Influence of forest age on forms of carbon in Douglas-fir soils in the Oregon Coast Range

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Abstract: The amount and type of carbon (C) in a forest soil reflects the past balance between C accumulation and loss. In an old-growth forest soil, C is thought to be in dynamic equilibrium between accumulations and losses. Disturbance upsets this equilibrium by altering the microclimate, the amount and type of vegetation growing on a site, and properties that affect organic matter decomposition. We measured total C and forms of soil C in the L, F, and H layers and in the light fraction of soil organic matter in the 0–10 cm of mineral soil in old-, second-, and young-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) soils in the Oregon Coast Range. Total C in L, F, and H layers and in organic material in the top 10 cm of mineral soil in old-growth forests was higher than in young- or second-growth forests. Old-growth forests had a higher lignin concentration and lower concentrations of sugar, hemicellulose, and cellulose in the L, F, and H layers and in the light fraction of organic material than second- or young-growth forests. Old-growth forests had greater amounts of fats, waxes, and oils, sugar, cellulose, and lignin, in the L, F, and H layers per square hectare and greater amounts of hemicellulose, cellulose, and lignin in the light fraction of organic matter in the 0–10 cm of mineral soil per square hectare than young- and second-growth forests. Concentrations of fats, waxes, and oils, sugar, and tannin in the light fraction of organic matter in the 0–10 cm of mineral soil did not differ with forest age.

Résumé : La quantité et le type de carbone élémentaire (C) dans un sol forestier reflète le bilan passé entre l'assimilation et la perte de C. Dans le sol d'une vieille forêt, on pense qu'il y a un équilibre dynamique entre les accumulations et les pertes de C. Les perturbations dérangent cet équilibre en modifiant le microclimat, la quantité et le type de végétation qui croît sur un site et les propriétés qui affectent la décomposition de la matière organique. Les auteurs ont mesuré le carbone total et les formes de C du sol dans les horizons L, F et H et dans la fraction légère de la matière organique du sol, dans les premiers 0 à 10 cm de sol minéral, dans les sols de vieilles forêts, de forêts de seconde venue et de jeunes forêts de douglas taxifoliés (*Pseudotsuga menziesii* (Mirb.) Franco) de la chaîne côtière en Oregon. Le carbone total dans les horizons L, F et H et dans la matière organique des premiers 10 cm de sol minéral était plus élevé dans les vieilles forêts que dans les forêts de seconde venue ou dans les jeunes forêts. Les vieilles forêts avaient une concentration plus élevée de lignine et des concentrations plus faibles de de sucres, d'hémicelluloses et de cellulose dans les horizons L, F et H et dans la fraction légère de la matière organique que les forêts de seconde venue ou les jeunes forêts. Les vieilles forêts avaient de plus grandes quantités à l'hectare de gras, de cires, d'huiles, de sucres, de cellulose et de lignine dans les horizons L, F et H et de plus grandes quantités à l'hectare d'hémicelluloses, de cellulose et de lignine dans la fraction légère de la matière organique des premiers 10 cm de sol minéral que les forêts de seconde venue et les jeunes forêts. Les concentrations de gras, de cires, d'huiles, de sucres et de tannins dans la fraction légère de la matière organique des premiers 10 cm de sol minéral ne variaient pas selon l'âge de la forêt. [Traduit par la Rédaction]

Introduction

Forest ecosystems represent the largest terrestrial C storage pool, containing from 82 to 86% of the global aboveground C (Dickson et al. 1994; Sedjo 1992). The amount and type of C in a forest soil reflects the past balance between C accumulation and loss. Accumulation of C in a forest soil is derived from litter fall and root input, while losses are the result of microbial degradation of organic matter, eluviation, solution losses, and erosion. In an old-growth forest, soil C is thought to be in dynamic equilibrium between accumulation and loss. As forest ecosystems mature they accumulate soil C to a maximum carrying potential, which is controlled by climate, topography, soil type, and vegetation (Harmon et al. 1990; Dewar 1991; Van Cleve and Powers 1995). Therefore, at equilibrium the amount of C added to the soil via vegetation is equal to the amount of C lost through organic matter degradation and other losses (Henderson 1995).

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Forest disturbance, especially timber harvesting, may alter the C equilibrium by changing the amount and type of vegetation, microclimate, and soil properties influencing microbial activity and organic matter decomposition (Gallet and Lebreton 1995). If the site is not burned after harvest, initially soil C will increase because of deposition of harvesting residues and root death (Johnson 1992). After the initial increase in decomposition, the rate of organic matter deposition from regrowing vegetation a forest will eventually achieve equilibrium with organic matter decomposition rates (Henderson 1995). Therefore, amount and type of vegetation growing on a site can have a substantial influence on the amount and type of C in a forest soil in a short period of time (Van Cleve and Powers 1995; Gallet and Lebreton 1995).

Plant species occurring in primary and secondary successional forest ecosystems often grow rapidly and have high nutrient concentrations and low concentrations of decay-resistant

Table 1. Site characteristics and harvesting procedures at MacDonald, Siuslaw, and Dunn sites with old-, second-, and young-growth *Pseudotsuga menziesii* stands.

		Site characteristics			Harvesting procedures	
Forest	Year*	Aspect	Slope (%)	Type	Site preparation	Reforestation
McDonald						
Old growth	—	West	26	—	—	—
Second growth	1939	West	32	Clearcut	Burn	Natural regeneration
Young growth	1973	Northwest	18	Clearcut	Burn	Planted *P. menziesii*
Siuslaw						
Old growth	—	Northwest	60	—	—	—
Second growth	1932	Southeast	55	Clearcut	Burn	Natural regeneration
Young growth	1967	North	50	Clearcut	Burn	Planted *P. menziesii*
Dunn						
Old growth	—	North	29	—	—	—
Second growth	1923	North	10	Clearcut	Burn	Natural regeneration
Young growth	1963	Northwest	18	Clearcut	Burn	Planted *P. menziesii*

*Year of stand establishment.

chemicals (Vitousek et al. 1989; Bryant et al. 1991; Entry et al. 1991; Van Cleve et al.1993). Nadelhoffer et al. (1983) reported that soil C accumulation in the L, F, and H layers and mineral soil was less when the regrowing vegetation was *Pinus resinosa* Ait., where organic matter degradation was faster, than when the regrowing vegetation was mature *Pinus strobus* L., where organic matter degradation was slower. Grigal and Ohman (1992) found that soil C accumulation was greater in soils supporting *Pinus banksiana* Lamb. than *Abies balsamea* (L.) Mill. *Pseudotsuga menziesii* (Mirb.) Franco stands in western Oregon had increasing amounts of C in the surface L, F, and H layers and the 0–10 cm of mineral soil as forest age increased (Entry and Emmingham 1995). As forest ecosystems in the Pacific Northwestern United States mature, an increasing amount of woody material is deposited on the forest floor. Woody material is more resistant to microbial decomposition than the conifer needles deposited in greater quantities by younger growth forests, and organic matter tends to accumulate on the forest floor as forests mature (Vesterdal et al. 1995).

Density fractionation is a useful method of separating organic matter into components that are physically and chemically distinct and are mineralized at different rates by soil microorganisms (Boone 1994; Christensen 1992). Density fractionation separates the light fraction, which is composed of partially decomposed roots and aboveground litter, from the heavy fraction, which is composed of the denser humic material (Boone 1994; Janzen et al. 1992). The light fraction is regarded as labile and is thought to be easily mineralized, while the heavy fraction represents humic material absorbed on mineral surfaces and is regarded as resistant to microbial mineralization (Theodorou 1990). Together the two fractions constitute nearly all of the organic matter in the soil (Boone 1994).

While separation of organic matter into light and heavy fractions is useful, further separation into proximate fractions of fats, waxes, and oils (FWO), sugars, hemicellulose, cellulose, lignin, tannins, and phenolic compounds is more complete. Chemical composition of soil C determines its rate of mineralization and thus nutrient turnover and storage (Melillo et al. 1989; Entry and Emmingham 1995). Each proximate fraction will decompose at a different rate and will often influence nutrient dynamics in forest soils (Melillo et al. 1982; McClaugherty et al. 1985). The objective of this study was to determine the influence of forest age on amount and form of C in the L, F, and H layers and in the light fraction in the 0–10 cm of mineral soil in forest soils.

Methods

Site descriptions

McDonald Forest

The McDonald Forest site (44°33′N, 123°15′W) is on a 18 to 32% east-facing slope in the McDonald Forest 3 km west of Corvallis, Oregon. Annual precipitation is 1100–1500 mm, 4% or less of which occurs as snowfall (Knezevich 1975). Mean annual air temperature is 12°C. The soil is a clayey, mixed mesic, Dystric Xerochrept (Knezevich 1975). The site is classified as a *Tsuga heterophylla/Acer circinatum/Gaultheria shallon* community type (Hubbard 1991). The old-growth stand has an overstory of 120-year-old *P. menziesii*, with *Tsuga heterophylla* (Raf.) Sarg., *Acer macrophyllum* Pursh, and *Taxus brevifolia* Nutt. as midstory trees. Depth of the L, F, and H layers ranges from 6 to 10 cm. The second-growth stand is dominated by 50- to 60-year-old *P. menziesii*; a few small *A. macrophyllum* and *T. heterophylla* compose the understory trees. Depth of the L, F, and H layers ranges from 4 to 10 cm. The young-growth stand is dominated by 15- to 20-year-old *P. menziesii*; understory species are *T. heterophylla, A. grandis*, and *Thuja plicata.* Depth of the L, F, and H layers ranges from 0 to 6 cm.

Siuslaw Forest

The Siuslaw Forest site (44°29′N, 123°31′W) is on a 50 to 60% north slope in the Siuslaw National Forest, 40 km west of Corvallis, Oregon. The soil is a clayey skeletal mixed mesic, Typic Haplumbrept (Knezevich 1975). Annual precipitation ranges from 1300 to 1900 mm, and average annual temperature is 12°C (Knezevich 1975). The site is classified as a *Tsuga heterophylla/Gaultheria shallon* community type (Hemstrom and Logan 1986). The overstory of the old-growth stand is 250-year-old and older *P. menziesii*; *A. macrophyllum, T. heterophylla*, and *Taxus brevifolia* compose the midstory. Depth of the L, F, and H layers varies from 7 to 12 cm. The second-growth stand at has an overstory of 60- to 80-year-old *P. menziesii* interspersed with a few scattered *A. macrophyllum*.

Table 2. Soil characteristics at sites with old-, second-, and young-growth *Pseudotsuga menziesii* stands.

		Soil characteristics								
		Mineral soil		Litter			Mineral soil (top 10 cm)			
Forest	Year*	Texture	Clay (%)	pH	C (%)	N (%)	pH	C (%)	N (%)	C/N (%)
McDonald										
Old growth	—	Gravely, silty, clay loam	75	4.6	41	1.07	5.2	11.0	0.72	15.3
Second growth	1939	Gravely, silty, clay loam	75	4.8	33	1.20	5.4	3.7	0.14	26.4
Young growth	1973	Gravely, silty, clay loam	75	4.6	18	1.04	5.4	5.6	0.31	18.1
Siuslaw										
Old growth	—	Gravely, clay loam	45	4.5	42	1.36	5.6	11.3	0.43	26.3
Second growth	1932	Gravely, clay loam	50	4.7	30	1.10	5.5	3.3	0.15	22.0
Young growth	1967	Gravely, clay loam	45	4.7	17	1.00	5.6	3.9	0.20	19.5
Dunn										
Old growth	—	Silty, clay loam	90	4.6	43	1.16	5.3	7.7	0.28	27.5
Second growth	1923	Silty, clay loam	85	4.8	26	1.08	5.5	4.2	0.18	23.3
Young growth	1963	Silty, clay loam	85	4.8	15	0.80	5.6	4.5	0.23	19.6

*Year of stand establishment.

Depth of the L, F, and H layers varies from 6 to 12 cm. The young-growth stand consists of 20- to 30-year-old *P. menziesii.* Depth of the L, F, and H layers ranges from 0 to 7 cm.

Dunn Forest

The Dunn Forest site (44°38′N, 123°21′W) is on a 10 to 30% north-facing slope within Dunn State Forest, 10 km north of Corvallis, Oregon. The soil is a clayey, mixed mesic Xeric Haplohumult (Knezevich 1975). Annual precipitation ranges from 1000 to 1500 mm, and annual temperature averages 12°C (Knezevich 1975). The site is classified as a *Tsuga heterophylla/Acer circinatum/Gaultheria shallon* community type (Hubbard 1991).

The old-growth stand has an overstory of 200-year-old *P. menziesii* and a midstory of *A. macrophyllum, T. heterophylla*, and *Taxus brevifolia*. Depth of the L, F, and H layers varies from 4 to 12 cm. The second-growth stand is dominated by an over story of 50- to 70-year-old *P. menziesii.* Depth of the L, F, and H layers varies from 4 to 10 cm. The young-growth stand consists of 20- to 30-year-old *P. menziesii.* Depth of the L, F, and H layers varies from 0 to 6 cm. Table 1 presents the site characteristics and harvesting procedures, and Table 2 presents the soil characteristics, for these three sites.

Experimental design

The experiment was arranged in a randomized block design (Kirk 1982). Soil samples were taken from three sites located in the Oregon Coast Range Mountains (blocks), each supporting forest stands of three ages (treatments): young-growth (age 25–35 years), second-growth (age 60–75 years), and old-growth (age 120–250 years). At each of these sites, we took 15 randomly selected 10 cm diameter soil cores consisting of the L, F, and H layers and the 0–10 cm of mineral soil (A horizon) at each site (block), within each stand age, for each season. A total of 540 soil cores were taken to measure total C in the L, F, and H layers and in 0–10 cm of mineral soil and forms of C in the L, F, and H layers and in the light fraction of the top 10 cm of mineral soil (3 forest ages (old-, second-, and young-growth) × 3 sites (McDonald, Siuslaw, and Dunn forests) × 15 locations in each age–site × 4 seasons).

Sampling procedures

Soil cores were taken each plot during winter (January 13), spring (March 15), summer (August 12), and autumn (November 15) in 1993. We sampled the stands each season to determine whether the amount and form of C in the L, F, and H layers would be affected by needle–leaf drop. The 0–10 cm of mineral soil was sampled because it is the most chemically and microbiologically active part of a forest mineral soil (Entry et al. 1991; Zvyagintsev 1994). Sampling locations were randomly chosen throughout each stand. Ten centimetre diameter cores were taken to a 10 cm mineral soil depth (50–200 g ovendry weight). Soil cores were then separated into the L, F, and H layers and the 0–10 cm of mineral soil. Woody material greater than 1.0 cm diameter was not measured. Carbon per hectare in the L, F, and H layers was estimated by measuring the amount of organic matter in 15 separate 25-cm^2 areas in each site × stand age × season.

Soil measurements

Separate 10 cm diameter soil cores were taken to measure bulk density and soil pH. The L, F, and H layers and mineral soil were separated. Bulk density was measured by dividing the volume of the sample by the ovendry weight (105°C for 48 h) (Blake and Hartage 1982). The pH of L, F, and H layers and soil was measured by using a 1:1 paste (McLean 1982). Total N was determined by using standard microkjeldhal procedures modified for nitrate (Bremner and Mulvaney 1982). Carbon/N ratios were calculated by dividing the weight of total C by total N.

Total carbon

The organic matter was collected, and roots greater than 1 mm diameter were removed by hand. Organic matter was dried at 80°C for 48 h, and then weighed. A 10-g subsample of the dried organic matter was ground finely enough to pass through a 1-mm opening, and another 1-g subsample was ashed at 525 ± 2°C. Total C was determined by loss on ignition (Nelson and Sommers 1982). The amount of C in the organic matter (OM) per square hectare of the L, F, and H layers was calculated from the following formula: $C = Mg\ OM \cdot ha^{-2} \times g\ C \cdot g\ OM$, where C is $Mg\ C \cdot ha^{-2}$ in surface organic matter, Mg OM is g C/g OM. Organic matter was assumed to contain 0.50 g C per gram organic matter on an ash-free basis (Nelson and Sommers 1982). Data from previous studies in this area have indicated that 0.50 g C per gram organic litter on an ash-free basis is an accurate measure of C in the L, F, and H layers and top 10 cm of mineral soil (McNabb et al. 1986; Strickland and Sollins 1987). Concentration of total C in the 0–10 cm of mineral soil was determined by loss on ignition at 525 ± 2°C. The amount of C per hectare of the 0–10 cm of mineral soil was calculated with the same formula as for the L, F, and H layers calculations, but organic material extracted from mineral soil was substituted for OM in the formula and with correction for soil bulk density.

Extraction of carbon (light fraction) from mineral soil

We separated the light fraction of organic matter in the 0–10 cm of mineral soil from the heavy organo-minerals using methods modified

Table 3. Total and percentage of carbon stored as fats, waxes, and oils, sugars, hemicellulose, cellulose, lignin, and tannins in the litter layer and top 10 cm of the light fraction (density ≥ 1.79 $Mg \cdot m^{-3}$) of mineral soil of old-, second-, and young-growth *Pseudotsuga menziesii* stands in western Oregon.

Stand type	Total C* (g C·kg soil^{-1})	LF/TC†	FWO‡	Sugars	Hemicellulose	Cellulose	Lignin	Tannins
Litter layer								
Old growth	487*a*	—	7.1*b*	2.0*b*	4.2*d*	40.2*b*	42.2*a*	4.3*a*
Second growth	377*b*	—	16.9*a*	7.1*a*	3.1*d*	49.7*b*	22.2*b*	1.0*b*
Young growth	311*b*	—	10.7*a*	6.6*a*	12.9*c*	64.9*a*	3.4*c*	2.1*b*
Mineral soil								
Old growth	115*c*	46*c*	4.8*b*	1.6*bc*	3.8*d*	39.0*c*	45.7*a*	5.1*a*
Second growth	47*d*	58*b*	5.8*b*	1.2*c*	18.9*b*	45.1*b*	25.6*b*	3.3*b*
Young growth	25*e*	64*a*	5.3*b*	1.3*c*	34.2*a*	47.6*b*	8.7*c*	2.9*b*

Note: In each column, values followed by the same letter are not significantly different as determined by the least square means test ($P \leq 0.05$; $n = 36$).

*Total C as determined by loss on ignition.

†Percent of soil carbon that is light fraction.

‡FWO, fats, waxes, and oils.

from Strickland and Sollins (1987). Fifty grams of equivalent dry weight of mineral soil was dispersed by a 350-mL NaI solution (density 1.75 $Mg \cdot m^{-3}$) and vigorously stirred by hand with a glass rod for 30 s, then centrifuged at 4080 g for 10 min. Organic material was then aspirated into a sidearm flask under water-drawn tension. Organic material was collected with a Gelman glass fiber prefilter on top of a Whatman No. 42 filter paper, rinsed with 100 mL deionized distilled water, dried at 70°C for 48 h, and weighed (Boone 1994; Strickland and Sollins 1987).

Carbon fractionation

Organic material from the L, F, and H layers or mineral soil was dried at 70°C for 48 h and ground to pass a 1-mm mesh. A 0.2-g subsample from each sample taken from the L, F, and H layers, and the light fraction extracted from each sample of mineral soil was used for C fractionation analysis following the method of Ryan et al. (1990). Soluble fats, waxes, and oils were removed using a series of dichloromethane washes (TAPPI 1975). Sugars and hemicellulose were removed and measured using methods described by Hanson and Moller (1975). Cellulose and lignin were determined gravimetrically (Effland 1977). Hot water extractable tannins were extracted and measured by methods described by Allen et al. (1974). Proximate carbon fractions were corrected for ash, and weight of ash was subtracted from the lignin fraction; therefore C fractions are presented as ash-free dry weight (Ryan et al.1990).

Statistical analysis

All data were subjected to a two-way (site × forest age × season) analysis of variance (ANOVA) for a randomized block design (Kirk 1982). The residuals were normally distributed with constant variance. SAS programs (SAS Institute Inc. 1986) were used to conduct the analysis of variance. Significance of treatment means were determined at $P \leq 0.05$ with the least square means test.

Results

Analysis of variance for total C, FWO, sugar, hemicellulose, cellulose, lignin, and tannin concentration both in the L, F, and H layers and in the light fraction of organic material in the 0–10 cm of mineral soil showed no significant differences among sites (McDonald, Siuslaw, or Dunn forests) or among seasons for any C form within a stand age. Therefore, only differences among forest ages will be discussed (Kirk 1982).

There was a greater amount of total C, FWO, sugar, hemicellulose, cellulose, lignin, and tannin concentration in the L, F, and H layers than in the light fraction of organic material extracted from the 0–10 cm of mineral soil regardless of forest age (Table 3). There was a greater amount of total C contained in the L, F, and H layers of old-growth forests than in those of young- or second-growth forests. Old-growth forests contained a greater concentration of lignin and tannins but lower concentrations of sugars, hemicellulose, and cellulose in the L, F, and H layers than young- or second-growth forests.

Old-growth forests contained more total C in the 0–10 cm of mineral soil than young- or second-growth forests (Table 3). Old-growth forests had a higher concentration of lignin and tannins but lower concentrations of hemicellulose and cellulose composing the light fraction of the organic material in the 0–10 cm of mineral soil than young- or second-growth forests. Second-growth forests contained a lower concentration of hemicellulose in the light fraction of the organic material in the 0–10 cm of mineral soil than young-growth forests. Concentrations of FWO, sugar, and tannin composing the light fraction of the organic material extracted from the 0–10 cm of mineral soil did not differ with forest age.

We found greater amounts of total C, FWO, cellulose, lignin, and tannin per square hectare in the L, F, and H layers than in the light fraction of the organic material extracted from the 0–10 cm of mineral soil in all forest ages (Table 4). Old-growth forests had a greater amount of total C in the L, F, and H layers and 0–10 cm of mineral soils per square hectare than young- or second-growth forests. Old-growth forests had greater amounts of FWO, sugar, cellulose, lignin, and tannins in the L, F, and H layers per square hectare than young- and second-growth forests. Second-growth forests had greater amounts of FWO, sugar, hemicellulose, cellulose, lignin, and tannins composing the L, F, and H layers per square hectare than young-growth forests. Old-growth forests had greater amounts of hemicellulose, cellulose, lignin, and tannins in the light fraction of the organic material in the 0–10 cm of mineral soil per square hectare than young- and second-growth forests. Second-growth forests had greater amounts of hemicellulose, cellulose, lignin, and tannins composing the light fraction of

Table 4. Total amount of carbon and total amount of carbon stored as fats, waxes, and oils, sugars, hemicellulose, cellulose, lignin, and tannin in the litter layer and the light fraction (density ≥ 1.75 Mg·m^{-3}) of the top 10 cm of mineral soil of old-, second-, and young-growth *Pseudotsuga menziesii* stands in western Oregon (Mg C·ha^{-2}).

Stand type	Total C*	FWO†	Sugars	Hemicellulose	Cellulose	Lignin	Tannin
				Organic layer			
Old growth	15.72*a*	1.11*a*	1.03*a*	0.36*a*	6.31*a*	6.63*a*	0.28*a*
Second growth	8.02*b*	1.36*b*	0.56*b*	0.29*a*	3.99*b*	1.73*b*	0.08*b*
Young growth	3.68*c*	0.40*c*	0.07*c*	0.13*b*	2.61*c*	0.13*d*	0.08*b*
				Mineral layer			
Old growth	1.35*d*	0.06*d*	0.02*c*	0.44*a*	0.53*d*	0.26*c*	0.04*c*
Second growth	0.87*e*	0.05*d*	0.01*c*	0.26*b*	0.39*e*	0.13*d*	0.03*c*
Young growth	0.47*f*	0.02*d*	0.06*c*	0.04*d*	0.22*f*	0.07*e*	0.01*c*

*Total C as determined by loss on ignition.

†FWO, fats, waxes, and oils.

‡In each column, values followed by the same letter are not significantly different, as determined by the least square means test ($P \leq 0.05$; $n = 36$)

the organic material in the 0–10 cm of mineral soil per square hectare than young-growth forests. The amounts of FWO and sugars in the light fraction organic material in the 0–10 cm of mineral soils did not differ with forest age.

Discussion

All three of the sites had old growth that was clear-cut and burned. Trees growing in all three second-growth stands were established to natural seeding from adjacent forests, while trees growing in young-growth stands were the result of planting bare-root *P. menziesii* seedlings (Table 1). The soil characteristics on these three sites contained substantial amounts of clay, which is a characteristic of soils in this region (Table 2).

Our study shows that old-growth conifer forests store substantially more total C in the L, F, and H layers and in the top 10 cm of mineral soil than do second- and young-growth forests. These findings were similar to C storage estimates from other studies. Homann et al. (1995) estimated that the organic layer and the top 20 cm of mineral soil in 86 soils in western Oregon contained from 10 to 14.7 Mg C·ha^{-2} and from 9 to 24.3 Mg C·ha^{-2}, respectively. The litter layer of soils in Michigan, Minnesota, and Wisconsin averaged 17 Mg·ha^{-2} (Grigal and Ohman 1992). Vogt et al. (1995) estimated that forest soils in the temperate region commonly average 17 Mg C·ha^{-2}.

We found that the amount of C stored in the L, F, and H layers and in the top 10 cm of mineral soil increases with forest ecosystem age. These results agree with many of the conclusions of Johnson (1992) and Schlesinger (1986). Johnson (1992) and Schlesinger (1986) reviewed several papers investigating the influence of timber harvesting and found that there is a small but significant decrease in soil C after timber harvesting and light-intensity burning followed by reforestation and there may be a large decrease in soil C after timber harvesting and a high-intensity burn. They also found that if trees were harvested and the site was not burned, there was no general trend toward lower soil C. Soil C in many of the studies reviewed by these authors were measured prior to and less than 3 years after harvesting. Organic material left on the site as a result of harvesting without burning for site preparation may not have degraded to a point where C input from litter fall was in equilibrium with organic matter degradation rates. Shortly after timber harvest without burning, soil C should increase as a result of increased organic material (slash) left on the site. Since there is less C input to soils due to a reduction in the amount of woody biomass on the site, there should be a drastic reduction in the amount of woody litter fall and woody root production. The amount of C that is resistant to microbial degradation added to the forest soil should be substantially reduced over a period of years and the rate at which organic material (C) is oxidized to CO_2 should be greater than the rate of organic material (C) supplied to the soil. Therefore, reductions in soil C after timber harvesting without burning may not be evident for many years.

In second-growth forest of western Oregon the light fraction of soil extracted with a density of ≥ 1.6 Mg·m^{-3} mineral soil represents from 25 to 53% of the total soil weight (Strickland and Sollins 1987; Sphyer et al. 1983). Our data show that as forests mature, significantly more C both in the L, F, and H layers and in organic material in the top 10 cm of mineral soil is stored in a more recalcitrant form. In old-growth forests, not only is there more C stored in the soil, but significantly more C is stored in a recalcitrant form (lignin) in young-growth forests. Forest soils have been estimated to contain approximately 60% of the C contained in terrestrial ecosystems (Sedjo 1992; Dickson et al. 1994). Greater percentages of recalcitrant compounds (lignin) in organic matter of old- and second-growth soils should result in slower organic matter decomposition and C turnover rates in the L, F, and H layers and in the organic material in the 0–10 cm of mineral soils in forests throughout the temperate region.

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