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Microbial respiration and biomass (substrate-induced respiration) in soils of old-growth and regenerating forests on northern Vancouver Island, British Columbia

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Abstract In studying the basal respiration, microbial biomass (substrate-induced respiration, SIR), and metabolic quotient (qCO_2) in western red cedar (*Thuja plicata* Donn ex D. Don)-western hemlock [(*Tsuga heterophylla* (Raf.) Sarg.] ecosystems (old-growth forests, 3- and 10-year-old plantations) on northern Vancouver Island, British Columbia, Canada, we predicted that (1) soil basal respiration would be reduced by harvesting and burning, reflecting the reduction in microbial biomass and activities; (2) the microbial biomass would be reduced by harvesting and slash-burning, due to the excessive heat of the burning or due to reduced substrate availability; (3) microbial biomass in the plantations would tend to recover to the pre-harvesting levels with growth of the trees and increased substrate availability; and (4) microbial biomass measured by the SIR method would compare well with that measured by the fumigation-extraction (FE) method. Decaying litter layer (F), woody F (Fw) and humus layer (H) materials were sampled four times in the summer of 1992. The results obtained supported the four predictions. Microbial biomass was reduced in the harvested and slash-burned plots. Both SIR and FE methods provided equally good estimates of microbial biomass in the samples [SIR microbial C (mg g^{-1})=0.227+0.458 FE microbial C (mg g^{-1}), r=0.63, P=0.0001] and proved suitable for microbial biomass measurements in this strongly acidic soil. Basal respiration was significantly greater in the old-growth forests than in the young plantations (P<0.05) in both F and H layers, but not in the Fw layer. For the 3- and 10-year-old plantations, there was no difference in basal respiration in F, Fw, and H layers. Basal respiration was related to changes in air temperature, precipitation, and the soil moisture contant at the time of sampling. The qCO_2 values were higher in the old-growth stands than in the plantations. Clear-cutting followed by prescribed burning did not increase soil microbial respiration, but CO_2 released from slash-burning and that contributed from other sources may be of concern to increasing atmospheric CO_2 concentrations.

Key words Basal respiration · Metabolic quotient (qCO_2) · Microbial biomass · Substrate-induced respiration (SIR) · Fumigation-extraction (FE) · Clear-cutting · Humus · Greenhouse effect

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Introduction

Clear-cutting of old-growth forests causes tremendous alterations to the forest ecosystem, through reduction of standing biomass (Smith et al. 1986), changes in energy and water fluxes (Yarie 1993), disturbance of surface soil and forest-floor materials (Boyle 1975; Entry et al. 1986), and increased or reduced input of litter and other organic C sources (Hendrickson et al. 1987). All of the above-mentioned factors have direct or indirect impacts on microbial communities and their activities in the forest floor and mineral soil of forest ecosystems. With growing concern about the importance of "greenhouse" gases on the global climatic system, increased attention has been given to the effect of forest clear-cutting on the evolution of CO_2 and other greenhouse gases from forest soils (Harmon et al. 1990; Fernandez et al. 1993).

The contribution of land use changes that eliminate large amounts of biomass to the rise in atmospheric CO_2 has been noticed (Detweiler and Hall 1988). This contribution may be only a one-time effect and the function of forest biomass in sequestering C and acting as a C sink (Sedjo 1989) may be restored once the next generation of forest is established. However, the effect of harvesting and site preparation on soil respiration may be long-lasting and may contribute greatly to the greenhouse effect. Further-

more, because of differences in the rate of vegetation reestablishment, inputs of C to soil from logging slash and deceased roots, the amount of disturbance, and the extent of microclimatic condition changes, it is difficult to generalize changes in soil respiration following harvesting for different ecosystems (Toland and Zak 1994). Therefore, individual studies must be conducted to evaluate the effect of harvesting and site preparation on soil basal respiration and microbial biomass of specific ecosystem types.

British Columbia, as one of the major producers of forest products in North America, cuts (mainly clear-cut) and slash-burns more than 40000 hectars of old-growth forests each year (Canadian Council of Forest Ministers 1995). In the coastal area, slash-burning is normally used to reduce logging residue in preparation for planting. It is therefore of importance to study the effect of clear-cutting and slash-burning on soil respiration in those sites. In a companion study in a clear-cut chronosequence, microbial biomass and N were studied using the chloroform fumigation-extraction (FE) method and was related to the mineralization of organic N in soil and the N nutrition and growth of crop trees in the field (Chang et al. 1995). The objectives of this work were (1) to quantify the effect of clear-cutting on soil respiration, the microbial biomass measured by the substrate-induced respiration (SIR) method and metabolic quotient; and (2) to compare the SIR method with the FE method for measuring microbial biomass in the acidic forest soil. We hypothesized that (1) soil basal respiration would be reduced by harvesting and slash-burning, reflecting the reduction in microbial biomass and activities; (2) microbial biomass would be reduced by harvesting and slash-burning, due to the effect of excessive heat from burning or due to reduced substrate availability; (3) microbial biomass in the plantations would tend to recover to the pretreatment levels with the growth of the trees and increased substrate availability; and (4) microbial biomass measured by the SIR method would compare well with that measured by the FE method, as reported for other soils (Sparling and West 1988; Cheng and Virginia 1993).

Material and methods

Site description

The study was conducted in the western red cedar (*Thuja plicata* Donn ex. D. Don)-western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] forest ecosystem in the very wet maritime Coastal Western Hemlock biogeoclimatic zone (Klinka et al. 1991) on northern Vancouver Island, British Columbia. The study sites were located on Tree Farm License 25 near Port McNeill (50°36′N, 127°15′W). Cedar-hemlock forests usually occupy the well to somewhat imperfectly drained middle or upper slope topographical situations. In the old-growth cedar-hemblock stands, cedar can reach diameters at breast height of greater than 2 m, ages of greater than 1000 years, and heights of 40–45 m (Keenan et al. 1993). The understory in these stands is dominated by salal, which can attain a height of greater than 1 m and is generally not very dense due to the limited amount of light available under the closed canopy. Less abundant understory species include deer fern (*Blechnum spicant*), blueberry (*Vaccinium* spp.), and bunchberry (*Cornus canadensis*) and salmonberry (*Rubus spectabalis*).

This area is characterized by a gently undulating topography which rarely exceeds 300 m in elevation (Lewis, T. 1982, unpublished data). Mineral soils found in cedar-hemlock stands are duric or orthic Humo-Ferric Podzols (Orthic Podzol of the FAO system) and Folisols (Histosol of the FAO system) (Agriculture Canada Expert Committee on Soil Survey 1987). Humus layers are well developed, mostly greated than 45 cm and sometimes greater than 1 m.

The climate of the study area is characterized by mild winters and cool moist summers. Annual precipitation is 1700 mm, most of which falls in the winter as rain. Drought is usually absent from the soils in all but exceptional years because precipitation usually occurs in each summer month (Lewis, T. 1982, unpublished data). Mean daily temperatures vary from 3.0 °C in January/February to 13.7 °C in July/August. The mean daily minimum temperature sometimes drops just below 0 °C in January and December.

Stand selection

Three replicates of old-growth cedar-hemlock stands in the area were selected according to their similarity in species composition, stand structure, and relative topographical location. Three stands each of 3- and 10-year-old western red cedar plantations on cedar-hemlock cutovers were also selected according to their similarity in topography and old red cedar stump appearance, to ensure that the clear-cut stands were similar to the old-growth stands. The sites for the plantations were all slash-burned after logging and then planted with western red cedar. The 3-year-old plantations has salal as the dominant understorey but this was usually not very dense and short; however, in the 10-year-old plantations, the salal was much denser and taller.

Field sampling

One composite sample of each of three detritus materials, decaying litter layer (F), woody F (Fw), and humus layer (H) materials, was taken from the surface organic layer in each selected stand on May 23, July 16, August 26, and October 18 in the summer of 1992. Each composite sample was a mixture of the same material randomly sampled from six or seven points within each stand. All samples were placed in a cooler on ice and transported to the laboratory within 3 days. The samples were stored at 4 °C before use.

The F material in the old-growth forests consists of partially decomposing fine twigs and leaf litter etc., and is usually about 5 cm thick just below the litter layer, while the F material in the 3- and 10-year-old plantations is usually 1–2 cm thick and is mainly the residue from burning. The Fw layer is partially decomposed woody material that retains its structure when rubbed between the fingers. The H material is well decomposed and is greater than 80% amorphous, has a greasy texture and dark color, is sometimes thicker than 1 m, and is the main component of the forest rooting zone (deMontigny 1992, unpublished data).

Laboratory analysis

The samples were sieved through an 8-mm screen and visible roots were removed. Subsamples of the homogenized material were removed to determine moisture content or were air-dried and sieved through a 2-mm screen for determination of mineralizable N, pH, and total N and C. Mineralizable N was measured by a 14-day anaerobic incubation at 30 °C (Waring and Bremner 1964) followed by Kjeldahl analysis; pH was measured in 1 : 1 (v/v) 0.01 *M* $CaCl_2$ solutions; total N was determined by Kjeldahl analysis with steam distillation and total C was analyzed using a LECO CR-12 C analyzer (Model 781-600, LECO Corporation 1981).

Basal respiration was measured on unmoistened fresh samples. A 4-g (dry basis) sample was lightly packed into a 55-mm plastic Buchner funnel (80 ml total volume) containing a glass-fiber filter (Whatman GF/A) at the bottom of the funnel. The samples were then placed in 1-liter chambers, sealed, and connected to a continuous flow-through 12-channel respiration apparatus as described in Setälä

et al. (1995). The chambers were maintained at a controlled temperature of 22 °C in an incubator. The total measurement time was 3 h, with the first 20–30 min used as a stabilization period (data obtained in that period were not used in calculations). During the 3-h measurement period, an automatic sequencer switched the sample gas stream to pass through a mass flow meter (Sierra Instruments Accu-Mass; output in liters per min at standard temperature and pressure) and a differential infrared gas analyzer (Analytical Development Company 225 MK-3) every 3 min. The results were recorded as μl CO_2 per min and means were calculated from five measurements for each sample.

For the microbial biomass measurements, a test was first conducted to determine the water-holding capacity of each of the F, Fw, and H samples at water potentials just under field capacity. Glucose solutions were prepared with appropriate concentrations so that the final glucose addition rates were 0, 40, 80, 160, and 200 mg g^{-1} sample. The results showed that the best choice was 80 mg glucose g^{-1} for F, Fw, and H, although the optimum addition rate differed slightly among the humus types.

For both the optimum glucose addition rate test and sample measurements, humus materials were packed and treated as those for basal respiration measurements. After 24 h at room temperature, an aliquot of 25 ml glucose solution (48 mg ml^{-1}) was poured onto the funnel, completely submerging the sample. After about 15 min, excess solution was removed to ensure adequate aeration and a final glucose addition rate of about 80 mg g^{-1} sample. The CO_2 evolved from the samples was measured in the same manner as for basal respiration. Microbial biomass C (mg g^{-1}) was calculated as 40 mg C per 1 ml CO_2 h^{-1} (Anderson and Domsch 1978). The metabolic quotient q for CO_2 (μg CO_2-C mg^{-1} microbial-C h^{-1}) was calculated by dividing basal respiration with microbial biomass C measured by the SIR method.

Microbial biomass (C) measurement by the FE method followed Vance et al. (1987a), and a detailed description of the procedures can be found in Chang et al. (1995).

Statistical analysis

Analyses of variance and simple linear regression analyses were performed using the General Linear Models (GLM) and regression analysis (REG) procedures of the SAS package (SAS Institute Inc. 1989). We treated the four sampling dates as a repeated measurement and performed the analysis of variance accordingly. Group means of independent variables were compared between treatments (age of stands) for each material type by using the LSMEANS statement under the GLM procedure, for each type of material sampled. Natural log transformations were performed before statistical analyses for all of the variables to normalize distributions and homogenize the variance of the data.

Results and discussion

Soil properties

Basic properties were similar in old-growth forests and in plantations, but differed by the material types (Chang et al. 1995). The humus material was quite acidic, with pH 3.16 in H, 3.31 in Fw, and 4.16 in F (Table 1). The lower pH in the H material was probably the result of accumulation of organic acids with decomposition. The total C content in the three types of humus material was not different, but the total N content was much lower in the Fw material, leading to a much greater C:N ratio for this material.

Table 1 Chemical properties of humus materials from old-growth forest (Chang et al. 1995); pH measured in 1:1 (v/v) 0.01 *M* $CaCl_2$

Organic material	pH	Total N (g kg^{-1})	Total C (g kg^{-1})	C:N ratio	Mineralizable N (mg kg^{-1})
F	4.16	9.4	48.0	51	394
Fw	3.31	2.2	52.1	235	40
H	3.16	10.3	48.7	47	148

Temperature and precipitation

The mean daily air temperature started to rise near the end of May (Fig. 1). The monthly mean temperature reached its annual peak in July (14.4 °C), remained high in August (14.2 °C), and declined in September (11.6 °C) and October (8.9 °C). Precipitation in the 6-month period (May 1 to October 31) accounted for 36.2% of the total annual precipitation. July was the driest month (11.2 mm) of the year and October the wettest month (299 mm) of the 6-month period (Fig. 1). The total precipitation for 1992 was 1906 mm, which was greater than a 30-year average of 1730 mm recorded between 1941 and 1970 (Lewis, unpublished data).

Heterotrophic soil respiration

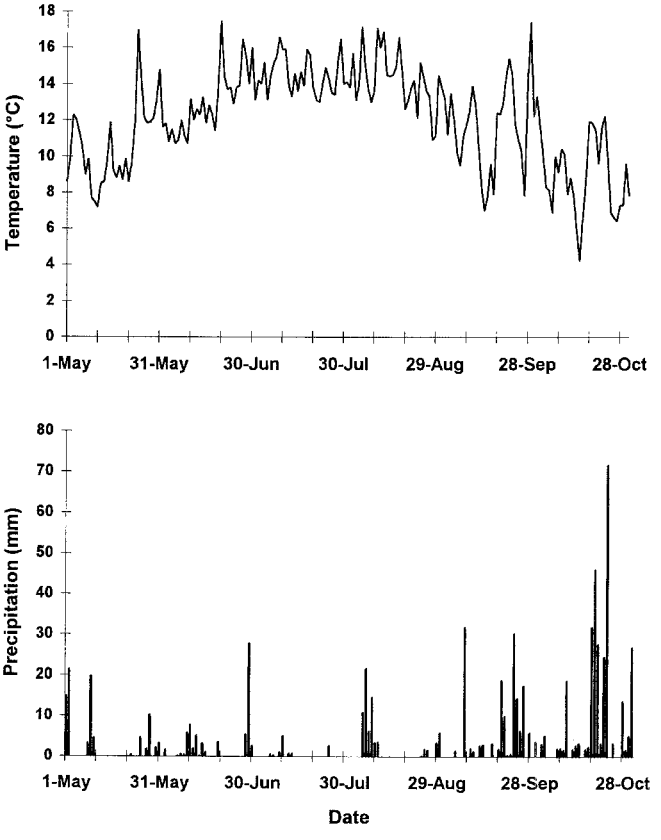

Fig. 1 Air temperature and precipitation at the study site in summer 1992. Climate data were obtained from the Port Hardy Airport 15 km away from the study site

Table 2 Analysis of variance results for soil respiration, microbial C (measured by substrate-induced respiration, *SIR*) and qCO_2-C (Metabolic quotient)

Source of variation	*df*	Basal respiration		Microbial C (SIR)		qCO_2-C	
		F	*P* value	*F*	*P* value	*F*	*P* value
Between subjects							
Stand type (S)	2	11.60	0.0007	8.38	0.0029	6.69	0.0072
Material (M)	2	43.60	0.0001	93.33	0.0001	6.80	0.0068
S×M	4	4.98	0.0077	2.36	0.0948	2.03	0.1353
Error (1)	18						
Within subjects							
Date (D)	3	18.40	0.0001	56.99	0.0001	3.57	0.0201
Linear	1	7.01	0.0169	13.80	0.0017	0.01	0.9475
Quadratic	1	5.96	0.0259	46.48	0.0001	7.71	0.0129
Cubic	1	43.89	0.0001	106.77	0.0001	8.82	0.0086
D×S	6	1.12	0.3622	1.41	0.2295	0.38	0.8908
D×M	6	3.03	0.0130	4.30	0.0014	4.06	0.0008
D×S×M	12	1.73	0.0877	0.93	0.5265	1.69	0.0980
Error (2)	54						

Table 3 Means of basal respiration, microbial biomass from substrate-induced respiration (*SIR*) and fumigation-extraction (*FE*) methods, and metabolic quotient across sampling dates (*mic-C* microbial C, means followed by the same *letter* do not differ significantly between stand types within a material type at $P=0.05$

Material type	Stand type	Basal respiration C ($\mu g\ g^{-1}$)	Microbial biomass (SIR) C ($mg\ g^{-1}$)	Microbial biomass (FE) C ($mg\ g^{-1}$)	qCO_2-C ($\mu g\ mg^{-1}$ mic-C h^{-1})
F	Old-growth	20.65a	4.91a	10.28a	4.70a
(litter)	3-year-old	6.56b	2.99b	5.07b	2.55b
	10-year-old	5.49b	3.30b	6.18c	1.99c
Fw	Old-growth	3.75a	1.13a	2.40a	3.66a
(woody litter)	3-year-old	2.47a	1.04a	1.89b	2.96a
	10-year-old	2.85a	1.21a	2.32a	2.45a
H	Old-growth	4.70a	2.58a	5.24a	2.02a
(humus)	3-year-old	2.60b	1.56b	3.59b	1.89a
	10-year-old	2.94ab	2.51a	5.08a	1.54a

We used CO_2 evolved from root-free fresh humus samples without any other treatment as a measure of microbial activities in the samples. Basal soil respiration differed by date, stand type, and material type, with significant stand type by material type and material type by date interactions (Table 2). Basal respiration in the F material was drastically decreased from the old-growth forests to the 3-year-old stands on each of the four sampling dates ($P<0.05$, Tables 2, 3 and Fig. 2). A significant difference between the 3- and 10-year-old stands was found only for the July 16 sampling. In the Fw material, the mean of basal respiration for the four samplings was also reduced from the old-growth forests to the 3-year-old stands (not significant; Tables 2 and 3); however, basal respiration was higher in the 3-year-old than in the 10-year-old stands on three of the four sampling dates and lower on the other sampling date (Fig. 2). Basal respiration patterns in the H material were very similar to that of the F material, with significantly less basal respiration in the 3- and 10-year-old stands than in the old-growth forests ($P<0.05$; Tables 2, 3) and no difference between the two plantations. Therefore, our first hypothesis that harvesting and burning would reduce potential rates of heterotrophic soil respiration was accepted. Thus it seems that clear-cutting followed by prescribed burning will not increase soil respiration under the conditions studied. However, under field conditions, total soil respiration is affected by environmental factors such as temperature and soil moisture content (Beyer 1991) and by root respiration, which are in turn affected by harvesting and slash-burning. Therefore, the main concern about increasing CO_2 concentrations in the atmosphere with forest harvesting and slash-burning may be the release of CO_2 from slash-burning and increased respiration due to increased root decomposition.

A reduction in heterotrophic soil respiration after harvesting or burning has been observed in many other studies (Pietikainen and Fritze 1993; Fritze et al. 1994), while the pattern of change in soil respiration over time has differed. Toland and Zak (1994) thought that after harvesting, soil respiration would decrease over time because the pool of labile C in soil would be metabolized by microorganisms. Our results suggest that the recovery of soil respiration in the burnt plots needed longer periods to recover to pretreatment levels than usually reported. This may be related to the severity of the slash-burning and other characteristics of the treated ecosystems. Pietikainen and Fritze (1993) reported that the intensity of forest fire influenced soil microbial activities.

In the present study, the soil respiration rate varied with sampling date. A detailed trend analysis showed that soil basal respiration followed a strong cubic trend ($P=0.0001$, Table 2). The highest respiration rate was usually observed for the August 26 sampling, the lowest for October 18, and a middle range for the May 23 and July 16 samplings

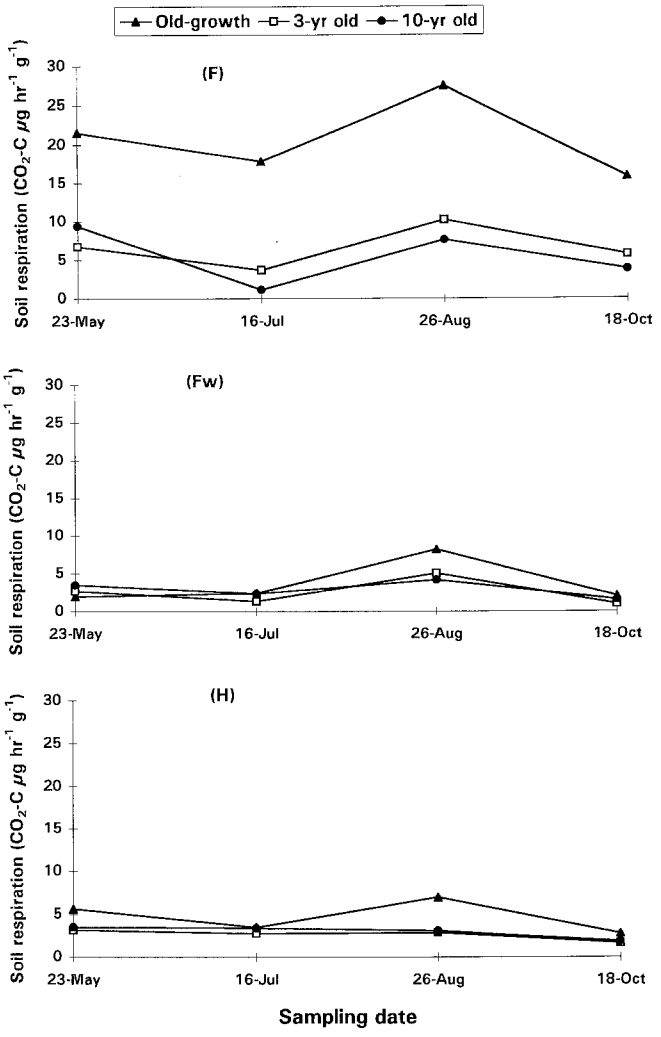

Fig. 2 Basal respiration in litter (*F*), woody litter (*Fw*), and humus (*H*) materials on various sampling dates (*yr* year)

(Fig. 2). During the August 26 sampling, the temperature was high and so was precipitation and the soil moisture content, and the highest respiration rate was obtained. With the October 18 sampling, although precipitation and the soil moisture content had increased from the previous sampling date, the air temperature was decreasing from the summer highs and so, probably, the soil temperatures. Therefore the lower respiration value on October 18 seemed to be mainly influenced by the temperature change. The same applies to the May 23 sampling. A close relationship between soil respiration and temperature and moisture content has been reported by many authors (O'Connell 1990; Fernandez et al. 1993). O'Connell (1990), studying the microbial decomposition of litter in eucalypt forests of south-western Australia, found that the moisture content and temperature of litter explained 93–94% of the variation in rates of CO_2 production.

Microbial biomass (SIR)

Microbial biomass measured by the SIR method was significantly affected by stand type, material type, and sampling dates. A significant interaction was found between material type and sampling date (Table 2). A closer look at the means of microbial biomass (SIR) across the sampling dates shows that the microbial biomass in the F material was significantly reduced in the harvested and slash-burned stands (Table 3). No stand type effect was found for the Fw material. For the H material, microbial biomass was significantly higher in the 10-year-old stands than in the 3-year-old stands and old-growth forests on the May 23 sampling (Fig. 3); on the next three sampling dates, the microbial biomass was higher in the old-growth forests than in the 10-year-old stands. However, this did not result in a significant stand type by sampling date interaction (Table 2), because the pattern of seasonal changes in microbial biomass was similar for different stands. The 3-year-old stands had the lowest microbial biomass throughout the sampling period. In all of the material types studied, the microbial biomass in the 10-year-old stands

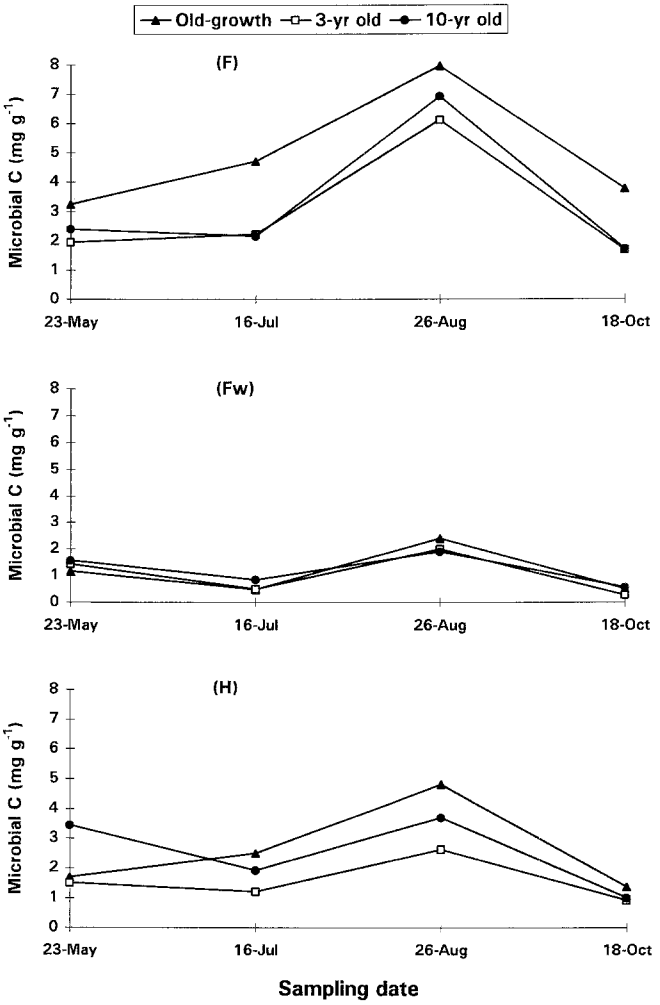

Fig. 3 Microbial biomass in F, Fw, and H materials measured by the substrate-induced respiration (*SIR*) method (for further explanations, see Fig. 2)

seemed to be recovering to levels in the old-growth forests (Table 3). Therefore our second and third hypotheses were accepted. The reason for the smaller amount of microbial biomass measured in the plantations compared with the old-growth forests may have been decline in substrate availability (Chang et al. 1995).

The highest value for microbial biomass was obtained on the August 26 sampling for F, Fw, and H material, regardless of the stand type (Fig. 3). Analysis of the date effect showed that the change in microbial biomass (SIR) followed strong cubic ($P=0.0001$), quadratic ($P=0.0001$), and linear ($P=0.0017$) trends (Table 2). A greater relative increase in microbial biomass from July 16 to August 26 in F compared with Fw and H material resulted in a significant material type by sampling date interaction.

Microbial biomass can now be measured by several methods, including direct counting, enzyme analysis, and fumigation-incubation, as well as FE and SIR (Beare et al. 1990). The fumigation-incubation method is generally regarded as unsuitable for strong acidic soils (Vance et al. 1987b). The FE method has proved suitable for measuring the microbial biomass in a wide range of soils (Vance et al. 1987a; Gallardo and Schlesinger 1990). However, the SIR method has not been thoroughly studied for strong acidic forest soils (Ross and Tate 1993). Comparing microbial biomass data obtained from the SIR method to those obtained from the FE method (Chang et al. 1995), we found a good correspondence. A simple regression analysis showed that microbial biomass measured by SIR=0.227+0.458 FE microbial C, $r=0.63$, $P=0.0001$ (Table 4). Therefore our last hypothesis was also accepted. We propose that the SIR and FE methods provided equally good estimates of microbial biomass in the present samples, because they gave consistent values between different samples and stand types.

SIR estimates of microbial biomass in the humus materials were considerably lower than those by the FE method. This problem may partly reflect the use of conversion factors both for SIR (to convert substrate-induced CO_2 evolution to microbial biomass) and for FE (K_c). Another possible reason for lower SIR than FE values is that the extraction method may remove non-microbial C (i.e., from live plant cells, waxes on plant surfaces) and C from recently dead or moribund microbial cells that would not respond to glucose additions. Underestimates of microbial biomass by the SIR method compared to the FE method were also reported by Ross and Tate (1993). Cheng and Virginia (1993) indicated that the FE procedure overestimated microbial biomass for soils of very high C:N ratios (60–90), which were very close to the C:N ratios found in our samples. Linear regression analysis on microbial biomass measured by SIR and FE methods for different types of organic materials showed that there is a best fit equation for each type of material studied (Table 4). A *t*-test for the linear equation slopes showed that while the slopes of the equations for F and H material were not different, the slope for Fw material was significantly different from those of the F and H material. This suggests that the C:N ratio of the materials does affect the estimation of microbial biomass by the two methods. The significantly higher slope for Fw than for F and H material shows that the higher the C:N ratio of the material, the greater the overestimate of the microbial biomass by the FE method compared with the SIR method. Further studies are thus needed to establish appropriate K_c factors for the FE procedure and calibration factors for SIR for the humus material types used in the present study.

Table 4 Models for the regression of microbial biomass (mg g^{-1}) measured by substrate-induced respiration (*SIRmic-c*) on that measured by fumigation-extraction (*FEmic-c*) method (*F* litter, *Fw* woody litter, *H* humus; *t*-test): the same uppercase letters represent no significant difference between the slopes of the compared linear equations

Material	Regression equation and statistics	*t*-test for slope
Pooled	SIRmic-c=0.227+0.458 FEmic-c	A
	$R^2=0.395$ $F=68.57$ $P=0.0001$ $n=108$	
F	SIRmic-c=1.435+0.320 FEmic-c	B
	$R^2=0.1334$ $F=5.23$ $P=0.0285$ $n=36$	
Fw	SIRmic-c=-0.530+0.761 FEmic-c	C
	$R^2=0.3873$ $F=20.86$ $P=0.0001$ $n=36$	
H	SIRmic-c=0.282+0.418 FEmic-c	AB
	$R^2=0.1301$ $F=5.08$ $P=0.0307$ $n=36$	

Metabolic quotient (qCO_2)

The ratios of the soil respiration rates to microbial biomass C (qCO_2) obtained in this study were comparable to and well within the range of values reported previously (Insam and Haselwandter 1989; Anderson and Domsch 1990; Santruckova and Straskraba 1991). The qCO_2 value was significantly greater in the old-growth forests than in the plantations (Fig. 4, Table 2). This was contradictory to the findings reported from some studies (Insam and Haselwandter 1989; Santruckova and Straskraba 1991). Santruckova and Straskraba (1991) noted that soil respiration was independent of microbial biomass, since it remained almost constant over a range of microbial biomass contents, resulting in a low microbial biomass with a high CO_2 evolution and thus a high qCO_2. This was not the case in our study. By comparing Figs. 3 and 4, it is obvious that higher basal respiration corresponds to higher microbial biomass (correlation coefficient $r=0.62$, $P=0.0001$). One of the possibilities is that the microbial activities (respiration) in the samples taken from the plantations were limited by low substrate availability caused by slash-burning or decreased litterfall and root exudate inputs. Even if the proportion of active cells in the young plantations (low microbial biomass) was higher than in the old-growth stands (high microbial biomass), as suggested by Santruckova and Straskraba (1991), no higher qCO_2 would be observed in the plantations if substrate availability was limited. Another possibility is that soil respiration was limited by the soil moisture content in samples from the young plantations compared to the old-growth forests, especially for F and Fw material, because sample moisture contents were not adjusted before measuring basal respira-

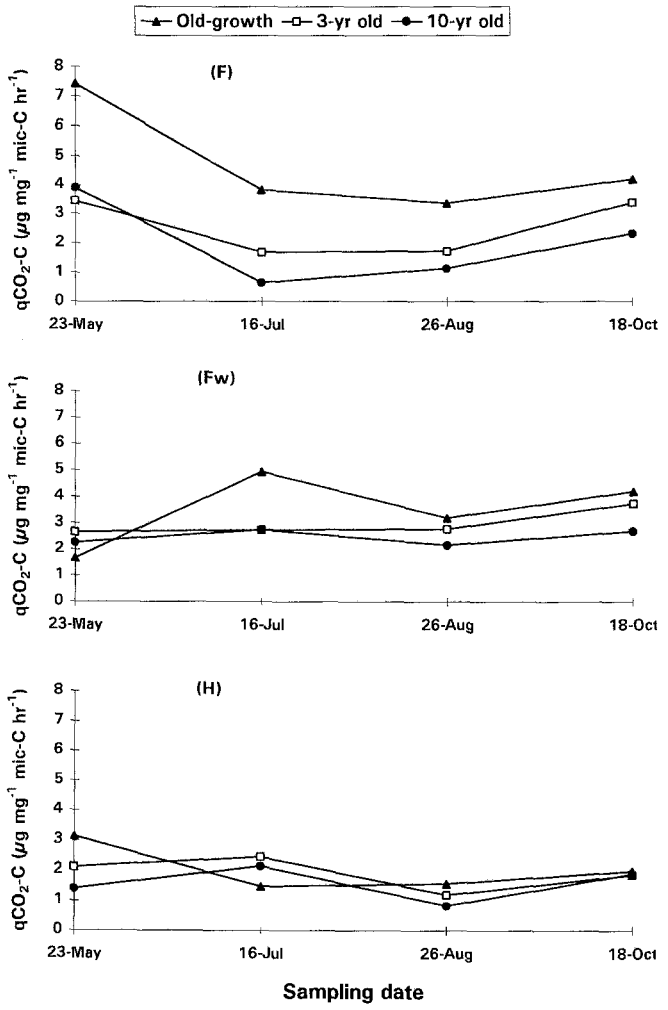

Fig. 4 Metabolic quotient (qCO_2) in F, Fw, and H materials on various sampling dates (*mic-C* microbial C; for further explanations, see Fig. 2)

tion. The soil moisture content was significantly higher in the forest floors of old-growth forests than of the plantations for F and Fw material throughout the sampling period (Chang et al. 1995), and the soil moisture content was always above 60% water-holding capacity in old-growth forests (except on August 26 for F material) but was below that in the 3- and 10-year-old plantations (except on October 18 for F material). The soil moisture content in the Fw material was slightly below 60% water-holding capacity on the first three sampling dates regardless of stand type. However, the soil moisture content of the H material was always above 60% water-holding capacity. Pietikainen and Fritze (1993) and Fritze et al. (1994) observed that when humus samples were adjusted to 60% water-holding capacity, the fresh-sample difference in respiration rate between treatments disappeared. Also, we cannot rule out the possibility that harvesting and slash-burning severely changed other properties of the forest ecosystems, which may have had more important effects on qCO_2.

The change in qCO_2 values in the clear-cut chronosequence may also be related to changes in ratio of fungal to bacterial biomasses. Sakamoto and Oba (1994) suggested that qCO_2 decreases with an increase in the fungal:bacterial biomass ratio. They proposed that the relationship was due to a higher efficiency of substrate C use by fungal flora relative to bacterial flora. However, this hypothesis could not be tested in the present study because the fungal and bacterial biomass was not measured separately.

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