In: *The Carbon Cycle* (eds Wigley TML, Schimel DS), pp. 93–101. Cambridge University Press, Cambridge, UK.

Sheldrick BH, Wang C (1993) Particle size distribution. In: *Soil Sampling and Methods of Analysis* (ed. Carter MR), pp. 499–511. Lewis Publishers, Boca Raton.

Smith TM, Cramer WP, Dixon RK *et al.* (1993) The global terrestrial carbon cycle. *Water Air and Soil Pollution*, **70**, 19–37.

Smith FW, Resh SC (1999) Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. *Forest Science*, **45**, 333–341.

Sommerfeld RA, Massman WJ, Musselman RC *et al.* Diffusional flux of CO₂ through snow: spatial and temporal variability among alpine-subalpine sites. *Global Biogeochemical Cycles*, **10**, 473–482.

Stocks BJ (1991) The extent and impact of forest fires in northern circumpolar countries. In: *Global Biomass Burning: Atmospheric, Climatic, and Biospheric Implications* (ed. Levine JS), pp. 197–202. The MIT Press, Cambridge, Mass.

Striegl RG, Wickland KP (2001) Soil respiration and photosynthetic uptake of carbon dioxide by ground-cover plants in four ages of jack pine forest. *Canadian Journal of Forest Research*, 31, 1540–1550.

Thierron V, Laudelout H (1996) Contribution of root respiration to total CO₂ efflux from the soil of a deciduous forest. *Canadian Journal of Forest Research*, **26**, 1142–1148.

Tinker DB, Turner MG, Romme WH *et al.* (Submitted) Aboveground biomass, net primary productivity, and leaf area in young postfire lodgepole pine stands, Yellowstone National Park, Wyoming. *Ecosystems*.

Toland DE, Zak DR (1994) Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. *Canadian Journal of Forest Research*, **24**, 1711–1716.

Trettin CC (1986) *Characterization of Soils in Yellowstone National Park*. Final Project Report, CX-1200-1-B027-233. Michigan Techological University, Ford. Forestry Center.

Turner MG, Baker WL, Peterson CJ *et al.* (1998) Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, **1**, 511–523.

Turner MG, Dale VH (1998) Comparing large, infrequent disturbances: what have we learned? *Ecosystems*, **1**, 493–496.

Turner MG, Hargrove WW, Gardner RH *et al.* (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, **5**, 731–742.

Turner MG, Romme WH, Gardner RH *et al.* (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs*, **67**, 411–433.

Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry*, **19**, 703–707.

Waring RH, Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*. Academic Press, San Diego.

Weber MG (1990) Forest soil respiration after cutting and burning in immature aspen ecosystems. *Forest Ecology and Management*, **31**, 1–14.

Whitlock C (1993) Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. *Ecological Monographs*, **63**, 173–198.

Xu M, DeBiase TA, Qi Y *et al.* (2001) Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. *Tree Physiology*, **21**, 309–318.

Xu M, Qi Y (2001) Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biology*, **7**, 667–677.