Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest

RICHARD D. BOWDEN[1]
Allegheny College, Department of Environmental Science, Meadville, PA 16335, U.S.A.
KNUTE J. NADELHOFFER
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, U.S.A.
RICHARD D. BOONE
Harvard Forest, Harvard University, Petersham, MA 01366, U.S.A.
JERRY M. MELILLO
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, U.S.A.
AND
JASON B. GARRISON
Allegheny College, Department of Environmental Science, Meadville, PA 16335, U.S.A.

Received June 11, 1992
Accepted November 26, 1992

BOWDEN, R.D., NADELHOFFER, K.J., BOONE, R.D., MELILLO, J.M., and GARRISON, J.B. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. **23**: 1402–1407.

Estimating contributions by root respiration and root litter to total soil respiration is difficult owing to problems in measuring each component separately. In a mixed hardwood forest in Massachusetts, we added or removed aboveground litter and terminated live root activity through construction of trenches and root barriers to determine the contribution of aboveground litter, belowground litter, and root respiration to total soil respiration. Annual soil respiration at control plots, measured by the soda-lime technique, was 371 g $C \cdot m^{-2} \cdot year^{-1}$. We used aboveground litter inputs (138 g $C \cdot m^{-2} \cdot year^{-1}$) and differences in carbon dioxide effluxes among treatment plots to calculate contributions to total soil respiration by live root respiration (33%) and by organic matter derived from aboveground (37%) and belowground (30%) litter. Newly deposited aboveground litter contributed 31% of the carbon dioxide emitted by total aboveground litter. This estimate is consistent with values published in litter decomposition studies. Nearly two thirds of soil respiration in this forest can be attributed to root activity, comparable with a previous study suggesting that live root respiration plus decomposition of root litter contributes 70–80% of total soil respiration across a wide range of forests.

BOWDEN, R.D., NADELHOFFER, K.J., BOONE, R.D., MELILLO, J.M., et GARRISON, J.B. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. **23** : 1402–1407.

Il n'est pas facile d'estimer la contribution de la respiration des racines et celle de la litière de racines à la respiration totale dans le sol à cause de la difficulté à mesurer séparément chacune des composantes. Dans une forêt feuillue du Massachusetts, nous avons ajouté ou enlevé la litière d'origine aérienne et stoppé l'activité des racines vivantes, en construisant des tranchées et des barrières pour les racines, dans le but de mesurer la contribution de la litière d'origine aérienne, celle de la litière d'origine souterrainne et celle de la respiration des racines à la respiration totale dans le sol. Dans les parcelles temoins, la respiration annuelle dans le sol, mesurée en trappant le dioxide de carbone, était de 371 g $C \cdot m^{-2} \cdot an^{-1}$. Nous avons utilisé l'apport de litière d'origine aérienne (138 g $C \cdot m^{-2} \cdot an^{-1}$) et la différence dans les émanations de dioxide de carbone entre les parcelles traitées pour calculer la contribution à la respiration totale dans le sol de la respiration des racines vivantes (33%) et de la matière organique dérivée aérienne (37%) et souterraine (30%). La litière d'origine aérienne déposée récemment contribuait pour 31% du dioxide de carbone émis par toute la litière d'origine aérienne. Cette estimation concorde avec les valeurs publiées dans les études de décomposition de litière. Près des deux tiers de la respiration dans le sol de cette forêt peut être attribué à l'activité des racines, ce qui est comparable aux résultats d'une étude antérieure qui suggérait que la respiration des racines vivantes et la décomposition de la litière de racines représentent 70–80% de la respiration totale dans les sols d'une grande variété de forêts.

[Traduit par la rédaction]

Introduction

Soil respiration is an important process in the flow of carbon in forest ecosystems. Large amounts of carbon are released to the atmosphere as CO_2 during decomposition of litter added to soil from aboveground and belowground sources, and additional CO_2 is released by respiration of living roots. Raich and Schlesinger (1992) estimate that global soil respiration by terrestrial ecosystems is 68 $Gt \cdot year^{-1}$, an order of magnitude greater than the 5.7 $Gt \cdot year^{-1}$ (in 1987) released through fossil fuel combustion plus industrial sources (Watson et al. 1990).

Estimates of soil respiration have been made in a variety of ecosystems and have been summarized in reviews by Schlesinger (1977), Singh and Gupta (1977), Raich and Nadelhoffer (1989), and Raich and Schlesinger (1992). Despite this increasing body of information, the relative contributions of autotrophic respiration (CO_2 released by respiring roots) and heterotrophic respiration (CO_2 released by decomposition of litter) are still poorly known. Carbon

[1]Author to whom all correspondence should be addressed.

Printed in Canada / Imprimé au Canada

dioxide from decomposition of aboveground litter can be estimated directly from measurements of aboveground litter fall, assuming that the system is in steady state (Reiners 1968; Schlesinger 1977; Raich and Nadelhoffer 1989). Identifying contributions by the different belowground sources has proven considerably more elusive, however. For example, root respiration estimates range from 4 (Phillipson et al. 1975) to 62% (Ewel et al. 1987*a*) of soil respiration.

Assessing autotrophic and heterotrophic contributions to soil respiration has been a problem owing to difficulties in measuring each source separately. Root respiration has been estimated by measuring respiration of soil from which roots were removed (e.g., Wiant 1967) or by measuring respiration of roots directly (Edwards and Sollins 1973; Edwards and Harris 1977). These approaches are limited by the effort involved in the root separation process, and perhaps compromised by considerable disturbances to the soil–root system. Root respiration can be estimated indirectly by subtracting root turnover, determined by the N-budget method (Aber et al. 1985; Nadelhoffer et al. 1985; Nadelhoffer and Raich 1993), from measured total soil respiration. This method, however, requires annual measurements of numerous carbon and nitrogen pools and fluxes, and is subject to accumulation of errors from each of those measurements.

Here we report an alternative approach to assess autotrophic and heterotrophic contributions to total soil respiration, where we use a series of manipulated forest plots (detritus input, removal, and trenching (DIRT) plots) to which aboveground litter has been added or removed, and where root activity has been terminated. The DIRT plots were established recently at the Harvard Forest in Massachusetts for long-term examinations of soil organic matter and nutrient dynamics in forest soils. The soil respiration findings reported here are the first results from these long-term study plots.

Site description

The 1.05-ha study site is an approximately 80-year-old mixed hardwood stand at the Harvard Forest in north central Massachusetts. The site, with a northwesterly aspect and gentle slope (4%), ranges in elevation from 331 m at the upslope position to 318 m at the downslope position. Predominant tree species (≥5 cm DBH), which form a relatively closed canopy, are northern red oak (*Quercus borealis* Michx. f.), red maple (*Acer rubrum* L.), and paper birch (*Betula papyrifera* Marsh.) and comprise 43, 19, and 15%, respectively, of the total basal area (29.7 $m^2 \cdot ha^{-1}$). Herbaceous ground cover is dominated by Canada mayflower (*Maianthemum canadense* Desf.) and several species of ferns. Ground cover is dense on the upper portion of the site and nearly absent at the lower portion.

Soil at the site is a moderately well-drained stony-loam of the Charlton series (Inceptisol) that averages about 3 m deep. It is derived from glacial till deposited over bedrock dominated by granite, gneiss, and schist. Duripans, though present in a stand approximately 100 m to the east, have not been found at the study site. The forest floor ranges from 3 to 8 cm thick and is a moder to mor type with a thin Oa horizon (1–3 cm thick). Most roots are concentrated in the forest floor with none observed below 70 cm (upper C horizon) in the mineral soil. Ground water, based on observations of soil pits, trenches, and soil sampling holes, occasionally occurs within a few centimeters of the soil surface at the lower end of the site after heavy rains in the fall. Mottling (5% coverage) was common in the B horizon over the entire area. The mineral soil does not indicate a plow layer. Based on records in the Harvard Forest archives, the site was a permanent pasture from 1733 to 1850, and was classified as old-field white pine in 1908 and as a white pine – transition hardwood in 1923. Today, mature pines are not found within the study area, although some are found on its margins.

Methods

The DIRT plots consist of a series of 3 × 3 m plots, free of trees or saplings, established in 1990. Treatments were as follows: control (normal annual aboveground litter inputs), no-litter (annual aboveground litter inputs excluded), 2×-litter (twice the annual aboveground litter input), no-roots (plots trenched and root regrowth into plots prevented), no-roots no-litter (plots trenched and annual aboveground litter excluded), no-OA (soil O and A horizons removed and replaced with B-horizon material from nearby excavations).

A stratified random approach was used to establish DIRT plots at upslope, midslope, and downslope positions within the site. One of each of the manipulated plots and two controls were located randomly at each of the slope positions. All plots except the no-OA plots were established by September 1990; the no-OA plots were completed in July 1991.

Litter inputs were intercepted in 1990 by placing plastic mesh shade cloth on all plots from early September until late October, the period when 95% of all litter fall occurs (A. Magill, personal observation). At the end of autumnal litter fall, litter was returned to the control and no-roots plots, but it was removed from the no-litter and no-roots no-litter plots. To double annual aboveground litter inputs for the 2×-litter plots, additional litter was obtained from collections made in either the no-litter or the no-litter no-roots plots in that block. Litter from the no-litter plots was used to estimate aboveground litter inputs. Fresh litter weights were converted to oven-dry weights (70°C), and carbon inputs were assumed to be 48% of oven-dry biomass. Our annual input estimate, 138 ± 21 g $C \cdot m^{-2} \cdot year^{-1}$ ($n = 3$) for 1990, was corrected for the 5% of litter fall that does not occur during autumn senescence.

At the no-roots plots, a 70–100 cm deep trench extending approximately 20 cm below the bottom of the rooting zone (the top of the C horizon) was dug 0.5 m outside the plot boundaries. Corrugated fiberglass sheets (3 mm thick) were placed into the trenches to prevent ingrowth of tree roots and the trenches were refilled. The no-OA plots were established by removing the O and A horizons and replacing the removed soil with B-horizon material excavated from soil pits nearby.

The plots were kept free of seedlings and herbaceous vegetation. Twice during the summer, all aboveground vegetation was clipped at the soil surface and removed. Newly fallen woody litter (≥1.0 cm diameter) was also removed from the plots during the field season.

Soil respiration was measured from June through August 1991 using a soda-lime technique (Edwards 1982; Raich et al. 1990). Carbon dioxide emitted from soil was absorbed for 24 h in 60 g of oven-dried (105°C) soda lime contained in soil tins placed beneath white plastic chambers that were 20 cm tall and 27.5 cm in diameter. Aluminum foil was placed over the chambers to minimize heating within the chamber. Plastic rings having the same diameter as the measurement chambers were placed on the forest floor 3 days prior to the first measurement to prepare an adequate seal between the soil surface and the chamber bottoms. One ring was placed on each plot, and the rings were left in place between flux measurements. Fluxes at each plot were measured once or twice per week from each plot from June through August, with the exception of the no-OA plots, which were sampled in July and August only. Mean fluxes for the summer were calculated for each chamber. Each sampling date was considered the midpoint of a sampling period, and the mean summer flux, weighted for sampling frequency, was calculated from the sum of all sampling periods.

Autotrophic and heterotrophic contributions to total forest soil respiration were estimated by comparing CO_2 efflux rates among the various treatments. Contributions from decomposing aboveground litter were assessed by comparing no-litter and 2×-litter plots to control plots, and root respiration was evaluated by comparing no-roots plots to control plots. The potential importance of B-horizon mineral soil was determined from respiration at the no-OA plots.

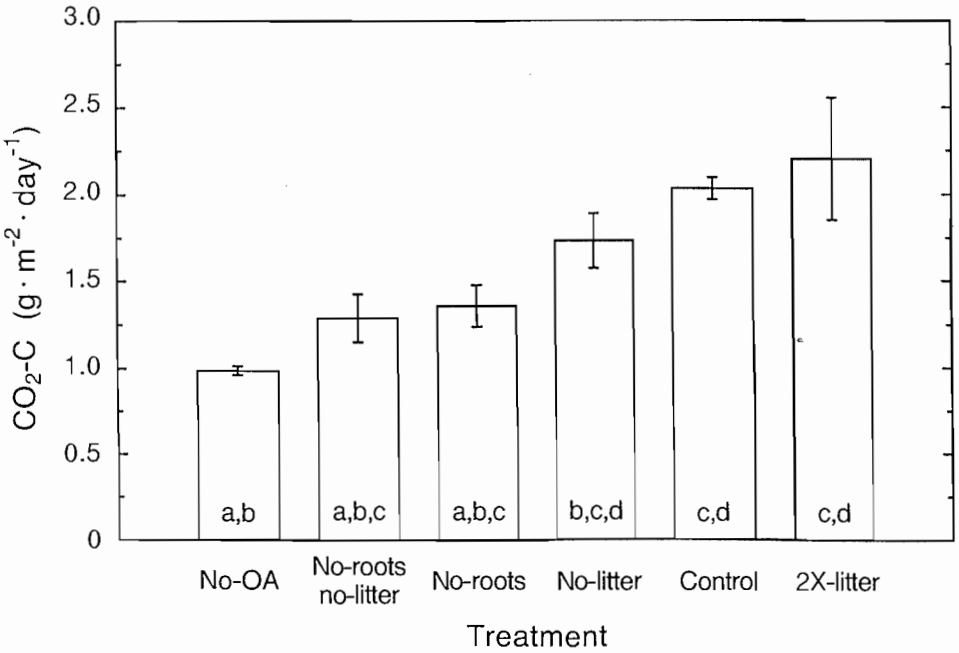

FIG. 1. Mean weighted CO_2 fluxes (± 1 SE) during study period (no-OA plots: July–August, 1991, all other plots June–August, 1991) ($n = 6$ for controls, $n = 3$ for all other treatments). Means with the same letter are not significantly different (ANOVA, Duncan's multiple range test).

Annual CO_2 fluxes for the plots were calculated by assuming that the daily CO_2 emission rates averaged over an entire year were half those for the summer months (June, July, and August) alone. This is in agreement with flux rates measured at an adjacent Harvard Forest mixed hardwood stand, where that the mean annual CO_2 flux rate (1.36 g $C \cdot m^{-2} \cdot day^{-1}$) was 53% of the mean flux rate for June, July, and August (2.57 g $C \cdot m^{-2} \cdot day^{-1}$; Bowden et al. 1993).

Results

Mean CO_2 effluxes (Fig. 1) showed a highly significant treatment effect ($F = 9.30$, df = 5, 15, $P < 0.001$), and were highest at the 2×-litter plots and lowest at the no-OA plots.

The contribution to total soil respiration from recent aboveground litter (litter added during the previous year), calculated as the mean difference in annual respiration between the control plots (371 g $C \cdot m^{-2} \cdot year^{-1}$) and 2×-litter plots (402 g $C \cdot m^{-2} \cdot year^{-1}$), and the control and no-litter plots (316 g $C \cdot m^{-2} \cdot year^{-1}$), was 43 g $C \cdot m^{-2} \cdot year^{-1}$, or 12% of the total CO_2 efflux for the control plots. Root respiration, the difference between the control and no-roots plots, was 123 g $C \cdot m^{-2} \cdot year^{-1}$, or 33% of total soil respiration. Differences among treatments were generally consistent throughout the summer (Fig. 2), with only the no-OA plots exhibiting a temporal trend. Carbon dioxide fluxes from the no-OA plots increased over the sampling season and were similar to fluxes from the no-roots and no-litter plots by mid to late August.

Discussion

The contribution of root respiration, 33%, to total soil respiration is comparable to estimates for a 50-year-old tulip-tree (*Liriodendron tulipifera* L.) forest in Tennessee, where direct measurements of roots removed from soil indicated that 35% of soil respiration was due to live root respiration (Edwards and Sollins 1973; Edwards and Harris 1977). It is considerably lower, however, than rates reported for several pine stands. For example, in Japan, Nakane et al. (1983), using cut and uncut pine forests (*Pinus densiflora* Seib. & Zucc.) and correcting for root decomposition, estimated that root respiration contributed 47–51% to total soil respiration. Also, Ewel et al. (1987*a*) estimated that root respiration was 62% of soil respiration in a 29-year-old slash pine (*Pinus elliottii* Engelm.) plantation in Florida, where trenched plots and estimates of root decomposition were used to estimate root respiration.

Our root respiration estimate is based on the assumption that root respiration is a constant proportion of total soil respiration throughout the year. If root respiration is a lower proportion of total respiration during dormant months, then extrapolation of the difference between control and no-roots plots from summer months to the entire year would overestimate the annual contribution by root respiration. Our data do not allow us to accurately constrain this potential error; however, we suggest that this error is probably low. Total respiration rates are drastically reduced during winter months (Reiners 1968; Edwards and Harris 1977; Bowden et al. 1993), and maintenance respiration, which may represent 30–40% of root respiration (M. Ryan, personal communication), would still be occurring during dormant periods.

We assume that CO_2 emissions from the trenched (no-roots and no-roots no-litter) plots include only CO_2 respired during decomposition of aboveground and belowground litter, and not CO_2 released during decomposition of roots killed during trenching. If our assumption is untrue, however (i.e., CO_2 emissions from the trenched plots include CO_2 from decomposition of the recently killed roots), then the difference between the control and no-roots plots is too small, and we have underestimated root respiration. We have attempted to constrain this error, however. Based on a mean fine root mass of 610 g $\cdot m^{-2}$ in a nearby Harvard Forest mixed hardwood site (Aber et al. 1985), a decomposition rate of 20% per year

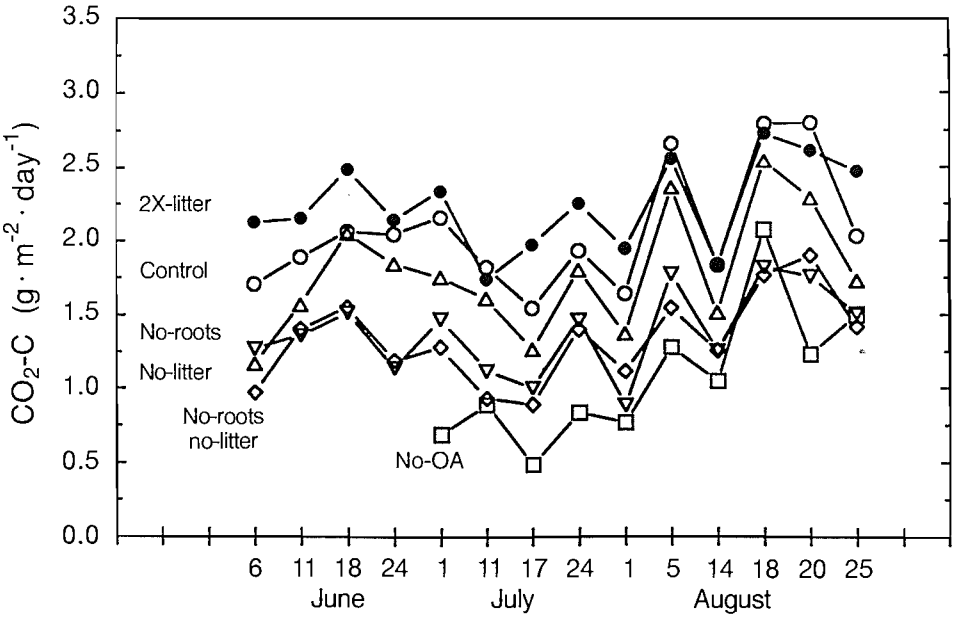

FIG. 2. Carbon dioxide fluxes from plots during 1991 study period (n = 6 for controls, n = 3 for all other treatments).

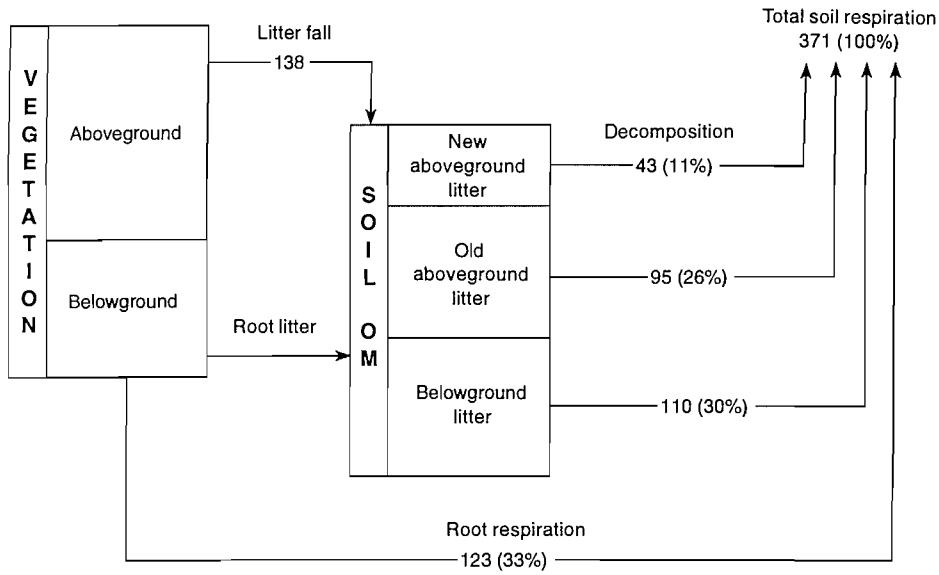

FIG. 3. Soil respiration budget for mixed hardwood forest at the Harvard Forest, Massachusetts. Numbers are flux rates (g $C \cdot m^{-2} \cdot year^{-1}$) and percentages (in parentheses) of total soil respiration for each component. OM, organic matter.

(McClaugherty et al. 1982), and a C content of 48%, root respiration might be up to 59 g $C \cdot m^{-2} \cdot year^{-1}$ greater than our estimate of 123 g $C \cdot m^{-2} \cdot year^{-1}$. This would increase our root respiration estimate from 33 to 49% of total soil respiration. We believe this is unlikely, however, because root decomposition rates were probably reduced drastically by the time we began our CO_2 flux measurements. Fahey et al. (1988), for example, found that the C content of decomposing, recently killed fine roots in a mixed hardwood forest in New Hampshire was relatively stable approximately 4 months after decay began. Our estimated root decomposition rate is the same as the rate reported by Fahey et al. (1988), suggesting that root decomposition probably did not strongly influence our flux measurements begun 9 months after trenching was completed. Additionally, Ewel et al. (1987*a*) found no effects of root decomposition on CO_2 effluxes 4 months after trenching was completed in a Florida pine plantation.

We do not know how our treatments may have influenced soil moisture in the study plots, nor do we know how potential changes in soil moisture may have influenced CO_2 flux rates. Cessation of root activity by trenching would have eliminated transpiration losses, thus resulting in higher soil moisture. Additionally, changes in soil texture caused by construction of the no-OA plots may have also influenced soil moisture. Although we did not measure soil moisture at the time of this study, previous work has shown that relatively large changes in soil moisture in this forest are necessary to influence soil respiration (R.D. Bowden, unpublished data).

Decomposition of recent (≤1 year old) aboveground litter fall contributed 12% of total soil respiration, similar to the 10.9% measured by Edwards and Harris (1977). Correspondingly, the release of 43 g $C \cdot m^{-2} \cdot year^{-1}$ indicates a 31% first-year decomposition rate for aboveground litter fall (138 g $C \cdot m^{-2} \cdot year^{-1}$). This compares well with a litter decomposition study in a nearby Harvard Forest mixed hardwood stand, which showed a 33% loss of northern red oak litter mass in the first year (Aber et al. 1990).

The balance of soil respiration (205 g $C \cdot m^{-2} \cdot year^{-1}$), after root respiration and decomposition of recent aboveground litter are subtracted from total respiration, results from decomposition of previously deposited aboveground litter fall (added prior to the previous year) and to decomposition of root litter (including all root-derived organic matter). The contribution from previous aboveground litter was estimated by assuming that, under approximately steady-state conditions, respiration by decomposing litter fall is equal to litter-fall C inputs. Subtracting recent aboveground litter from total aboveground litter provides an estimate of 95 g $C \cdot m^{-2} \cdot year^{-1}$ derived from decomposition of previously deposited aboveground litter. Release from belowground litter (110 g $C \cdot m^{-2} \cdot year^{-1}$) was calculated by subtracting total aboveground litter decomposition (138 g $C \cdot m^{-2} \cdot year^{-1}$) and root respiration (123 g $C \cdot m^{-2} \cdot year^{-1}$) from total soil respiration.

Fluxes from our no-OA plots indicate that B-horizon soil contains a labile pool of soil organic matter; however, the contribution of this pool to total soil respiration in an undisturbed plot is unknown. Respiration from these plots may have been affected by the massive soil disturbance created during construction of these plots, including changes in soil structure and moisture. We do not think that much of the respiration from the no-OA plots came from root respiration because most roots in this forest are located in the O and A soil horizons that had been removed and replaced with B-horizon soil. There was also insufficient time for recolonization of roots into the added B-horizon material.

Results of our study are in agreement with much more laborious means of determining contributions to total soil respiration. Our estimates indicate that total soil respiration in this temperate mixed hardwood forest is composed of approximately equal contributions of carbon dioxide from aboveground litter (37%), belowground litter (30%), and root respiration (33%) (Fig. 3). A large fraction (63%) of soil respiration in this forest is due to belowground processes, in agreement with recent work indicating that root respiration plus belowground litter decomposition combined contribute 70–80% of total soil respiration across a wide range of forests (Raich and Nadelhoffer 1989; Nadelhoffer and Raich 1992).

Factors controlling relative contributions to total soil respiration in different forests are not well understood. The absolute rate of total soil respiration from forest soils is influenced by a number of factors, including moisture and temperature (Schlentner and Van Cleve 1985; Weber 1985), soil pH (Kowalenko et al. 1978), soil nitrogen content (Söderström et al. 1983), litter quality (Rout and Gupta 1989) and content (Van Cleve and Sprague 1971), forest development and soil organic matter content (Ewel et al. 1987*a*, 1987*b*; Gordon et al. 1987; Rout and Gupta 1989), and management practices (deJong et al. 1974; Weber 1985, 1990; Gordon et al. 1987). These factors may also influence the relative contributions to soil respiration. For example, respiration in a recently clear-cut forest may be dominated by soil organic matter decomposition, with only a small contribution by root respiration. Increased understanding of these factors is needed to predict relative contributions to total soil respiration in different forest ecosystems.

Acknowledgements

This research is a contribution to the Harvard Forest Long-Term Ecological Research program, and was supported by the National Science Foundation (Grant BSR-8811764), the Pew Midwest Science Cluster, the Howard Hughes Medical Institute, and the Department of Energy (Northeast Regional Center of the National Institute for Global Environmental Change). We thank Michael Buckley, Martha Downs, Jenn Ellis, Kasey Keith, Alison Magill, Cathy Millikin, Steve Newman, Andrea Ricca, Pete Spooner, and Susanna Walter, for their field and laboratory assistance. We also thank John Aber and two anonymous reviewers for useful comments on initial drafts of this manuscript.

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A., and Pastor, J.D. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of methods. Oecologia, **66**: 317–321.

Aber, J.D., Melillo, J.M., and McClaugherty, C.A. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. **68**: 2201–2208.

Bowden, R.D., Castro, M.C., Melillo, J.M., Steudler, P.A., and Aber, J.D. 1993. Fluxes of greenhouse gases between soils and the atmosphere in a temperate forest following a simulated hurricane blowdown. Biogeochemistry. In press.

deJong, E., Schappert, H.J.V., and MacDonald, K.B. 1974. Carbon dioxide evolution from virgin and cultivated soil as affected by management practices and climate. Can. J. Soil. Sci. **54**: 299–307.

Edwards, N.T. 1982. The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia, **23**: 321–338.

Edwards, N.T., and Harris, W.F. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology, **58**: 431–437.

Edwards, N.T., and Sollins, P. 1973. Continuous measurement of carbon dioxide from partitioned forest floor components. Ecology, **54**: 406–412.

Ewel, K.C., Cropper, W.P., Jr., and Gholz, H.L. 1987*a*. Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. Can. J. For. Res. **17**: 330–333.

Ewel, K.C., Cropper, W.P., Jr., and Gholz, H.L. 1987*b*. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. Can. J. For. Res. **17**: 325–329.

Fahey, T.J., Hughes, J.W., Pu, M., and Arthur, M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. **34**: 744–768.

Gordon, A.M., Schlentner, R.E., and Van Cleve, K. 1987. Seasonal patterns of soil respiration and CO_2 evolution harvesting in the white spruce forests of interior Alaska. Can. J. For. Res. **17**: 304–310.

Kowalenko, C.G., Ivarson, K.C., and Cameron, D.R. 1978. Effect of moisture content, temperature, and nitrogen fertilization on carbon dioxide evolution from field soils. Soil Biol. Biochem. **10**: 417–423.

McClaugherty, C.A., Aber, J.D., and Melillo, J.M. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology, **63**: 1481–1490.

Nadelhoffer, K.J., and Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology, **73**: 1139–1147.

Nadelhoffer, K.J., Aber, J.D., and Melillo, J.M. 1985. Fine root production in relation to net primary production along a nitrogen

availability gradient in temperate forests: a new hypothesis. Ecology, **66**: 1377–1390.

Nakane, K., Yamamoto, M., and Tsubota, H. 1983. Estimation of root respiration in a mature forest ecosystem. Jpn. J. Ecol. **33**: 397–408.

Phillipson, J., Putman, R.J., Steel, J., and Woodell, S.R.J. 1975. Litter input, litter decomposition, and the evolution of carbon dioxide in a beech woodland—Wytham Woods, Oxford. Oecologia, **20**: 203–217.

Raich, J.W., and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology, **70**: 1346–1354.

Raich, J.W., and Schlesinger, W.S. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus, **44B**: 81–99.

Raich, J.W., Bowden, R.D., and Steudler, P.A. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci. Soc. Am. J. **54**: 1754–1757.

Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology, **49**: 471–483.

Rout, S.K., and Gupta, S.R. 1989. Soil respiration in relation to abiotic factors, forest floor litter, root biomass, and litter quality in forest ecosystems of Siwaliks in northern India. Acta Oecologia, **10**: 229–244.

Schlentner, R.E., and Van Cleve, K. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can. J. For. Res. **15**: 97–106.

Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. Annu. Rev. Ecol. Syst. **8**: 51–81.

Singh, J.S., and Gupta, S.R. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. **43**: 449–528.

Söderström, B., Bååth, E., and Lundgren, B. 1983. Decrease in soil microbial activity and biomasses owing to nitrogen amendments. Can. J. Microbiol. **29**: 1500–1506.

Van Cleve, K., and Sprague, D. 1971. Respiration rates in the forest floor of birch and aspen stands in interior Alaska. Arct. Alp. Res. **3**: 17–26.

Watson, R.T., Rodhe, H., Oeschinger, H., and Siegenthaler, U. 1990. Greenhouse gases and aerosols. *In* Climate change: the IPCC scientific assessment. *Edited by* J.T. Houghton, G.J. Jenkins, and J.J. Ephraums. Cambridge University Press, Cambridge. pp. 1–40.

Weber, M.G. 1985. Forest soil respiration in eastern Ontario jack pine ecosystems. Can. J. For. Res. **15**: 1069–1073.

Weber, M.G. 1990. Forest soil respiration after cutting and burning in immature aspen ecosystems. For. Ecol. Manage. **31**: 1–14.

Wiant, H.V., Jr. 1967. Contribution of roots to forest "soil respiration." Adv. Front. Plant Sci. **18**: 163–167.