Biol Fertil Soils (1997) 25:196–201

ORIGINAL PAPER

R. Jandl · P. Sollins

Water-extractable soil carbon in relation to the belowground carbon cycle

Received: 11 December 1995

Abstract We investigated the role of water-extractable carbon (C-extr) as potential substrate for forest soil microorganisms by comparing belowground C fluxes at a plot with the forest floor removed (no-litter) and at a control plot. One-third lower soil respiration rates at the no-litter plot gave evidence that the forest floor was the source of considerable amounts of microbially degradable C. Laboratory incubation of C-extr, fractionated into neutral and acid moieties, showed that part of the C-extr was degraded rapidly, and that the high-molecular-weight acid fraction was much less degradable than the neutral C. To the extent that the degradable portion of the water-extractable C can be regenerated quickly, it may supply much of the substrate for heterotrophic soil respiration.

Key words Water-extractable carbon fractions · Biodegradation · Belowground carbon dynamics · Soil respiration · Dissolved organic carbon

Introduction

Although a role is well established for dissolved organic carbon (DOC) in soil formation (Ugolini and Dahlgren 1987; Pohlman and McColl 1988) and in nutrient and heavy-metal transport (Qualls and Haines 1991; Guggenberger et al. 1994), its role in the belowground C economy remains less clear. Fluxes of organic C downward in solution are generally small relative to inputs in litterfall and root death (Sollins and McCorison 1981; Cronan 1985; McDowell and Likens 1988; Guggenberger 1992). Even levels of water-extractable C, typically larger than the amount of C transported downward in solution through the soil profile but of similar chemical composition (Jardine et al. 1989), are small compared to that respired over the course of a 7-day incubation (Davidson et al. 1987). Despite several recent studies on the role of DOC as substrate for soil microbial respiration (McGill et al. 1986; Zsolnay and Steindl 1991; Cook and Allan 1992 a, b; Nelson et al. 1994), the degradability of DOC remains unclear (Qualls and Haines 1992; Boissier and Fontvielle 1993). None of these results, moreover, rule out the possibility that some portion of the water-extractable C is both degraded quickly and regenerated rapidly from particulate organic matter (OM). If true, then water-extractable C could still be a significant substrate for microbial metabolism.

Here was measured amounts and composition of water-extractable C (C-extr) in two forest plots from which the forest floor and leaf litter inputs were or were not excluded. We also measured rates of CO_2 evolution from the forest floor, and soil pCO_2 levels. In a laboratory incubation experiment we determined rates of degradation of the C-extr. We hoped to understand better the dynamics of C-extr in relation to inputs and losses of C from the soil.

Materials and methods

Site description

The study site is at an elevation of 630 m in the Andrews Experimental Forest in the central Cascade Mountains of Oregon, United States, on a gently north-facing slope (Table 1). The stand, designated L 108 A, consists of dense Douglas fir planted and established naturally after old-growth was clear cut and the site slash-burned in 1952. The site was replanted in fall.

Litter removal

In June 1993, the entire O horizon (referred to hereafter as litter layer) was removed from a rectangular 4-m^2 area (the no-litter plot) chosen to be clear of stumps and coarse woody debris. The nearest

R. Jandl
Forstliche Bundesversuchsanstalt, A-1130 Vienna, Austria

P. Sollins
Department of Forest Science, Oregon State University Corvallis, OR, 97331, USA

R. Jandl (✉)
Seckendorff – Gudent Weg 8, A-1131 Vienna, Austria
Fax: (1) 877 59 07; e-mail: rjandl@mail.boku.ac.at

similar area, about 10 m distant, served as a control plot. Freshly fallen litter was collected manually and removed from the no-litter plot every 2 weeks for 1 year. Respiration, soil CO_2 concentration, and C-extr were measured periodically at both plots during the year.

Respiration from forest floor

Glass jars (diameter = 10 cm, $n = 3$ plot^{-1}) containing about 30 g oven-dried soda lime were placed under a bucket (23-cm diameter) and exposed to CO_2 outgassing from the soil for 24 h (Edwards 1982). The jars were then closed, oven dried, and reweighed. The released C ($mol \cdot m^{-2}$) was then calculated from the increase in weight of $CaCO_3$. Monthly respiration was calculated assuming that the measured respiration represents the average respiration rate for the entire month. Work published after our field work was completed (Nay et al. 1994) indicates that the method underestimates values at high flux rates, but the error is small relative to the differences that we found between plots.

Soil atmosphere pCO_2

We sampled soil air using steel tubes with an inner diameter of 6 mm and numerous perforations of 2 mm diameter in the side walls about 2 cm from the bottom. We pushed the tubes 15 and 30 cm into the soil, then drew soil air through a rubber septum at the top. We assumed that the atmosphere in the steel tube was in equilibrium with the soil atmosphere. Gas samples were injected into Vacutainers and analyzed by gas chromatography (GC) (HP 5730 A GC with an HP 3380 A integrator and a thermal conductivity detector (TCD) within 6 h. To account for losses of CO_2 during transport, we drew three to five samples from a container with standard gas, which were handled and analyzed the same as those from the experimental plots.

Carbon extraction and fractionation

Material from the entire forest floor and mineral soil (0–5, 5–10, 10–20, and 20–30 cm) was collected at the end of each season (June, September, and December 1993; March and June 1994). Field moist soil (50 g) was extracted with 150 ml distilled water. Soils were shaken overnight, centrifuged (Sorvall centrifuge, GSA rotor, 6500 *g*, 30 min), then sterilized by filtration through 0.2-µm polycarbonate membranes (Poretics). The threshold of 0.2-µm was chosen instead of the more commonly used 0.45 µm to exclude microbes and submicron organomineral particles. Viruses were presumably not excluded. DOC was measured on an aliquot with a Dohrman DC-80 carbon analyzer after acidification to pH 2 with phosphoric acid to purge inorganic C. Carbon compounds in the water extracts were fractionated by a modification of methods of Leenheer (1981), which separate acids, bases and neutrals with hydrophilic (Hi) and hydrophobic (Ho) groups. Following Guggenberger et al. (1994), who summarized earlier work (Thurman 1985; Qualls and Haines 1991; Vance and David 1991 a), we assumed that hydrophobic acids (HoAs) are derived from plant biomass and include "ligno-cellulose degradation products and a mixture of complex polyfunctional aliphatic and aromatic acids." The hydrophilic acids (HiAs) are similar to hydrophobic acids but contain more aliphatic acids (e.g., fatty acids), more carboxyl groups per C atom and more microbially derived polysaccharides. Hydrophilic neutrals (HiNs) are a mixture of carbohydrates, polyfunctional alcohols, and simple sugars and ketones, all of both microbial and plant origin.

Solutions were concentrated with a rotary evaporator at 45 °C to obtain a 150-ml sample volume with a concentration of ca. 20 mg C l^{-1}. Samples were then acidified to pH 2 and passed through a sequence of four columns with different macroreticular exchange resins. Resins were industrial grade and had to be cleaned by Soxhlet extraction (Leenheer 1981; Aiken 1988; Malcolm 1990). Amberlite XAD-8 retains hydrophobic acids (HoAs), Amberlite XAD-4 retains hydrophilic acids (HiAs), Bio-RAD (AG MP-50) scavenges cations, and Duolite retains any remaining anions. Hydrophilic neutrals (HiNs) are the C compounds that pass through all four resins. The HoA and HiA fractions were desorbed from the XAD columns with 0.1 *M* NaOH, after which the eluent was pumped through the Bio-RAD resin to remove salts. Since hydrophobic acids (XAD-8), hydrophilic acids (XAD-4) and hydxrophilic neutrals commonly compose up to 90% of the C-extr in soil (Donald et al. 1993; Vance and David 1991 b), minor components such as hydrophobic neutrals and hydrophobic and hydrophilic bases were neglected. Although the XAD-8 is quite efficient, the XAD-4 is not, so we tried to use the Duolite column as a back-up. The Duolite tended to bleed organics during desorption, however, so data were not included.

Degradation of water-extractable C

Biodegradability of C fractions from litter and soil extracts was tested in a laboratory experiment. Fractions (HoA, HiA, and HiN) from the no-litter and control samples were combined to obtain sufficient volume. Solutions (30 ml) with a DOC concentration of ca. 20 mg l^{-1} were placed in autoclaved 50-ml glass bottles sealed with rubber septa. Solutions had already been filtered (0.2 µm) so resupply of dissolved C from POC was prevented. Air present initially in the headspace was replaced with commercially available CO_2-free air, which was bubbled through the liquid for several minutes at low pressure and allowed to escape through a cannula. Because the filtration had excluded most organisms, 20 µl inoculum containing 10 mg l^{-1} DOC was added. The inoculum was prepared from a water extract of litter and mineral soil material from which we separated a 0.2- to 5-µm-size fraction, which should include bacteria and some fungal spores and hyphal fragments but exclude most grazers (Frey et al. 1985). We sequentially passed the water extract through a 5-µm and a 0.2-µm membrane filter. The material trapped on the 0.2-µm filter was resuspended in water and used as inoculum. The amount of C added as inoculum was negligible relative to the amount of C in the XAD-fractionated sample, so degradation of the inoculum should not have confounded results.

Carbon degradation was found to be strongly N limited in an initial of incubations, which was to be expected as our fractionation method yielded organics free of inorganic N. To prevent N limitation, we lowered the C:N ratio to a favorable level ($\sim$10) by adding NH_4NO_3. We added no other nutrients. Samples were incubated at 22 °C for 120 days. CO_2 was drawn from the headspace after 3 days, then every 2 weeks thereafter, and analyzed by GC. Supersaturation of the sample solution with CO_2 was minimized by shaking the bottle gently for 30 min before gas sampling. An asymptotically increasing exponential function was fit to cumulative respiration over time with the SAS statistical package (Proc NLIN, DUD method). One replicate of each incubated fraction was left uninoculated; we observed no CO_2 evolution from these sterile samples.

Determination of microbial biomass

Biomass of soil bacteria and soil fungi was determined 1 year after litter removal on litter-layer samples from the control plot and on mineral soil (0- to 5-cm) samples from both plots. Total and active biomass of fungi and bacteria, and length of hyphae, were determined by microscopy (Frey et al. 1985; Ingham et al. 1991).

Results and discussion

Litter removal

Litter material removed initially amounted to 500 g OM m^{-2} (150 g C m^{-2}). Subsequent periodic litter removal accounted for an additional 213 g C m^{-2} over the course of the 13-month study, with the majority consisting of needles removed in March 1994.

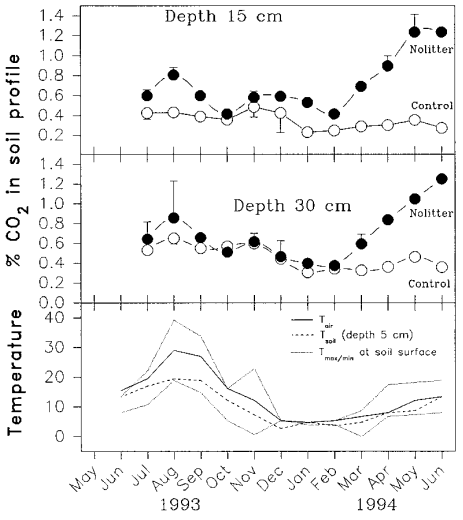

Fig. 1 Soil CO_2 partial pressure at two depths in the no-litter and control plots. Air and soil temperature shown at bottom

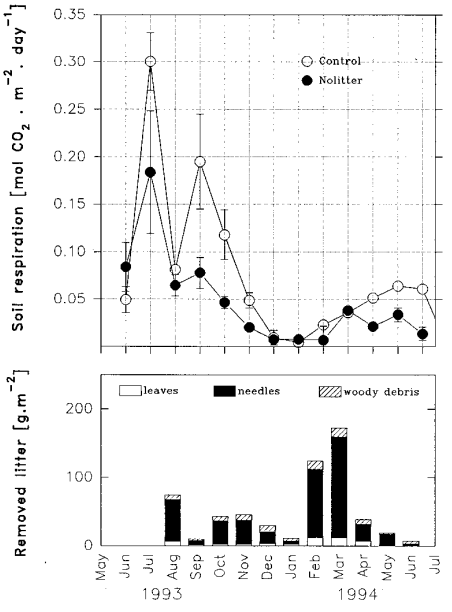

Fig. 2 Soil respiration at no-litter and control plots and dry weight of Douglas fir litter removed. Error bars denote 1 SD (omitted where SD was small), $n = 3$

Soil respiration and soil atmosphere pCO_2

Soil atmosphere pCO_2 varied with season and depth at the control plot (Fig. 1). The pCO_2 was consistently higher in the lower horizon and declined in both horizons during the cold months, due presumably to reduced root and microbial activity. Initially pCO_2 was somewhat higher in the no-litter plot, likely a result of the disturbance. Later pCO_2 declined. Unexpectedly high concentrations of CO_2 built up in the soil atmosphere in the no-litter plot in spring 1994, suggesting reduced diffusivity. A possible explanation is that the soil surface, unprotected by a litter layer, became sealed by clay particles during the moist winter and spring months. Unlike Hart and Firestone (1991), we observed no differences in soil water content between the two plots.

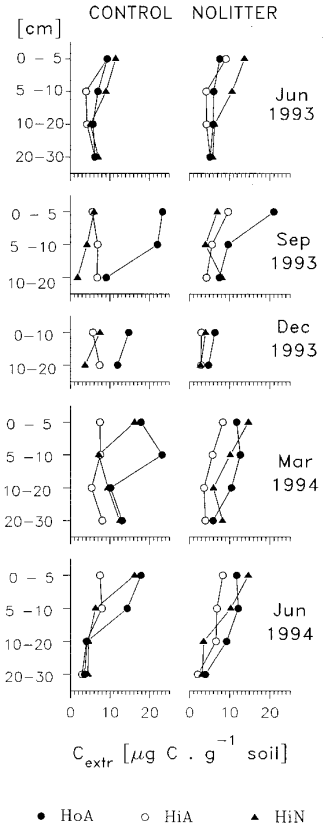

Fig. 3 Water-extractable C by fraction at several depths in mineral soil in the no-litter and control plots

Total soil respiration measured with soda lime between June 1993 and June 1994 summed to 380 g C m^{-2} at the control plot vs 226 g C m^{-2} at the no-litter plot. The respiration rate was initially quite high at the no-litter plot (Fig. 2), possibly an effect of site disturbance, but then decreased rapidly. Given that soil pCO_2 built up at the no-litter plot, we suspect that considerable CO_2 may have escaped around the sides of the disturbed area. We are unable to estimate how much though; thus we do not draw inferences from the differences in CO_2 flux between the plots. CO_2 evolution rates were low in August, likely due to soil dryness, and during the cool winter months. Measured field respiration rates and soil CO_2 levels fell within ranges reported previously (Castelle and Galloway 1990; Bowden et al. 1993; Fernandez et al. 1993; Mattson and Smith 1993).

Carbon extractions and fractionations

Extractable carbon averaged about 17–34 g C g^{-1} in the mineral soil (averaging across both plots, Fig. 3), but about 370 g C g^{-1} in the litter layer (control plot only – Fig. 4). These values represent about 1.5% of total C in the litter layer, but only 0.05% of total C in mineral soil.

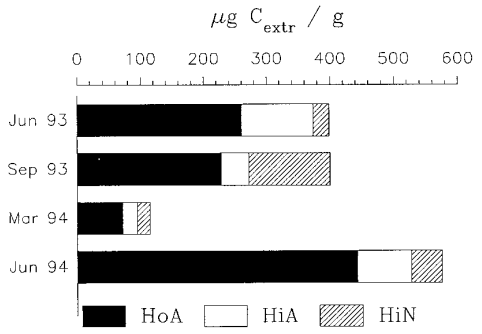

Fig. 4 Amount and composition of water-extractable C in the litter layer (control plot only) through time. Values are means of two replicates which differed by <10%

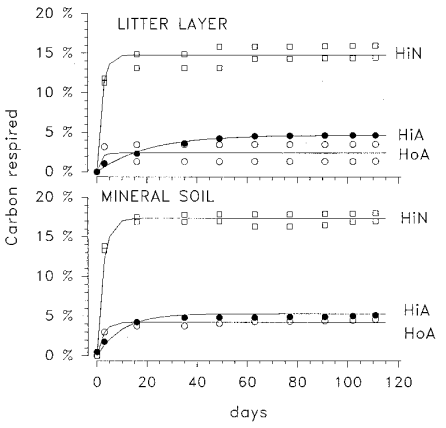

Fig. 5 Cumulative C respired from water-extractable C fractions during a laboratory incubation

Amounts of all three C fractions decreased between litter and mineral soil and with depth in the mineral soil. For all samples, regardless of depth, time, or plot, HoA was the largest contributor to C-extr (Figs. 3, 4). The trend through time was inconsistent. Extracts from litter and mineral soil differed markedly in percentage composition: 62.9% HoA, 20.6% HiA, and 16.4% HiN for litter vs 42.3%, 25.5%, and 32.2% averaging over all mineral soil samples. Pairwise *t*-tests of the percentages showed that differences were significant ($P<0.05$) for HoA and HiA only. Figure 3 suggests that there was proportionately less HoA and more HiN in the upper mineral soil of the no-litter plot than the control plot. We consider this to be treatment effect, because litter leachate is dominated by HoA (Easthouse et al. 1992; Pohlman and McColl 1988; Vance and David 1991b) whereas the other sources of C (microbial tissues, root exudates, and decaying roots) yield more microbially derived polysaccharides, which appear in HiA and HiN (Guggenberger et al. 1994).

To assess differences in C composition between plots, we divided proportion of C in each fraction in the no-litter plot by proportion of C accounted for by that particular fraction in the control plot (e.g. percentage of HoA at the no-litter plot divided by percentage of HoA at the control plot). By horizon, such ratios were widest for the uppermost mineral-soil layer. By fraction, the ratios were widest for HoA and narrowest for HiN. For the HiA fraction, the ratio widened initially, but returned to near 1 a year after litter removal.

Incubation experiment

As little hyphal growth was noted, the incubations reflect mainly bacterial activity and thus may be a conservative estimate of C degradability. Cumulative respiration differed between litter and mineral soil extracts and between the three fractions (Fig. 5). For both the litter and mineral soil extracts, HoA was slightly less degradable than HiA, whereas HiN degraded the fastest. An exponential function generally failed to describe the early part of the incubation, which suggests a two-stage process of C degradation with the majority of the degradation occurring within the first 2 or 3 days. That amounts of C in the three fractions vary more over time in the absence of litter is to be expected: the overriding effect of leaf leachate (HoA) is missing; thus the contribution of other sources of C-extr should become more apparent. Faster degradation of HiN than HoA is reasonable because the former is mainly carbohydrate (largely microbial in origin), whereas the latter derives mainly from leaf tissue rich in structural materials. The amounts and degradation rate of HiA are less easily interpreted as both its nature and source are unclear. Degradation rates measured in this study are very rapid for the portion of the pool dominated in carbohydrates (HiN), whereas the acidic macromolecular remnants of lignin and cellulose (HiA, HoA) were more recalcitrant. Thus, even though HiN is not the dominant C-extr fraction, it contributes the largest part of respired C.

Table 1 Description of the soil profile (by Dr. T. Dyrness)

O_i	4–3 cm	twigs, needles
O_a	3–0 cm	humus layer
A	0–23 cm	silty loam, moist 10 YR, stones medium gravel, friable, non-sticky, non-plastic, many fine and medium roots, clear wavy boundary
B_{w1}	23–55 cm	silty loam, friable, weak medium subangular blocks, slightly sticky, plastic, common fine, medium, and coarse roots, gradual smooth boundary
B_{w3}	55–120 cm	silty clay loam, friable, weak coarse subangular blocks, sticky, very plastic

Microbial biomass

Biomass of fungi and bacteria was higher in the control plot than in the no-litter plot, due entirely to the microbial content of the litter layer (Table 2). For the mineral soil alone, values were slightly in the no-litter plot, especially for bacterial biomass and length of fungal hyphae. The higher microbial biomass in the mineral soil at the no-lit-

Table 2 Bacterial and fungal biomass and fungal hyphal length

Parameter	Control		No litter
	Forest floor	0–5 cm	0–5 cm
Fungal biomass			
Total (μg g^{-1})	2000	520	690
Active (μg g^{-1})	59	3	8
Length of hyphae			
Total (cm g^{-1} soil)	69500	17900	17400
Active (cm g^{-1} soil)	2000	100	200
Bacterial biomass			
Total (μg g^{-1})	7.7	3.7	7.4
Active (μg g^{-1})	7.4	3.0	4.3
Carbon in fungi			
Total (μg C g^{-1})	538	138	184
Active (μg C g^{-1})	16	0.8	2.1
Carbon in bacteria			
Total (μg C g^{-1})	3.2	1.3	1.8
Active (μg C g^{-1})	3.1	1.3	1.8

ter plot (Table 2) is also consistent with the higher proportions of HiN at that plot.

General discussion

To what extent could C-extr constitute the substrate for microbial respiration in soil and litter? For C-extr to be the main source for microbial respiration and assuming that litter layer and mineral soil contribute equally to soil respiration, C-extr would have to turn over about 1000 times annually in the litter layer and 4500 times in the mineral soil. Degradation of freshly extracted C has rarely been measured. Dahm (1981) reported that some 20% of the C freshly leached from alder foliage was respired within 48 h, after an initial lag of about 6 h, during which no respiration occurred. Rapid degradation of C freshly desorbed from marine sediments has also been reported (Keil et al. 1994). Qualls and Haines (1992) incubated DOC collected with soil lysimeters and found loss of only 5–10% in the first 2 days. The highest degradation rates were reported in the few experiments in which degradation of desorbed C was followed sequentially during the first few days after desorption (Qualls and Haines 1992; Keil et al. 1994; this study).

Seto and Yanagiya (1983) found a very close relation ($r = 0.95$) between C-extr and respiration for 65 forest and agricultural soils. Although the C-extr was sufficient to supply only 3 h of respiration, it was replaced rapidly; weekly extractions showed no detectable decrease in C-extr over a 6-week period once an initial loss phase had ended after the 1st week. More recently, Cook and Allan (1992a) incubated sieved (root-free) soil for 210 days. They found close correlations between levels of C-extr and soil respiration at 14 and 35 days into the incubation, but not thereafter.

On the control plot, C-extr averaged about 7.8 g m^{-2} counting both litter and mineral soil (to 30 cm depth). Our degradation results suggest that only about 15% of this is degradable, but that most of the degradation takes place within 3 days. This degradation rate extrapolates to respiration of about 360 mg C m^{-2} day^{-1}, or about 120 g m^{-2} day^{-1}, quite close to the soil respiration rate we measured at the control plot. The measured value, however, includes CO_2 produced by roots, which may account for as much as half of soil respiration (Ewel et al. 1987; Bonan 1993; Bowden et al. 1993).

Critical is the rate at which the C-extr might be replenished by dissolution of particulate OM and thus become available for microbial degradation. To determine this replenishment rate is difficult, however, because virtually any sort of laboratory experiment creates highly artificial conditions. In most such experiments, water was added regularly to leach the soil of C-extr. Vance and David (1991b) added artificial throughfall to intact litter/soil profiles weekly for a full year and measured the DOC leached. Total over 1 year ranged from 4.8 to 144 g C m^{-2} depending on the type of soil and the soil horizons included in the profile. Cronan (1985), in a similar experiment, found slightly lower rates of DOC leaching. The total soluble C available for degradation thus does seem to be of the same order as the measured respiration rate, suggesting that soluble C might in fact account for a significant proportion of the microbial substrate. Obviously, however, combining results from laboratory experiments on New England soils with data from our study cannot provide definitive answers, but the evidence suggests that the role of water-extractable C as a substrate for microbial respiration merits further attention.

Acknowledgements We wish to thank E. Ingham for microbial biomass determinations, J. Baham, R. Griffiths, and P. Homann for insightful comments, C. Glassman and B. Caldwell for excellent technical help, and Ted Dyrness for soil pit descriptions. Financial support was provided by the Austrian and US National Science Foundations and by the Andrews Long-Term Ecological Research program.

References

Aiken GR (1988) A critical evaluation of the use of macroporous resins for the isolation of aquatic humic substances. In: Frimmel FH, Christman RF (eds) Humic substances and their role in the environment. John Wiley&Sons, New York, pp 15–28

Boissier JM, Fontvieille D (1993) Biodegradable dissolved organic carbon in seepage waters from two forest soils. Soil Biol Biochem 25:1257–1261

Bonan GB (1993) Physiological controls of the carbon balance of boreal forest systems. Can J For Res 23:1453–1471

Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, Garrison JB (1993) Contributions of aboveground litter, below ground litter and root respiration to total soil respiration in a temperate mixed hardwood forest. Can J For Res 23:1402–1407

Castelle AJ, Galloway JN (1990) Carbon dioxide dynamics in acid forest soils in Shenandoah National Park, Virginia. Soil Sci Soc Am J 54:252–257

Cook BD, Allan DL (1992a) Dissolved organic carbon in old field soils: Total amounts as a measure of resources available for soil mineralization. Soil Biol Biochem 24:585–594

Cook BD, Allan DL (1992b) Dissolved organic carbon in old field soils: Compositional changes during the biodegradation of soil organic matter. Soil Biol Biochem 24:595–600

Cronan CS (1985) Comparative effects of precipitation acidity on three forest soils: Carbon cycling responses. Plant and Soil 88:101–112

Dahm CN (1981) Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. Can J Fish Aquatic Sci 38:68–76

Davidson EA, Galloway LF, Strand MK (1987) Assessing available carbon: Comparison of techniques across selected forest soils. Commun Soil Sci Plant Anal 18:45–64

Donald RG, Anderson DW, Stewart JWB (1993) Potential role of dissolved organic carbon in phosphorus transport in forested soils. Soil Sci Soc Am J 57:1611–1618

Easthouse KB, Mulder J, Christophersen N, Seip HM (1992) Dissolved organic carbon fractions in soil and stream water during variable hydrological conditions at Birkenes, Southern Norway. Water Resour Res 28:1585–1596

Edwards NT (1982) The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia 23:321–330

Ewel KC, Cropper WSP, Gholz HL (1987) Soil CO_2 evolution in Florida slash pine plantations: II. Importance of root respiration. Can J For Res 17:330–333

Fernandez I, Son Y, Kraske CR, Rustad LE, David MB (1993) Soil carbon dioxide characteristics under different forest types and after harvest. Soil Sci Soc Am J 57:1115–1121

Frey JS, McClellan JF, Ingham ER, Coleman DC (1985) Filter-outgrazers (FOG): A filtration experiment for separating protozoan grazers in soil. Biol Fertil Soils 1:73–79

Guggenberger G (1992) Eigenschaften und Dynamik gelöster organischer Substanzen (DOM) auf unterschiedlich immissionsbelasteten Fichtenstandorten. Bayreuther Bodenkundliche Abhandlungen 26, Lehrstuhl für Bodenkunde und Bodengeographie der Universität Bayreuth

Guggenberger G, Zech W, Schulten HR (1994) Formation and mobilization pathway of dissolved organic matter: Evidence from chemical structural studies of organic matter fractions in acid forest floor solutions. Organic Geochem 21:51–66

Hart SC, Firestone MK (1991) Forest floor-mineral soil interactions in the internal nitrogen cycle of an old-growth forest. Biogeochemistry 12:103–127

Ingham ER, Griffiths RP, Cromack K, Entry JA (1991) Comparison of direct vs fumigation incubation microbial biomass estimation from ectomycorrhizal mat and non-mat soils. Soil Biol Biochem 23:465–471

Jardine PM, Weber NL, McCarthy JF (1989) Mechanisms of dissolved organic carbon adsorption on soil. Soil Sci Soc Am J 53:1378–1385

Keil RG, Montlucon DB, Prahl FG, Hedges JI (1994) Sorptive preservation of labile organic matter in marine sediments. Nature (London) 370:549–551

Leenheer JA (1981) Comprehensive approach to preparative isolation and fractionation of dissolved organic carbon from natural waters and waste waters. Environ Sci Technol 15:578–587

Malcolm RL (1990) Variations between humic substances isolated from soils, stream waters, and groundwaters as revealed by ^{13}C-NMR spectroscopy. In: Humic substances in soil and crop sciences; selected Readings. Am Soc Agron and Soil Sci Soc Am (ed), pp 13–35

Mattson KG, Smith HC (1993) Detrial organic matter and soil CO_2 efflux in forests regenerating from cutting in West Virginia. Soil Biol Biochem 25:1241–1248

McDowell WH, Likens GE (1988) Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook Valley. Ecol Monogr 58:177–195

McGill WB, Cannon KR, Robertson JA, Cook FD (1986) Dynamics of soil microbial biomass and water-soluble organic C in Breton L after 50 years of cropping to two rotations. Can J Soil Sci 66:1–19

Nay MS, Mattson KG, Bormann BT (1994) Biases of chamber methods for measuring CO_2-efflux demonstrated with a laboratory apparatus. Ecology 75:2460–2463

Nelson PN, Dictor MC, Soulas G (1994) Availability of organic carbon in soluble and particle-size fractions from a soil profile. Soil Biol Biochem 26:1549–1555

Pohlman AA, McColl JG (1988) Soluble organics from forest litter and their role in metal dissolution. Soil Sci Soc Am J 52:265–271

Qualls RG, Haines BL (1991) Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. Soil Sci Soc Am J 55:1112–1123

Qualls RG, Haines BL (1992) Biodegradability of dissolved organic matter in forest throughfall, soil solution, and stream water. Soil Sci Soc Am J 56:578–586

Seto M, Yanagiya K (1983) Rate of CO_2 evolution from soil in relation to temperature and amount of dissolved organic carbon. Jpn J Ecol 33:199–205

Sollins P, McCorison FM (1981) Nitrogen and carbon solution chemistry of an old growth coniferous forest watershed before and after cutting. Water Resour Res 17:409–1418

Thurman EM (1985) Organic geochemistry of natural waters. W. Junk, Boston, Dordrecht

Ugolini FC, Dahlgren RA (1987) The mechanisms of podzolization as revealed by soil solution studies. In: Righi D, Chauvel A (eds) Podzols and podzolization. Association Francaise pour L'Etude du Sol, INRA, Paris, pp 185–203

Vance GF, David MB (1991a) Chemical characteristics and acidity of soluble organic substances from a northern hardwood forest floor, central Maine, USA. Geochim Cosmochim Acta 55:3611–1625

Vance GF, David MB (1991b) Forest soil response to acid and salt additions of sulfate: III. Solubilization and composition of dissolved organic carbon. Soil Sci 151:297–305

Zsolnay A, Steindl H (1991) Geovariability and biodegradability of the water-extractable organic material in an agricultural soil. Soil Biol Biochem 23:1077–1082