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Additional carbon sequestration following repeated urea fertilization of second-growth Douglas-fir stands in western Washington

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Abstract

We examined whether N fertilization of Douglas-fir (*Psuedotsuga menziesii* (Mirb.)) plantations in western Washington State could affect C sequestration in both the vegetation and soils. Three sites, which received a total of 896–1120 kg ha^{-1} over a 16-year-period, were compared with adjacent unfertilized control sites. Carbon contained in the soil, understory vegetation and snags was measured in 1993. Since the tree biomass started at different levels (treated versus controls), C biomass and increment was analyzed dynamically from 1969–1993. There was 6.2% more C (8 Mg ha^{-1}) stored in the sum of non-tree components, but the difference was not statistically significant. The N treatment added an average of 26.7 Mg ha^{-1} (significant at 0.01 level) to the live tree component. On average, the entire forest system of the fertilized plots added 34.7 Mg C ha^{-1}. When considered individually, there was no significant difference between the amount of C stored in the snags, understory vegetation and all sampled soil horizons and depths to 85 cm in the control and fertilized plots. However, the urea-treated plots did contain on average 34% more C in the O horizon (20 versus 15 Mg of C ha^{-1}). A large portion of the soil C was found in deeper horizons. When sampling to a depth of 85 cm, 75% of soil C was found below the A horizon and 40% below 25 cm. This result illustrates how failing to sample below surface horizons can cause soil C to be underestimated in these forest ecosystems. However, these soil layers changed little in C concentration due to the treatment. This study suggests that N fertilization of commercial forests in western Washington could increase C stored in these forest ecosystems, though the absolute effect of widespread fertilization on stands of varying properties was not evaluated in this study. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Forest fertilization; Urea; Carbon sequestration; Douglas-fir

1. Introduction

Human activities during the last century, including the burning of fossil fuels and changes in land use patterns, have raised atmospheric CO_2 levels, a factor implicated in accelerated global climate change (Post et al., 1990). Developing mechanisms for slowing this increase has been a goal of both policy makers and scientists in recent years. It has been suggested that by raising the productivity of forest systems, more C may be removed from the atmosphere and stored in the terrestrial system (Sedjo, 1989; Johnson and Kern,

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1990; Smith et al., 1993; Dixon et al., 1994). Nitrogen fertilization has been found to commonly increase the productivity of commercial Douglas-fir stands in the coastal Pacific Northwest (Barclay and Brix, 1985; Stegemoeller and Chappell, 1990), potentially increasing C storage in aboveground tree biomass. However, it is not known how the addition of N into the total ecosystem will affect the C storage or decomposition rates of the soil and the forest floor. An increase in aboveground productivity of forests might increase inputs of C to the soil; however, N fertilization may also increase the soil CO_2 efflux due to the narrowing of the C:N ratio and increased decomposition (Harrison et al., 1996) or lowered C allocation to root systems. Sequestration of C in soils is important because it may remain for long time periods while C sequestered in live trees might remain for a shorter time period depending on land use (Wilding et al., 1983; Harrison et al., 1994).

A review by Johnson (1992) cited several studies which observed increases in tree biomass and soil C after N fertilization. Van Cleve and Moore (1978) found increases in tree growth, soil organic matter, and soil biological activity after the addition of N and P to quaking aspen (*Populus tremuloides* Michx.) stands in Alaska. They also observed an increase in soil biological activity attributed to increased soil organic matter and higher levels of soil N and P. Nohrstedt et al. (1989) found increases of 10–26% in absolute amount of C per square meter of forest floor and stand productivity after N fertilization of a Swedish pine forest. Baker et al. (1986) compared the growth of *Pinus radiata* D. Don on sand dunes in New Zealand when a mixed fertilizer (including N, P, K, S, Ca and Mg) was added, and found that the fertilized area had higher soil C. Others have found no increase in soil C due to the presence of N fixing species (Paschke et al., 1989) or after N fertilization (Harding and Jokela, 1994). Currently there have been no published studies comparing the C sequestration in the vegetation, detritus and soils of paired urea-fertilized and unfertilized Douglas-fir stands.

The purpose of this study was: (1) to quantify C sequestered in 62–69-year-old control and urea-fertilized Douglas-fir stands, and (2) to determine whether urea-fertilized stands sequestered more C in live trees, snags, understory vegetation, forest floor, and mineral soil than corresponding adjacent unfertilized Douglas-fir stands.

2. Materials and methods

2.1. Site description

In 1969 the Regional Forest Nutritional Research Project (RFNRP) established studies in the Pacific Northwest to evaluate the response of coastal Douglas-fir to urea-N fertilization. Our study utilized one control and one fertilized plot at three of the RFNRP sites located in the Cascade Mountains of western Washington. These stands were 30–40 years old when first fertilized, and the studies were designed to see if such stands would respond to fertilization. Though plots that included thinning treatments were included in the original studies, only unthinned stands were utilized in this study.

The soil types selected include three important soils used for forest production. Sites 1 and 2 were in the Cedar River watershed, approximately 60 km SE of Seattle. Both sites contained low fertility outwash soils common in western Washington. Site 3 was located near Skykomish, about 75 km NE of Seattle. It also contained low fertility soils, but with parent material of volcanic ash.

All of the fertilized plots received 448 kg N ha^{-1} as urea in 1969, and 224 kg N ha^{-1} in 1977 and 1981. The fertilized plots in Site 3 received as additional 224 kg ha^{-1} in 1985. Thus, Sites 1 and 2 received a total of 896 kg ha^{-1} of N over 12 years and Site 3 received a total of 1120 kg ha^{-1} of N over 16 years. Tables 1 and 2 contain specific site and soil information for these sites.

2.2. Determination of soil bulk density and gravel content

Because of the rocky nature of the soils at Sites 1 and 2, soil bulk density could not be accurately determined using standard soil core or clod methods. Instead a method, similar to the one described by Huntington et al. (1989), was used at all sites. Three soil pits (50 cm×50 cm×85 cm deep) for each site and treatment were hand excavated and measured. The O and A horizons were individually removed and all

Table 1
Site characteristics in 1993

Parameters	Site 1 (RFNRP #1)	Site 2 (RFNRP #5)	Site 3 (RFNRP #43)
	Control/treated	Control/treated	Control/treated
Age	67	62	69
Trees per ha	725/925	1350/1250	2125/1300
Quadratic mean dbh (cm)[a]	37/36	26/30	22/28
Total height (m)[b]	37/39	32/36	33/38
Basal area (m^2 ha^{-1})	52/61	51/58	75/79
Elevation (m)	344	274	457
Mean annual precipitation (mm)	2032	1778	2667
Soil series	Alderwood	Everett	Teneriffe
Location	S8 T22N R8E 121°45′W, 47°40′N	S22 T22N R7E 121°45′W, 47°40′N	S26 T26N R12E 121°15′W, 47°40′N

[a] Calculated by summing squares of DBH, the taking square root.
[b] Average total height of tallest 99 trees per hectare.

material brought back to the soil analysis lab at the University of Washington. Soil E horizons were generally not present or very thin and bulked into the A horizon. These soil genetic horizons were separated individually since they had abrupt boundaries and the O and A are typically high in C concentration.

The B and C horizons were excavated by depth rather than by genetic horizon using the following sampling depths: the top of the B horizon to 25 cm, 25–55 cm, and 55–85 cm (Fig. 1). After each measured layer was excavated, all soil material was weighed in the field and a representative 7 l subsample was weighed in the field and brought back to the laboratory. Soil moisture content, percent coarse particles and soil bulk density were determined. After excavation of each horizon or layer, the volume was

Table 2
Profile descriptions of soils at study sites

Horizon	Depth (cm) in control	Depth (cm) in fertilized	Description
Site 1. Inceptisol, Alderwood, dystric entic Durochrept, slope 5% (SCS, 1973)			
O	3.25–0	2.75–0	Fresh and decomposed moss, needles, twigs, logs, etc.
A	0–4.75	0–4.00	10-year 2/3, gravelly loam
Bw1	4.75–18	4.00–18	10-year 3/3, very gravelly sandy loam
Bw2	18–48	18–48	10-year 3/4, very gravelly sandy loam
BC	48–85	48-depth	10-year 4/4, very gravelly, coarse OS?
Site 2. Inceptisol, Everett, dystric Xerochrept, slope 10% (SCS, 1973)			
O	2.75–0	3.00–0	Fresh and decomposed moss, needles, twigs, logs, etc.
A	0–2.75	0–2.25	10-year 2/2, loam
Bw	2.75–25	2.25–25	10-year 3/3, gravelly sandy loam
BC	25–85	25–85	10-year 3/4, very gravelly sandy loam
Site 3. Spodosol, Teneriffe, typic Haplorthod, slope 10% (SCS, 1992)			
O	5.25–0	2.25–0	Fresh and decomposed moss, needles, twigs, logs, etc.
A	0–1.50	0–2.00	7.5-year 4/2, fine silt
E	1.5–7.25	2.00–4.00	7.5-year 6/2, fine silt
Bw1	7.25–34	4.00–34	10-year 4/6, sandy loam
Bw2	34–59	34–59	10-year 3/4, loamy sand
BC	59–85	59–85	10-year 4/4, loamy sand

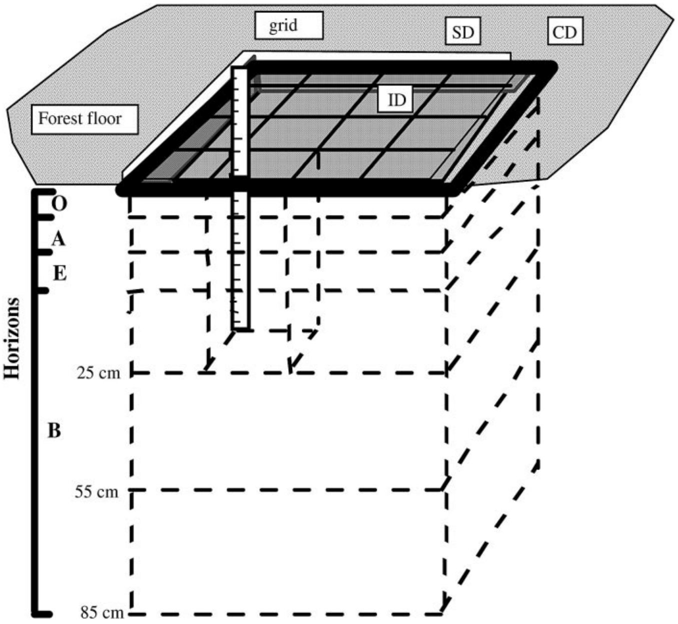

Fig. 1. Diagram of the pit excavated to determine soil bulk density. Individual horizons and depths were removed. Twenty depth measurements at grid corners were used to estimate horizon volumes.

estimated by placing a grid with 16 12.5 cm^2 squares over the pit and depths measured at the corners of each square (Fig. 1). The volume of the horizon was determined by applying Eq. (1) to the measured depths (corner depth=CD, side depths=SD, interior depths=ID).

$$\frac{(\mathrm{CD}\times 1)+(\mathrm{SD}\times 2)+(\mathrm{ID}\times 4)\,\mathrm{cm}}{64}\times(125\,\mathrm{cm})^2 \tag{1}$$

When large rocks protruded from the pit wall, they and the material below them were not excavated and these weights and volumes were not included in subsequent calculations.

Soil material was dried at 70°C to constant weight and the dry soil weight used to determine bulk density. A separate study determined that drying the soil at 70°C was identical to drying at 105°C. All but the O horizon material were sieved to 2 mm and weighed again to determine the <2 mm fraction. Organic material which did not pass through the 2 mm sieve was combined with the <2 mm soil material.

2.3. Carbon concentrations and contents

An equal amount of material from the entire depth of each horizon or layer of each pit was collected and oven dried at 70°C to constant weight. Soil O horizons were then ground in a Wiley mill using a 1 mm mesh. All other samples were sieved to 2 mm and coarse tree roots removed because they were included in the tree biomass equations calculated separately. The <2 mm material was finely ground with a mortar and pestle and analyzed for total C using a CHN analyzer (Perkin–Elmer 2400, Norwalk, CT). A separate study showed that these humid-region soils did not contain carbonate, thus the C in these soils can be assumed to be of organic origin.

2.4. Understory C

Six understory samples were taken at each plot in July 1993. A metal frame 1 m×1 m was placed randomly on the forest floor and all understory plants clipped at the base. Roots were not sampled as they were included in the soil samples. Samples were oven dried at 70°C to constant weight and ground to 1 mm using a Wiley mill. Samples were analyzed for C concentration using a CHN analyzer (Perkin–Elmer 2400, Norwalk, CT).

2.5. Tree and snag C

The stem diameter at 1.3 m of all live trees (DBH) on each plot was measured in 1969, 1977, 1985 and 1993, and tree biomass, including coarse roots and foliage, was estimated using allometric equations developed by Gholz et al. (1979). The plots contained primarily Douglas-fir with some western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). When allometric equations for the western hemlock and western redcedar of a particular size class were not available, the equations for Douglas-fir of that size were used instead.

The estimates of biomass in bark, bolewood, branches (live and dead), snags, foliage and roots generated from the equations of Gholz et al. (1979) were then multiplied by the average C concentrations of six samples of each tissue collected from these plots in September 1999. The C concentrations of these samples ranged from 0.481–0.546 g C g^{-1}, with an average C concentration of 0.509 g C g^{-1}. These results compared well to the data for overall average C concentrations (0.512 g C g^{-1}) of Douglas-fir trees in the Pacific Coast and Rocky mountains region (Birdsey, 1992).

Other studies of forest fertilization have shown differential increases in foliage and branches compared to the bole (Jokela et al., 1989; Chappell and Bennett, 1993; Mitchell et al., 1996). The equations of Mitchell et al. (1996) were used to calculate biomass estimates for fertilized and unfertilized stands; however, there was only an estimate of 0.3% difference in total biomass due to differential C allocation. Since Mitchell et al. (1996) measured young stands (24 year old), with smaller average diameters than the stands in this study, the limits of the equations were exceeded and the equations of Gholz et al. (1979) were used for this study. Thus, no effect of differences in C allocation in plant parts due to N fertilization were accounted for in this study.

The stands were undergoing considerable self-thinning due to high stocking, and nitrogen fertilization would be expected to increase mortality. Thus, measurement of snags was considered to be very important in this study. All snags were measured in 1993. Unfortunately, snag data was not available for years previous to 1993. Because no allometric equations exist for the calculation of snag biomass, an alternative method was used based on the allometric equations for live trees and snag density. The DBH of each snag was measured and its decay stage recorded (Maser et al., 1984). The live tree allometric equations were used to calculate a tree biomass. If the decay class of the snag was higher than 3, then live branches were not included. If the decay class was greater than 4, then live and dead branches as well as bark were not included and the biomass estimate was adjusted for the lower density of a dead tree.

The biomass was multiplied by the estimated density of a snag (Spies et al., 1988) and divided by the density of a live tree (Hartman et al., 1976). The adjusted biomass estimate was then multiplied by the average C concentration of live Douglas-fir used in the live biomass estimates because the C concentration of decaying wood has been found to remain fairly constant (Sollins et al., 1987).

2.6. Statistical analysis

The data from the three soil pits in each plot were averaged, as were the understory sample data from each plot. Estimates of differences in live-tree additional C increments due to N fertilization were calculated according to Eq. (2), and were compared for 1993.

$$\begin{aligned}\text{C increment} = {} & (\text{fertilized}_{1993} - \text{control}_{1993}) \\ & - (\text{fertilized}_{1969} - \text{control}_{1969}) \qquad (2)\end{aligned}$$

This gave a sample size of n=3 for each system component. A paired Student's *t*-test analysis was performed on the data (SYSTAT, 1990).

3. Results and discussion

When compared to the control plots, the non-tree pools in the fertilized plots contained on average 8 Mg ha^{-1} more C (Table 3); however, results are not statistically significant for understory vegetation, snags, or any combination of soil horizons or depths. The C content in the understory vegetation was about

Table 3
Per hectare C contents of non-tree components.

Component	Treatment ($\mathrm{Mg\ ha^{-1}}$)		
	Control	N fertilized	Difference[a]
O horizon	15	20	5
A Horizon	12	11	−1
0–25 cm	39	41	2
25–55 cm	24	22	−2
55–85 cm	15	14	−1
Understory	5	5	0
Snag	13	18	5
Sum of components	123	131	8

[a] Difference=N fertilized−control.

the same in both treatments, $5\ \mathrm{Mg\ ha^{-1}}$. There was 35% more C in snags in fertilized plots. The O horizon and 0–25 cm depth in the fertilized plots contained 33 and 5% more C, respectively, while the A horizon, 25–55, and 55–85 cm depths in the control plots contained 8, 8 and 7% less carbon, respectively, than the fertilized plots.

A dynamic analysis of C increase in trees was developed using previous stem measurements and the biomass estimation equations of Gholz et al. (1979). As is typical of studies of natural stands, initial stand stocking was not the same. Control plots had $11.7\ \mathrm{Mg\ ha^{-1}}$ less C than N fertilized, before any N was added. However, the periodic increment increased in all three stands due to the N treatment, resulting in 24.7, 23.7 and $31.6\ \mathrm{Mg\ ha^{-1}}$ additional C in Site 1, 2 and 3, respectively, for an average of $26.7\ \mathrm{Mg\ ha^{-1}}$ additional C from the 1969–1993 growth period (Table 4). Differences continued to increase during each 8-year measurement period. The total average amounts of $200\ \mathrm{Mg\ C\ ha^{-1}}$ for the whole-tree estimate would equate to $394\ \mathrm{Mg\ ha^{-1}}$ of dry organic matter in the total-tree, and $331\ \mathrm{Mg\ ha^{-1}}$ in the above-ground portion only, using the biomass equations of Gholz et al. (1979). Thus, our estimates of 62–69-year-old stands are comparable at 13% higher than the organic matter estimates of $294\ \mathrm{Mg\ ha^{-1}}$ for the above-ground only portion of a 73-year-old Douglas-fir stand (Turner and Singer, 1976).

Results of this study compare with those of Harding and Jokela (1994) who found no increase in soil organic matter after a single N application produced increased aboveground productivity in a Florida forest. However, our findings contrast with several studies which found statistically significant increases in soil C after N fertilization (Van Cleve and Moore, 1978; Baker et al., 1986; Nohrstedt et al., 1989). Two of three sites showed an increase in O horizon C after fertilization, however, the 33% increase in our study was not statistically significant (0.05 level) due to high variation among sites.

Seventy-five percent of soil C to 85 cm was found below the A horizon and 40% was found below 25 cm (Table 3). This result demonstrates how failing to sample below the surface soil horizons may give underestimates of soil C on an area basis. A study by Hammer et al. (1995) found that subsurface soil C (sampling depth ranged from 94–191 cm) exceeded that of surface C in a forest-prairie ecotone. Stone et al. (1993) also found that C stored in Florida Spodosols was commonly underestimated, due largely to shallow sampling. However, results of this study indicate that N fertilization did not significantly change that underground C pool.

Table 4
Increase in biomass in trees vs. time and treatment ($\mathrm{Mg\ C\ ha^{-1}}$)

Growth year	Site 1			Site 2			Site 3			Average		
	Control	N fertilized	N increased[a]	Control	N fertilized	N increased[a]	Control	N fertilized	N increased[a]	Control	N fertilized	N increased[a]
1969	175.4	19.12		108.9	124.5		121.3	125.0		135.2	146.9	
1977	207.5	230.7	7.4	144.2	171.7	11.9	143.0	155.1	8.4	164.9	185.8	9.2
1985	226.3	255.4	13.3	168.0	199.1	15.6	166.7	191.2	20.7	187.0	215.2	16.5
1993	228.5	269.0	24.7	193.4	232.7	23.7	178.8	214.1	31.6	200.2	238.6	26.7

[a] Calculated as $(\mathrm{fertilized}_{\mathrm{year}} - \mathrm{control}_{\mathrm{year}}) - (\mathrm{fertilized}_{1969} - \mathrm{control}_{1969})$.

Though further study is necessary to evaluate the implications of N fertilization over the entire area of the Douglas-fir zone, additional C sequestration may be an additional benefit of widespread N fertilization in additional to higher production of commercial volume.

4. Conclusions

1. Fertilization with N increased C stored in three 62–69-years-old Douglas-fir forests by an average of 34.8 Mg ha^{-1}.
2. The addition of urea–N fertilizer did not significantly change the individual C content of the understory vegetation or any of the sampled soil horizons or depths, but did significantly increase ($p=0.01$) the increase in C increment of the live-tree component.
3. A large portion of the total and soil C was found below the surface soil horizons.

References

Baker, T.G., Oliver, G.R., Hodgkiss, P.D., 1986. Distribution and cycling of nutrients in *Pinus radiata* as affected by past lupine growth and fertiliser. For. Ecol. Manage. 17, 169–187.

Barclay, H.J., Brix, H., 1985. Effects of high levels of fertilization with urea on growth of thinned and unthinned Douglas-fir stands. Can. J. For. Res. 15, 730–733.

Birdsey, R.A., 1992. Carbon storage accumulation in United States forest ecosystems. General Technical Report WO-59. US Department of Agriculture, Forest Service, Global Change Research, Northeastern Forest Experiment Station, Radnor, PA.

Chappell, H.N., Bennett, W.S., 1993. Young true-fir trees response to Nitrogen fertilization in western Washington and Oregon. Soil Sci. Soc. Am. J. 57, 834–838.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Lab, Oregon State University, Corvallis, OR.

Hammer, R.D., Henderson, G.S., Odawatta, R.P., Brandt, D.K., 1995. Soil organic carbon in the Missouri forest-prairie Ecotone. In: McFee, W.W., Kelly, J.M. (Eds.), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Madison, WI. pp. 201–232.

Harding, R.B., Jokela, E.J., 1994. Long-term effects of forest fertilization on site organic matter and nutrients. Soil Sci. Am. J. 58, 216–221.

Harrison, R.B., Dongsen, X., Henry, C.L., Cole, Dale W., 1994. Long-term effects of heavy applications of biosolids to coarse-textured soils: nutrients and general soil properties. For. Ecol. Manage. 66, 165–177.

Harrison, R.B., Gessel, S.P., Zabowski, D., Henry, C.L., Xue, D., Cole, D.W., Compton, J.E., 1996. Mechanisms of negative impacts of three forest treatments on nutrient availability. Soil Sci. Soc. Am. J. 60, 1622–1628.

Hartman, D.A., Atkinson, W.A., Bryant, B.S., Woodfin, R.O., 1976. Conversion Factors for the Pacific Northwest Forest Industry; Converting Forest Growth to Forest Products. Institute of Forest Products, Seattle, WA.

Huntington, T.G., Johnson, C.E., Johnson, A.H., Siccama, T.G., Ryan, D.F., 1989. Carbon, organic matter, and bulk density relationships in a forested Spodosol. Soil Sci. 148, 380–386.

Johnson, D.W., 1992. Effects of forest management on soil carbon storage. Water, Air Soil Pollut. 64, 83–120.

Johnson, M.G., J.S. Kern, 1990. Sequestering Carbon in Soils: A Workshop to Explore the Potential for Mitigating Global Climate Change. US EPA Environmental Research Laboratory, Corvallis, OR.

Jokela, E.J., Harding, R.B., Nowak, C.A., 1989. Long-term effects of fertilization on stem form, growth relations, and yield estimates of slash pine. For. Sci. 35, 832–842.

Maser, C., Trappe, J.M., Cline, S.P., Cromack, K., Jr., Blaschke, H., Sedell, J.R., Swanson, F.J., 1984. The seen and unseen world of the fallen tree. General Technical Report PNW-164. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Mitchell, A.K., Barclay, J.J., Brix, H., Pollard, D.F.W., Benton, R., DeJong, R., 1996. Biomass and nutrient element dynamics in Douglas-fir: effects of thinning and nitrogen fertilization over 18 years. Can. J. For. Res. 26, 376–388.

Nohrstedt, H.-Ö., Arnebrant, K., Bååth, E., Söderström, B., 1989. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Can. J. For. Res. 19, 323–328.

Post, W.M., Peng, T.H., Emanuel, W.R., King, A.W., Dale, V.H., DeAngelis, D.L., 1990. The global carbon cycle. Am. Scientist 78, 310–326.

Paschke, M.W., Dawson, J.O., David, M.B., 1989. Soil nitrogen mineralization in plantations of *Juglans nigra* interplanted with actinorhizal *Elaeagnus umbellata* or *Alnus glutinosa*. Plant and Soil 118, 33–42.

Sedjo, R.A., 1989. Forests to offset the greenhouse effect. J. For., July, 12–15.

Smith, T.M., Cramer, W.P., Dixon, R.K., Leemans, R., Neilson, R.P., Solomon, A.M., 1993. The global terrestrial carbon cycle. Water, Air Soil Pollut. 70, 19–37.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., Spycher, G., 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. 17, 1585–1595.

Spies, T.A., Franklin, J.F., Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69, 1689–1702.

Stegemoeller, K.A., Chappell, H.N., 1990. Growth response of unthinned and thinned Douglas-fir stands to single and multiple applications of nitrogen. Can. J. For. Res. 20, 343–349.

Stone, E.L., Harris, W.G., Brown, R.B., Kuehl, R.J., 1993. Carbon storage in Florida Spodosols. Soil Sci. Soc. Am. J. 57, 179–182.

SYSTAT, 1990. Version 5.1. SYSTAT, Evanston, IL.

Turner, J., Singer, M.J., 1976. Nutrient distribution and cycling in a sub-alpine coniferous forest ecosystem. J. Appl. Ecol. 13, 295–301.

Van Cleve, K., Moore, T.A., 1978. Cumulative effects of nitrogen, phosphorus, and potassium fertilizer additions on soil respiration, pH and organic matter content. Soil Sci. Soc. Am. J. 42, 121–124.

Wilding, L.P., Smeck, N.E., Hall, G.F. (Eds.), 1983. Pedogenesis and Soil Taxonomy II. The Soil Orders. Elsevier, New York, pp. 236–244.