

CARBON IN FOREST SOILS—RESEARCH NEEDS

DALE W. JOHNSON

Desert Research Institute, P.O. Box 60220, Reno, NV 89506 USA
and
Department of Range, Wildlife, and Forestry, College of Agriculture,
University of Nevada, Reno, NV 89512 USA

(Received for publication 5 November 1992; revision 30 March 1993)

ABSTRACT

General areas of research needed for soil carbon include, but are not limited to, (1) effects of forest management, (2) effects of climate change, and (3) effects of elevated carbon dioxide. The research requirements to investigate these topics include: (1) a co-ordinated study with specific protocols for sampling and analyses to either confirm or negate the results of a recent review which showed little average change in soil carbon with harvesting, but increased soil carbon with improved nutrient status; (2) process-level studies involving temperature and moisture manipulations combined with gradient studies; (3) studies of litter quality effects (including roots) using actual incubation and/or litterbag experiments to assess potential litter and soil carbon changes with increasing carbon dioxide; (4) a realistic soil carbon fractionation method to complement all new studies; and (5) studies of factors affecting soil carbon dioxide partial pressures ($p\text{CO}_2$) along with an evaluation of the effects of soil $p\text{CO}_2$ on tree seedling root growth.

Keywords: organic matter; respiration; forest management; climate change; carbon dioxide; soil carbon; sampling.

INTRODUCTION

Soil organic matter has a major influence upon site productivity because of its effects upon physical (bulk density, water holding capacity), biological (microbial populations), and chemical (cation exchange capacity) properties of soils (Chen & Aviad 1990). Recently, there have also been claims as to the benefits of dead wood to forest ecosystems (Maser *et al.* 1988). As with all nutrients, however, too much carbon in soils can have negative effects, especially with regard to nitrogen immobilisation (Bollen 1974).

In addition to issues regarding site productivity, the global carbon / climate change issue has greatly heightened interest in the effects of land management practices on terrestrial carbon balances. Of particular interest is the "missing sink" of carbon, which arises from the difference between carbon dioxide release by fossil fuels (approximately 6×10^{15} g) and the annual carbon dioxide increase in the atmosphere (approximately 3.4×10^{15} g) (Lugo 1992). One of the major problems in identifying this sink is that background or "natural" pools and fluxes are much larger than both the release from fossil fuels and the observed increases in the atmosphere. Estimates of carbon fixation by photosynthesis, autotrophic, and heterotrophic

respiration (120 , 60 , and 60×10^{15} g, respectively) are an order of magnitude greater than either fossil fuel emissions or atmospheric carbon dioxide increase (Post *et al.* 1990). Given the uncertainties with estimated carbon budgets even on a plot level, it would seem to be an impossible task to discover the “missing sink” for fossil fuel. Thus, it is not surprising that the literature is full of contradictions, some estimates showing the terrestrial ecosystem as a net sink (Bolin 1977; Tans *et al.* 1990) and some showing it as a net source (Woodwell *et al.* 1978; Watson 1992; Broecker & Peng 1992).

In that the soil contains a very large reserve of carbon in organic matter (approximately 1500 – 1600×10^{15} g, as compared to 500 – 800×10^{15} g in terrestrial vegetation and 750×10^{15} g in the atmosphere), there is justifiable concern over the soil carbon balance and the potential effects of human activities upon this balance. Some immediate research needs can easily be identified, and that is the purpose of this paper.

EFFECTS OF FOREST MANAGEMENT ON SOIL CARBON

In a recent review, data from a variety of studies were summarised to examine the effects of harvesting, site preparation, fire, and fertiliser treatment on soil carbon (Johnson 1992). Many problems in this assessment arose from differences in sampling intensity in the vertical, horizontal, and temporal dimensions among the studies reviewed. Some authors compared changes in carbon in the top 2–5 cm of soil (e.g., Ellis & Graley 1983), whereas others compared changes in the top metre of soil (e.g., Johnson *et al.* 1991)*. Horizontal sampling intensity also varied enormously. Some studies had sufficient sample replicates to detect a change of less than 10% (Johnson *et al.* 1991), whereas others lacked the power to detect changes of as much as 40%. Perhaps most serious of all, temporal trends were seldom addressed. With varying amounts of slash left to decompose, temporal trends in mineral soil carbon are very likely to occur, yet very few studies addressed this issue. Most studies involved sampling only once (usually within 1–3 years of harvesting), and those few that addressed longer-term temporal trends of soil carbon after harvesting were mostly chronosequences with all the assumptions and uncertainties associated with that approach.

Most studies showed very little change in soil carbon with harvesting, regardless of sampling intensity or time since harvest. There were significant exceptions where soil carbon increased or decreased after harvest, but the overall pattern of little average change was convincing. Thus, the early assumption that large (35–50%) losses of soil carbon normally occur after forest harvesting (e.g., Houghton *et al.* 1983) appears to be largely unjustified. Harvesting followed by reforestation appears to have little effect on soil carbon unless forests are converted to agriculture (Mann 1986).

This review clearly pointed out the need for co-ordinated studies of the effects of harvesting (and other forest management practices) on soil carbon. Given the uncertainties in the comparisons made, significant trends (either upward or downward) may easily have been missed. Also, forest floor changes were not included in the overall assessment, which may have been a significant omission in northern/boreal forest ecosystems.

One striking aspect of this literature summary was the uniform increase in soil carbon with fertiliser treatment or the introduction of nitrogen-fixers. The increased soil carbon with

* In order to try to standardise the depth effect somewhat, the percentage changes for the entire soil profile sampled were calculated when not reported.

nutrient addition could have been due to increased productivity, increased stabilisation of soil organic matter by chemical co-ordination with nitrogen and calcium, or both. This pattern of increased soil carbon with fertiliser or nitrogen-fixers poses an interesting problem: Is the carbon content of a given soil ultimately determined by texture, topographic position, and climate, or can it be "permanently" changed by the addition of nutrients or the introduction of nitrogen-fixers? This question might be addressed by resampling of long-term fertiliser and mixed species trials.

EFFECTS OF CLIMATE CHANGE

Soil Carbon Accumulation

There are two basic ways in which the effects of climate change on soil carbon have been studied: (1) process-level studies in the laboratory or in the field, and (2) gradient studies. Each has its advantages and disadvantages. Process-level studies offer the most basic knowledge and the greatest hope for extrapolation to future scenarios. However, process-level studies are typically short-term and often involve very artificial conditions.

Several experiments have been conducted (Van Cleve *et al.* 1990; Anon. 1992) under field conditions in order to provide some understanding of the effects of climate warming on soil processes. These experiments necessarily involve the imposition of sudden increases in temperature, possibly creating conditions that would not occur with the more gradual changes resulting from climate warming. Soil micro-organisms have much less time to adapt to changes in a warming experiment than during climate change, for example. Also, heating of soil without heating of air and vegetation is likely to produce artifacts, especially with regard to changes in primary productivity and litter inputs. Finally, there are likely to be problems in terms of sorting out the effects of heating from attendant changes in moisture and nutrient status. Thus, it seems unlikely that soil warming studies alone will adequately address the process-level issues associated with climate change; ancillary laboratory studies with more tightly controlled moisture and nutrient conditions would be helpful, if not necessary additions to field studies of soil warming.

Gradient studies provide little if any process-level understanding, but they may offer a more realistic alternative to short-term process-level studies (Vitousek & Matson 1991). The classic studies by Jenny *et al.* (1949) and early modelling by Olson (1963) still provide useful guidelines and some process-level insights into the effects of climate change on litter and soil carbon. Olson's (1963) classic model of the effects of climate on productivity and decomposition using a simple decay equation seems to have withstood the test of time, although refinements have been added (Meetenmeyer 1978; Melillo *et al.* 1982). Olson's analysis indicated that, while both decomposition and productivity increase with increasing temperature, litter carbon will decrease because the former increases at a greater rate than the latter.

The simple decay model he proposed appears to be very useful in predicting times to quasi-steady-state and final forest floor biomass; however, has the model, with or without the refinements mentioned, been tested? This is especially pertinent to the question of mineral soil carbon responses to climate change: will it follow the same pattern as Olson's ideal litter pool? Soil organic matter (OM) accumulation is strongly affected by factors other than temperature and moisture. For instance, soil organic matter stability is strongly affected

by binding with polyvalent cations (Oades 1988) and abiotic reactions with nitrogen (Mortland & Wolcott 1965; Paul & Clark 1989). Thus, it would seem unlikely that soil organic matter will follow the same idealised decay curves as fresh litter does. Nonetheless, Post *et al.* (1982) found some fairly straightforward relationships among soil organic matter, precipitation, temperature, and the ratio of potential evapotranspiration to precipitation in a global-scale gradient study. They found that soil organic matter increased with increasing precipitation, decreasing temperature (at constant precipitation), and decreasing evapotranspiration to precipitation ratio.

This poses the question as to how important soil physical (e.g., clay content) and chemical (e.g., cation and nitrogen reactions) properties are in determining the overall patterns of soil organic matter. Is climate, after all, the overriding factor?

Post *et al.* (1985) addressed the nitrogen issue to some extent in a later paper which examined global patterns of nitrogen and carbon/nitrogen ratios as well as carbon. They found relatively large amounts of nitrogen and low carbon/nitrogen ratios (often <10) in tropical soils, which they attributed to the accumulation of recalcitrant humus forms. They found moderate nitrogen and variable carbon/nitrogen ratios in temperate soils, and did not make any specific generalisations about these systems. Finally, they noted high carbon, nitrogen, and carbon/nitrogen ratios in wet tundra regions, which were interpreted as being due to slow decomposition.

Local-scale gradient studies can also be very useful in evaluating the potential effects of climate change on soils. The study of Amundson *et al.* (1990) in the Mojave desert is a good illustration. They studied the effects of climate on soil carbon content, decomposition, and soil carbon dioxide partial pressure along an elevational gradient from 2150 m to 840 m (fir-pine to creosote bush). Among other things, they found a clear pattern of decreasing soil carbon (and plant cover) with decreasing elevation, which could then be correlated with temperature and precipitation (Fig. 1). This information alone cannot provide response data to temperature and moisture individually, however, and thus ancillary, small-scale, process-level studies would be useful.

Effects of Climate Change on Other Soil Processes

Soil carbon dioxide partial pressure and root growth

There are several important soil processes—both biological and chemical—that will be strongly affected by increases in soil temperature. For instance, there may be important plant physiological responses to elevated soil carbon dioxide partial pressure ($p\text{CO}_2$) resulting from increased soil respiration. Observations of increased crop growth with carbonation of irrigation water and with polyethylene mulch led to speculation that plant roots can take up carbon dioxide and stimulated several studies on the effects of elevated soil $p\text{CO}_2$ on plant growth. Results were extremely variable, depending upon species and $p\text{CO}_2$ level. Stolwijk & Thimann (1957) noted $p\text{CO}_2$ on root growth of peas (*Pisum sativum* L. var. Alaska), but no response in oats (*Avena sativa* L.). The response of peas was especially interesting: there was a slightly positive growth response (10% greater than controls) from ambient atmospheric up to 1.5% $p\text{CO}_2$, and a decidedly negative growth response from 1.5% to 6% (70% less than controls). Baron & Gorski (1986) found increased growth in eggplant (*Solanum melongena* L.) with $p\text{CO}_2$ levels up to 15% under some day-length and light-level conditions, but reduced growth under other conditions. Using $^{14}\text{CO}_2$, they established that the plants were

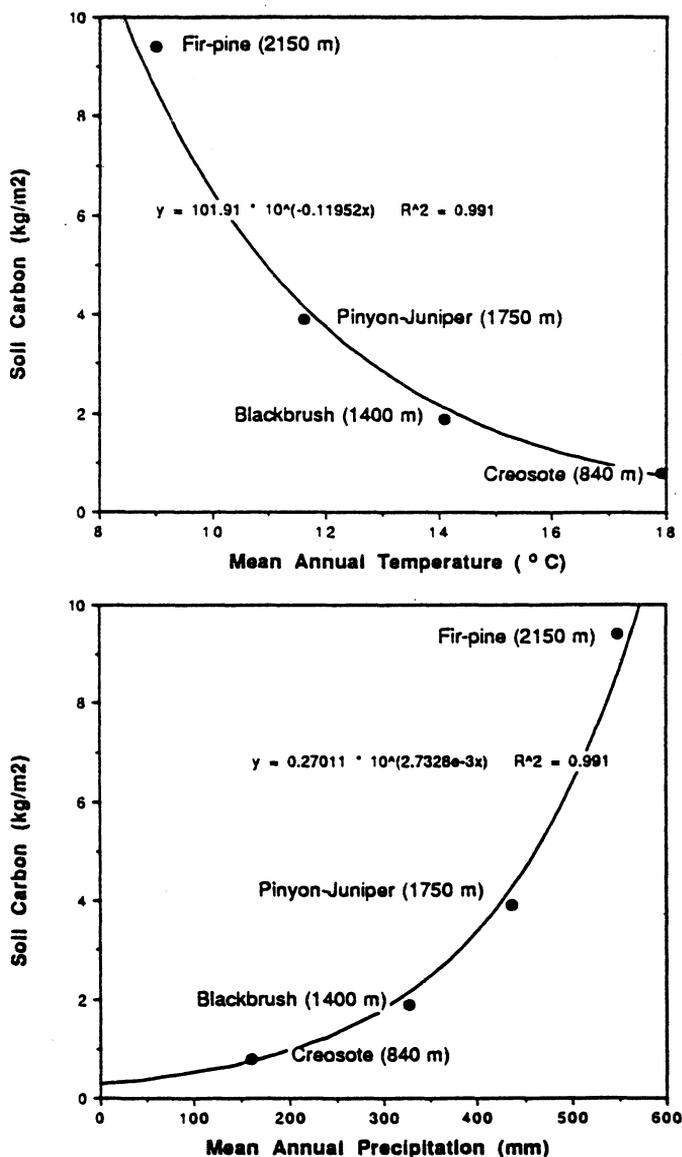


FIG. 1—Soil carbon as a function of mean annual temperature (top) and precipitation (bottom) along an elevational transect in the Mojave desert (from Amundsen *et al.* 1991).

able to take up carbon dioxide in roots and translocate it to shoots. Mauney & Hendrix (1988) found that irrigation with $p\text{CO}_2$ -saturated water resulted in significantly greater growth than controls in cotton (*Gossypium hirsutum* L.). Unlike Baron & Gorski (1986), however, they found no evidence of root uptake of $^{14}\text{CO}_2$.

The above studies raise several interesting questions, both in terms of soil carbon responses and in terms of any management practices that might alter soil $p\text{CO}_2$. Firstly, there

is a clear need to determine whether forest species respond to differences in soil $p\text{CO}_2$ or not, and, if so, how the responses compare to $p\text{CO}_2$ determined in the field. If tree species respond to $p\text{CO}_2$ as crop species do, there will be a need to determine how various forest management practices affect soil $p\text{CO}_2$, in addition to the climate change questions. In this context, it is essential to note that soil $p\text{CO}_2$ is a function not only of respiration, but (even more importantly) of soil carbon dioxide diffusivity. Soil carbon dioxide diffusivity is in turn a function of soil porosity, water content, and the presence or absence of any significant barrier to carbon dioxide diffusion (e.g., plastic mulch, snow pack) (Wesseling 1962). Thus, a pertinent line of totally unexplored forest soils research might be as follows: (1) how do forest tree species respond to variations in soil $p\text{CO}_2$; and (2) how does forest management affect soil $p\text{CO}_2$ either by changing respiration or by changing diffusivity—for instance, by causing changes in porosity or changes in litter characteristics?

Soil and soil solution chemical processes will likely be strongly affected by soil warming, especially in humid regions. In temperate soils that are not extremely acidic, increased $p\text{CO}_2$ in the soil atmosphere will stimulate increased carbonic acid leaching (McColl & Cole 1968; Johnson *et al.* 1977), which will also tend to increase soil acidification*. This can be shown from the following equations describing the dissolution of carbon dioxide in solution and the dissociation of carbonic acid:

$$[\text{H}_2\text{CO}_3] = (\text{Kh})(p\text{CO}_2) \quad (1)$$

$$\frac{[\text{HCO}_3^-][\text{H}^+]}{[\text{H}_2\text{CO}_3]} = K_1 \quad (2)$$

where Kh = Henry's Law constant

K_1 = First dissociation constant for carbonic acid.

Combining and solving for $[\text{HCO}_3^-]$ yields:

$$[\text{HCO}_3^-] = \frac{(K_1)(\text{Kh})(p\text{CO}_2)}{[\text{H}^+]} \quad (3)$$

Thus, bicarbonate concentration (and, therefore, cation leaching associated with bicarbonate) is a function of the partial pressure of carbon dioxide ($p\text{CO}_2$) in the soil atmosphere and soil solution pH (Johnson 1975). McColl & Cole (1968) artificially increased $p\text{CO}_2$ in soil columns, and demonstrated increased carbonic acid leaching. Johnson *et al.* (1977) found that elevated $p\text{CO}_2$ resulting from greater biological activity in soils at a tropical site (La Selva, Costa Rica) caused greater carbonic acid leaching rates than in more northern forest soils with lower $p\text{CO}_2$.

Ulrich (1980) noted some time ago that nitrification was stimulated during warm dry years, giving an acid "push" and mobilisation of aluminium in soils of the Solling site in Germany. Johnson *et al.* (1991) noted the same phenomenon in red spruce (*Picea rubens* Sarg.) sites in the Great Smoky Mountains of North Carolina. Soil warming studies now in progress show that soil $p\text{CO}_2$ levels increase with temperature, thus creating an increase in carbonic leaching potential (Anon. 1992).

In northern and subalpine soils that are dominated by organic acid leaching (Johnson *et al.* 1977), warming will likely lead to a decrease in organic acid leaching and an increase in

* Carbonic acid leaching will not increase the leaching of aluminium, however, because carbonic acid is a weak acid and does not dissociate at pH where aluminium comes into solution.

carbonic and/or nitric acid leaching, depending on soil nitrogen status. Studies of soil leaching processes in different climates indicate that a shift from organic to carbonic acid dominance occurs with increasing mean annual temperature (Johnson *et al.* 1977). Laboratory incubation studies on forest floor material from a cold Spodosol showed that warming caused a marked increase in pH and, presumably, decreased inorganic acid production (Fig. 2). Thus, a significant increase in soil temperature in cold-region soils may well lead to a shift from organic to carbonic acid dominance, with attendant changes in soil solution pH (increase) and iron and aluminium transport by chelation (decrease).

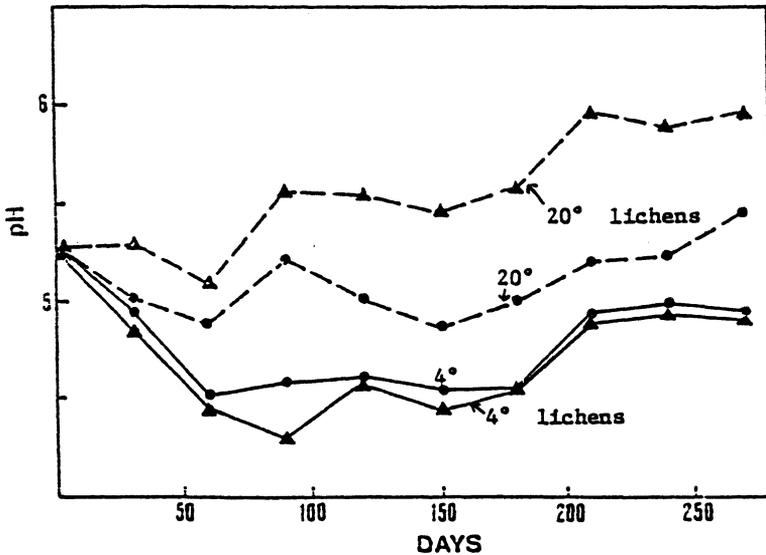


FIG. 2—pH of leachates from decomposing *Abies amabilis* needles incubated at 4°C (solid lines) and 25°C (dashed lines), with and without lichens (from Johnson 1975).

Warming may also increase the capacity of soils to adsorb anions (e.g., Singh 1984) and decrease the leaching of sulphate and phosphate. Finally, warming, along with the increased production of acids as described above, will likely result in an increase in the rate of primary mineral weathering, which may offset the potential acidification of soils by the increased carbonic and/or nitric acid production.

All of the above processes merit investigation in soil warming experiments, in the laboratory, in the field, or both. However, the limitations of short-term, square-wave-type warming experiments in simulating actual climate warming must be borne in mind when interpreting results. This is an especially important concern with respect to nitrogen transformations and nitrate leaching.

Litter Production, Quality, and Decomposition

Much of the study of the effects of elevated carbon dioxide has been devoted to plant response, especially under nutrient or water limitations (*see* review by Strain 1985). There are two aspects of the carbon dioxide question that pertain to soil carbon, however—(1)

potential changes in litter quality, and (2) potential increases in allocation of primary production to roots. Some investigators have noted decreased foliar nitrogen concentrations with increased carbon dioxide (Norby, O'Neill & Luxmoore 1986; Norby, Pastor & Melillo 1986; Brown 1991) whereas others have found little effect (Luxmoore *et al.* 1986; Campagna & Margolis 1989). Whether or not changes in foliar nitrogen concentration will result in significant changes in litter quality is not clear. Nambiar & Fife (1991) argued that litter nitrogen is closely coupled to foliar nitrogen, and Norby, Pastor & Melillo (1986) found that leaves from carbon dioxide-fumigated white oak (*Quercus alba* L.) seedlings had lower lignin but higher tannin and sugars than leaves from unfumigated trees. However, Norby, O'Neill & Luxmoore (1986) concluded that rates of litter decomposition will not be greatly affected by carbon dioxide, based upon lignin:nitrogen and lignin:phosphorus ratios. Clearly, direct studies of decomposition rates and nutrient mineralisation rates from carbon dioxide-fumigated trees are needed to test the generality of the conclusions of Norby, O'Neill & Luxmoore (1986) for white oak.

Couteaux *et al.* (1991) conducted a detailed study of the effects of increased carbon dioxide on decomposition of chestnut (*Castanea*) leaf litter. They found that carbon dioxide enrichment (from 350 to 700 $\mu\text{l/l}$) caused increased litter carbon/nitrogen ratios (from 40 to 75), but there were no differences in lignin, cellulose + hemicellulose, or hydrosoluble compounds. The litter from both elevated and ambient carbon dioxide-treated plants was sterilised and inoculated with known decomposer organisms, and then incubated. The authors divided their results into two basic periods during the incubation. During the first period (2–3 weeks), litter quality effects dominated results: untreated (ambient carbon dioxide) leaves had greater respiration (released more carbon as carbon dioxide) and nitrogen mineralisation (nitrogen released as dissolved organic nitrogen) than treated (elevated carbon dioxide) leaves. During the second period, respiration in the treated litter was greater than in untreated litter owing to differences in organism composition (increased presence of white-rot fungi which are better able to use lignin and aromatic polymer-protein as sources of nitrogen). The results, which are far more detailed than can be adequately summarised here, indicated that decomposition is not merely a function of traditional initial parameters of litter quality such as carbon:nitrogen and lignin:nitrogen ratios, but also of the dynamics of microbial populations as they develop on the litter substrate. In practical terms, the results strongly indicate the need for actual incubation studies of carbon dioxide-enriched litter as well as simple evaluations of initial litter quality.

Nambiar & Fife (1991) suggested that translocation in roots prior to senescence is virtually nil, so that changes in root litter quality would be directly manifested in root decomposition rates. Coupled with the often-observed disproportionate increase in root biomass with elevated carbon dioxide (Norby, O'Neill & Luxmoore 1986; Norby, Pastor & Melillo 1986; Luxmoore *et al.* 1986; Higginbotham *et al.* 1985), one might expect an increase in soil carbon via root turnover under an elevated carbon dioxide environment.

A question regarding direct carbon dioxide effects that has not yet been addressed is, what effects have increases since the industrial revolution (approximately 50% increase) already had on plant growth, nutrient cycling, and soil carbon accumulation rates? All studies to date on effects of carbon dioxide have involved increases from current levels; it would be very instructive to complement these studies with some in which carbon dioxide was brought to pre-industrial levels as well.

TOOLS FOR SOIL CARBON RESEARCH

One of the most immediate needs in the way of basic tools for soil carbon research is a soil carbon fractionation method. Both chemical (Schnitzer & Schuppli 1989) and physical (Young & Spycher 1979; Anderson *et al.* 1981; Tiessen & Stewart 1983) methods are available but have not been widely tested in forest soils. Recent developments combining physical fractionation with ^{13}C NMR analyses apparently hold promise (J. Baldock, pers. comm.).

It would be extremely useful if instantaneous soil carbon accumulation rates could be estimated from soil carbon budgets. This would allow rapid assessments of the effects of various treatments on soil carbon. However, there is a major problem with obtaining soil carbon budgets—separation of root from soil respiration. The methods currently available for separation of soil and root respiration involve substantial physical disturbance such as litter removal (Johnson *et al.* 1975; Ewell *et al.* 1987a, b) or the incubation of excised samples in the laboratory (Edwards 1975).

Raich & Nadelhoffer (1989) offered a way of estimating root respiration by subtracting litterfall from total soil respiration, assuming litter and soil carbon accumulation are either negligible or measurable. Rates of soil carbon accumulation are, in fact, typically smaller than typical rates of litterfall or soil respiration: Schlesinger (1990) gave an overall long-term soil carbon accumulation of $2.4 \pm 0.7 \text{ g C/m}^2/\text{yr}$ compared to typical litterfall rates of 70–500 $\text{g C/m}^2/\text{yr}$ and typical soil respiration rates of 330–1600 $\text{g C/m}^2/\text{yr}$ (Raich & Nadelhoffer 1989). However, in that negligible soil carbon accumulation is inherently assumed, the Raich & Nadelhoffer (1989) model is, by definition, not useful for estimating soil carbon accumulation rates. Also, in ecosystems with rapidly accumulating forest floors, litter accumulation rates (including woody litter) can be of the order of 95 $\text{g C/m}^2/\text{yr}$ (e.g., Turner 1981), making the assumption of negligible soil and litter carbon questionable, if not invalid. (Raich and Nadelhoffer did not take woody litter into account in their model.)

Measurements of total soil plus root respiration are most often done by either static or dynamic chamber methods (Edwards 1975; Johnson 1975; Ewell *et al.* 1987a, b). There is an alternative, however, that deserves further investigation, and which may be of some use in separating soil and root respiration—the soil carbon dioxide profile method (de Jong & Schappert 1972; de Jong *et al.* 1979). This involves measurement of soil pCO_2 and calculation of flux from the diffusion equation:

$$q = -D_s \frac{dc}{dz} \quad (4)$$

where q = flux ($\text{g C/m}^2/\text{hr}$)
 D_s = diffusion coefficient (cm^2/s)
 c = soil carbon dioxide concentration (g/cm^3)
 z = depth (cm).

D_s can be calculated from the diffusion coefficient of carbon dioxide in air (D_a) and effective porosity (p , or fraction of air-filled pore space) (Wesseling 1962):

$$D_s = D_a(0.9p - 0.1) \quad (5)$$

This method involves the assumption that carbon dioxide evolution is a diffusion process, of course, and neglects “pumping” of soil gas during rain events. It offers the decided

advantage of allowing calculation of carbon dioxide production and fluxes within the soil profile, as long as $p\text{CO}_2$, porosity, and water content data are available.

De Jong *et al.* (1979) compared the static and dynamic chamber methods, the soil $p\text{CO}_2$ method, and the micrometeorological method of estimating soil carbon dioxide flux in a prairie soil. They found that the $p\text{CO}_2$ profile method gave considerably higher results than either of the chamber techniques, but could not offer a satisfactory explanation for the differences. They called for further comparisons of these methods.

CONCLUSIONS

Some (but by no means all) of the research needs in forest soil carbon can be summarised as follows.

- A co-ordinated multi-site study of the effects of harvesting and other management practices (e.g., nitrogen-fixers, fertiliser) on soil carbon, employing strict common sampling protocols, is needed to establish whether these practices have any consistent effect on soil carbon.
- A combination of field gradient studies and laboratory and field process-level studies is needed to test current hypotheses and models as to the effects of climate change on soil carbon and related processes (i.e., leaching, acidification).
- Basic research on the factors controlling soil $p\text{CO}_2$ and tree responses to variations in soil $p\text{CO}_2$ is needed, both in the context of soil carbon research and in order to fill a basic knowledge gap in our understanding of forest ecosystems.
- Research is needed to determine the effects of both increased and decreased (to pre-industrial levels) carbon dioxide on plant nutrient uptake, litter quality (root and leaf), and decomposition rates. It is vital to determine decomposition in addition to litter quality effects in that the latter take the effects of microbial community changes into account.

Research is also needed in order to develop some basic tools for further soil carbon research, namely:

- A meaningful soil carbon fractionation method
- A realistic method for separation of soil and root respiration so that soil carbon budgets can be constructed
- Further comparisons of soil respiration methods (chambers *v.* $p\text{CO}_2$ profiles).

ACKNOWLEDGMENTS

Research supported by (1) the National Council of the Paper Industry for Air and Stream Improvement, Inc; (2) the Electric Power Research Institute (RP 3041), the Desert Research Institute, and the Nevada Agricultural Experiment Station, College of Agriculture, University of Nevada, Reno.

REFERENCES

- AMUNDSON, R.G.; CHADWICK, O.A.; SOWERS, J.M. 1990: A comparison of soil climate and biological activity along an elevational gradient in the eastern Mojave Desert. *Oecologia* 80: 395–400.

- ANDERSON, D.W.; SAGGAR, S.; BETTANY, J.R.; STEWART, J.W.B. 1981: Particle size fractions and their use in studies of soil organic matter. I: The nature and distribution of forms of carbon, nitrogen, and sulfur. *Soil Science Society of America Journal* 45: 767–72.
- ANON. 1992: Soil-warming experiments in global change research. Report of a Workshop held in Woods Hole, Massachusetts, September 27–28, 1991. National Science Foundation, Washington, D.C.
- BARON, J.J.; GORSKI, S.F. 1986: Response of eggplant to a root environment enriched with CO₂. *HortScience* 21: 495–8.
- BOLIN, B. 1977: Changes of land biota and their importance for the carbon cycle. *Science* 196: 613–5.
- BOLLEN, W.B. 1974: Soil microbes. Pp. B-1–B-41 in Cramer, O.P. (Ed.) Environmental effects of forest residues management. *USDA Forest Service General Technical Report PNW-24*.
- BROECKER, W.S.; PENG, T.-H. 1992: Interhemispheric transport of carbon dioxide by ocean transport. *Nature* 356: 587–92.
- BROWN, K.R. 1991: Carbon dioxide enrichment accelerates the decline in nutrient status and relative growth rate of *Populus tremuloides* Michx. seedlings. *Tree Physiology* 8: 161–73.
- CAMPAGNA, M.A.; MARGOLIS, H.A. 1989: Influence of short-term CO₂ enrichment on growth, allocation patterns, and biochemistry of black spruce seedlings at different stages of development. *Canadian Journal of Forest Research* 19: 773–82.
- CHEN, Y.; AVIAD, T. 1990: Effects of humic substances on plant growth. Pp. 161–86 in McCarthy, P.; Clapp, C.E.; Malcolm, R.L.; Bloom, P.R. (Ed.) "Humic Substances in Soil and Crop Sciences: Selected Readings". American Society of Agronomy, Madison, Wisconsin.
- COUTEAUX, M.-M.; MOUSSEAU, M.; CELKERIER, M.-L.; BOTTNER, P. 1991: Increased atmospheric CO₂ and litter quality decomposition of sweet chestnut litter with animal food webs of different complexities. *Oikos* 61: 54–64.
- de JONG, E.; SCHAPPERT, H.J.V. 1972: Calculation of soil respiration and activity from CO₂ profiles in the soil. *Soil Science* 119: 328–33.
- de JONG, E.; REDMANN, R.E.; RIPLEY, E.A. 1979: A comparison of methods to measure soil respiration. *Soil Science* 127: 300–6.
- EDWARDS, N.T. 1975: Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. *Soil Science Society of America Proceedings* 39: 361–5.
- ELLIS, R.C.; GRALEY, A.M. 1983: Gains and losses in soil nutrients associated with harvesting and burning eucalypt rainforest. *Plant and Soil* 74: 437–50.
- EWELL, K.C.; CROPPER, W.P.; GHOLZ, H.L. 1987a: Soil CO₂ evolution in slash pine plantations. I. Changes through time. *Canadian Journal of Forest Research* 17: 325–9.
- 1987b. Soil CO₂ evolution in slash pine plantations. II. Importance of root respiration. *Canadian Journal of Forest Research* 17: 330–3.
- HIGGINBOTHAM, K.O.; MAYO, J.M.; L'HIRONDELLE, S.; KRSTOFIAK, D.K. 1985: Physiological ecology of lodgepole pine (*Pinus contorta*) in an enriched CO₂ environment. *Canadian Journal of Forest Research* 15: 417–21.
- HOUGHTON, R.A.; HOBBIIE, J.E.; MELILLO, J.M.; MOORE, B.; PETERSON, B.J.; SHAVER, G.R.; WOODWELL, G.M. 1983: Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO₂ to the atmosphere. *Ecological Monographs* 53: 235–62.
- JENNY, H.; GESSEL, S.P.; BINGHAM, F.T. 1949: Comparative study of decomposition rate of organic matter in temperate and tropical regions. *Soil Science* 68: 419–32.
- JOHNSON, C.E.; JOHNSON, A.H.; HUNTINGTON, T.G.; SICCAMI, T.G. 1991: Whole-tree clear-cutting effects on soil horizons and organic matter pools. *Soil Science Society of America Journal* 55: 497–502.
- JOHNSON, D.W. 1975: Processes of elemental transfer in some tropical, temperate, alpine, and northern forest soils: Factors influencing the availability and mobility of major leaching agents. Ph.D. Thesis, University of Washington, Seattle.

- 1992: The effects of forest management on soil carbon storage. *Water, Air, and Soil Pollution* 64: 83–120.
- JOHNSON, D.W.; COLE, D.W.; GESSEL, S.P. 1975: Processes of nutrient transfer in a tropical rain forest. *Biotropica* 7(3): 208–15.
- JOHNSON, D.W.; COLE, D.W.; GESSEL, S.P.; SINGER, M.J.; MINDEN, R.V. 1977: Carbonic acid leaching in a tropical, temperate, subalpine, and northern forest soil. *Arctic and Alpine Research* 9: 329–43.
- JOHNSON, D.W.; VAN MIEGROET, H.; LINDBERG, S.E.; HARRISON, R.B.; TODD, D.E. 1991: Nutrient cycling in red spruce forests of the Great Smoky Mountains. *Canadian Journal of Forest Research* 21: 769–87.
- LUGO, A.E. 1992: The search for carbon sinks in the tropics. *Water, Air, and Soil Pollution* 64: 3–9.
- LUXMOORE, R.J.; O'NEILL, E.G.; ELLS, J.M.; ROGERS, H.H. 1986: Nutrient uptake and growth responses of Virginia pine to elevated atmospheric carbon dioxide. *Journal of Environmental Quality* 15: 244–51.
- MANN, L.K. 1986: Changes in soil carbon storage after cultivation. *Soil Science* 142: 279–88.
- MASER, C.; TARRANT, R.F.; TRAPPE, J.M.; FRANKLIN, J.F. (Ed.) 1988: From the forest to the sea: A story of fallen trees. *USDA Forest Service General Technical Report PNW-GTR-229*.
- MAUNEY, J.R.; HENDRIX, D.L. 1988: Responses of glasshouse grown cotton to irrigation with carbon dioxide-saturated water. *Crop Science* 28: 835–8.
- MCCOLL, J.G.; COLE, D.W. 1968: A mechanism of cation transport in a forest soil. *Northwest Science* 42: 132–40.
- MEETENMEYER, V. 1978: Microclimate and lignin control of litter decomposition rates. *Ecology* 59: 465–72.
- MELILLO, J.M.; ABER, J.; MURATORE, J.F. 1982: Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621–6.
- MORTLAND, M.M.; WOLCOTT, A.R. 1965: Sorption of inorganic nitrogen compounds by soil materials. Pp. 150–97 in Bartholomew, W.V.; Clark, F.E. (Ed.) "Soil Nitrogen". *American Society of Agronomy, Madison, Wisconsin, Agronomy* 10.
- NAMBIAR, E.K.S.; FIFE, D.N. 1991: Nutrient translocation in temperate conifers. *Tree Physiology* 9: 185–208.
- NORBY, R.J.; O'NEILL, E.G.; LUXMOORE, R.J. 1986: Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiology* 82: 83–9.
- NORBY, R.J.; PASTOR, J.; MELILLO, J.M. 1986: Carbon-nitrogen interactions in CO₂-enriched white oak: Physiological and long-term perspectives. *Tree Physiology* 2: 233–41.
- OADES, J.M. 1988: The retention of organic matter in soils. *Biogeochemistry* 5: 35–70.
- OLSON, J.S. 1963: Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44: 322–31.
- PAUL, E.A.; CLARK, F.E. 1989: "Soil Microbiology and Biochemistry". Academic Press, New York.
- POST, W.M.; EMANUEL, W.R.; ZINKE, P.J.; STANGENBERGER, A.G. 1982: Soil carbon pools and world life zones. *Nature* 298: 156–9.
- POST, W.M.; PASTOR, J.; ZINKE, P.J.; STANGENBERGER, A.G. 1985: Global patterns of soil nitrogen storage. *Nature* 317: 613–6.
- POST, W.M.; PENG, T.-H.; EMMANUEL, W.R.; KING, A.W.; DALE, V.H.; DEANGELIS, D.L. 1990: The global carbon cycle. *American Scientist* 78: 310–26.
- RAICH, J.W.; NADELHOFFER, K.J. 1989: Belowground carbon allocation in forest ecosystems: Global trends. *Ecology* 70: 1346–54.
- SCHLESINGER, W.H. 1990: Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348: 232–4.

- SCHNITZER, M.; SCHUPPLI, P. 1989: Method for the sequential extraction of organic matter from soils and soil fractions. *Soil Science Society of America Journal* 53: 1418–24.
- SINGH, B.R. 1984: Sulfate adsorption by acid forest soils. 4. Kinetics and effects of temperature and moisture. *Soil Science* 138: 346–53.
- STRAIN, B.R. 1985: Physiological and ecological controls on carbon sequestering in terrestrial ecosystems. *Biogeochemistry* 1: 219–32.
- STOLWIJK, J.A.J.; THIMANN, K.V. 1957: On the uptake of carbon dioxide and bicarbonate by roots, and its influence on growth. *Plant Physiology* 32: 513–20.
- TANS, P.P.; FUNG, I.Y.; TAKAHASHI, T. 1990: Observational constraints on the global atmospheric CO₂ budget. *Science* 247: 1431–8.
- TIESSEN, H.; STEWART, J.W.B. 1983: Particle size fractions and their use in studies of soil organic matter: II. Cultivation effects. *Soil Science Society of America Journal* 47: 509–14.
- TURNER, J. 1981: Nutrient cycling in an age sequence of western Washington Douglas-fir stands. *Annals of Botany* 48: 159–69.
- ULRICH, B. 1980: Production and consumption of hydrogen ions in the ecosphere. Pp. 255–82 in Hutchinson, T.C.; Havas, M. (Ed.) "Effects of Acid Precipitation on Terrestrial Ecosystems". Plenum Press, New York.
- VAN CLEVE, K.; OECHEL, W.D.; HOM, J.L. 1990: Response of black spruce (*Picea mariana*) ecosystems to soil temperature modifications in interior Alaska. *Canadian Journal of Forest Research* 20: 291–302.
- VITOUSEK, P.M.; MATSON, P.A. 1991: Gradient analysis of ecosystems. Pp. 287–98 in Cole, J.; Lovett, G.; Findlay, S. (Ed.) "Comparative Analyses of Ecosystems". Springer-Verlag, New York, Heidelberg, London.
- WATSON, A. 1992: Conveying that sinking feeling. *Nature* 356: 561.
- WESSELING, J. 1962: Some solutions of the steady state diffusion of carbon dioxide through soils. *Netherlands Journal of Agricultural Science* 10: 109–17.
- WOODWELL, G.M.; WHITTAKER, R.H.; REINERS, W.A.; LIKENS, G.E.; DELWICHE, C.C.; BOTKIN, D.B. 1978: The biota of the world carbon budget. *Science* 199: 141–6.
- YOUNG, J.L.; SPYCHER, G. 1979: Water-dispersible organic-mineral particles: I. Carbon and nitrogen distribution. *Soil Science Society of America Journal* 43: 324–8.