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Belowground carbon pools and processes in different age stands of Douglas-fir

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Summary Forest floor material and soil organic matter may act as both a source and a sink in global CO_2 cycles. Thus, the ecosystem processes controlling these pools are central to understanding the transfers of carbon (C) between the atmosphere and terrestrial systems. To examine these ecosystem processes, the effect of stand age on temporal carbon source–sink relationships was examined in 20-year-old, 40-year-old and old-growth stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Cascade Mountains of south-central Washington State. Belowground C and nitrogen (N) storage and soil respiration were measured. In addition, nylon mesh bags containing homogenized soils from each site were buried at the respective sites to quantify root ingrowth and potential C sequestration and loss. The sites supporting the 20- and 40-year-old stands had soil C stores reflecting the C contributions from logging residue, coarse woody debris and stumps left after harvest. Because the N-fixer red alder (*Alnus rubra* Bong.) comprised 33% of the 40-year-old stand, this site had significantly greater concentrations and pools of N in the forest floor than sites without red alder. This N-rich site had consistently lower soil CO_2 efflux rates during the growing season than the sites supporting the 20-year-old and old-growth stands. Estimated annual soil C efflux was 1367, 883 and 1194 g m^{-2} for the sites supporting the 20-, 40- and old-growth stands, respectively. These values are higher than previously reported values. Root ingrowth was significantly less in the 40-year-old stand than in the 20-year-old stand, and both young stands showed markedly less fine root growth than the old-growth stand. At the sites supporting the young stands, C and N were lost from the soil bags, whereas there was an increase in C and N in the soil bags at the site supporting the old-growth stand. The fine root growth and soil respiration data support the hypothesis that belowground C allocation decreases with increasing fertility. Quantification of the source–sink relationship of soil C at the three stands based on litterfall, relative root ingrowth and soil respiration measurements was compromised because of significant CO_2 flux from decaying organic matter in the young stands.

Keywords: CO_2, forest floor, litterfall, old-growth, Pseudotsuga menziesii, root growth, soil carbon, soil nitrogen, soil respiration, Tsuga heterophylla, western hemlock.

Introduction

Carbon (C) stored below ground comprises more than two-thirds of the C in terrestrial ecosystems (Post et al. 1982) and more than twice that in the atmosphere (Schimel 1995, Rustad et al. 2000). Almost 10% of the atmosphere's CO_2 passes through the soil annually (Raich and Potter 1995). This transfer process is important because the soil C pool is expected to show the greatest response to climate change. However, accurate inventories of this pool are scarce and there are even fewer data on temporal changes in this pool (Sarmiento and Wofsy 1999). Schlesinger and Andrews (2000) conclude that a large increase in the soil C pool is unlikely to mitigate increases in atmospheric CO_2 concentration [CO_2] during this century. Furthermore, global warming (Mitchell et al. 1990) may result in a net export of ecosystem C (as CO_2) as soil respiration increases (Schleser 1982, Jenkinson et al. 1991, Anderson 1992, Trumbore 1996, Raich and Tufekcioglu 2000). However, whether the soil becomes a significant source or sink for atmospheric CO_2 depends on its ecosystem type, successional stage, geographic location and legacy (Schimel et al. 1994, Trumbore et al. 1996, Field and Fung 1999, Jobbágy and Jackson 2000, Schlesinger and Andrews 2000). Climate-driven interannual variability further increases this source– sink complexity (Bousquet et al. 2000, Fung 2000).

In the conterminous United States, the Pacific Northwest coniferous forests have the greatest amount of belowground C storage and flux of any forest ecosystem type (Kern 1994, Turner et al. 1995, Vogt et al. 1995). Research has focused on these and other forest ecosystems because climate warming may have a large effect on their C stores (e.g., Bonan 1991, Peterson and Waring 1994, Turner et al., 1995, Garten et al. 1999, Lin et al. 1999). Relatively small changes in forest soil C inventories may have substantial influence on the global C budget (Rustad et al. 2000). To predict future C dynamics in forest ecosystems, it is therefore essential to quantify the soil and forest floor C pools and to document the processes controlling these pools (Frey 1996).

Following cutting (or other major disturbances such as fire (Johnson 1992)), there is a significant loss of aboveground C through harvesting, and an increase in forest floor belowground C through unharvested slash and tree roots that enter the detrital pool. The ecosystem acts as a C source until pri-

mary production surpasses autotrophic and heterotrophic respiration. Johnson and Curtis (2001) report that sawlog harvesting of coniferous species had positive effects on soil C; however, they did not compare net fluxes of C. Soil CO_2 efflux is a function of the activity of autotrophic roots and associated rhizosphere organisms (e.g., mycorrhizae), heterotrophic bacteria and fungi acting primarily as decomposers, and soil fauna. A stand's total soil CO_2 efflux is thus related to both the amount of live roots and the amount and quality of the soil C pools. It follows that this major source of C loss from the ecosystem will differ according to the structure and age of the stand.

In this study, forest floor and belowground C storage and release were determined in 20-year-old, 40-year-old and old-growth stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Cascade Mountains of south-central Washington. Specifically, intrasystem storage of belowground C was measured, efflux of C through soil respiration was quantified, and sources of C input into the belowground system were estimated. The data were used to test the hypothesis that belowground C pools are sources of atmospheric C for a significant period of time following cutting and dominate the sink–source equation.

Materials and methods

The research was undertaken in an old-growth Douglas-fir ecosystem located at the Wind River Canopy Crane Research Facility (WRCCRF; hereafter the old-growth site) and in 20- and 40-year-old Douglas-fir stands in the surrounding Gifford Pinchot National Forest. The old-growth site is situated at 355 m elevation and the sites supporting the 20- and 40-year-old stands are at approximately 500 m. Soils are classified as medial, mesic, Entic Vitrands. These soils are deep, well-drained, medium-textured sandy loams. The parent material is mixed volcanic ejecta. Soil pH ranges from 4.0 at the 20-year-old stand to 4.2 at the 40-year-old stand and 5.1 at the old-growth stand. Bulk density of the upper 20 cm at the old-growth stand is between 0.70 and 0.92 g cm^{-3}, increasing with depth, and is between 0.9 and 1.1 g cm^{-3} at the other stands. These organic-rich Andisols are capable of holding more than 100% of their weight with water. A typical soil profile has only 2 to 4 cm of forest floor material above the mineral soil. This shallow layer has a mull type of humus that is incorporated into the surface layer of the mineral soil and is characteristic of areas with rapid decomposition as a result of favorable water and temperature conditions. The area is in the rain-on-snow zone of the Cascade Mountains. The climate is temperate winter wet, summer dry with over 2500 mm of annual precipitation, with less than 10% falling between June and September. Mean annual snowfall is 2330 mm. Mean annual temperature is 8.7 °C at the old-growth site and slightly lower at the young stands. Soils at the site supporting the 40-year-old stand were consistently wetter than at the other sites.

The old-growth site is dominated by 450- to 550-year-old Douglas-firs and western hemlocks (*Tsuga heterophylla* (Raf.) with the tallest trees averaging 55 to 65 m (maximum 67 m). Other tree species include western red cedar (*Thuja plicata* Donn), western white pine (*Pinus monticola* Dougl. ex D. Don), Pacific silver fir (*Abies amabilis* (Doug.) Forb.) and grand fir (*Abies grandis* (Doug.) Lindl.). The 40-year-old stand is composed of Douglas-fir mixed with 33% red alder (*Alnus rubra* Bong.) and 13% western hemlock. This site has been described as one of the most productive in the forest and had some of the largest trees in the district when it was harvested. Some of the logs (> 2 m diameter) were so large that they could not be moved and were left behind when harvesting was completed (C. Harrington, USDA Forest Service, personal communication). The 20-year-old stand is dominated by Douglas-fir, with western hemlock and some Pacific silver fir. When it was cable-logged, up to 80 Mg ha^{-1} of woody residue was left on site. Both young stands were established following harvest of old-growth stands (C. Harrington, personal communication). Much of the unharvested larger material (stumps, logs) at the site supporting the 40-year-old stand (hereafter the 40-year site) is still present, whereas the site supporting the 20-year-old stand (hereafter the 20-year site) is covered with soil. There is a large amount of coarse wood debris present at all three sites (Janisch and Harmon 2002). Understory vegetation (e.g., Oregon grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh) on the 20-year site and old-growth sites is typical of that of the Washington southern Cascades on well-drained soils, whereas that on the 40-year site is characterized by a rich herbaceous flora characteristic of more moist and nutrient-rich stands. A detailed description of the WRCCRF can be found at http://depts.washington.edu/wrccrf.

Nutrient pools

The three sites were sampled for organic C and total N content of the forest floor material and soils. Each of the 4 ha surrounding the centrally located crane at the WRCCRF is divided into 16 25 × 25-m permanently marked grids. Six grids in each quadrant were randomly selected, yielding a total of 24 sampling points. For the young stands, 12 randomly stratified locations placed in a 1-ha plot were sampled. Samples of the forest floor material were taken using 0.25 × 0.25-m frames and separated into the O_a, O_e and O_i horizons. Soil samples were taken to a depth of 0–10 and 10–20 cm from an area around the forest floor plots. Each sample consisted of a composite of five subsamples to account for soil heterogeneity. Soil nutrient pool sizes were calculated based on bulk density measurements obtained by excavating a 25-cm deep pit from beneath the forest floor samples. A cylinder of known dimensions was inserted horizontally into the wall of the pit (at 5 and 15 cm), extracted and extending soil trimmed. The cylinder containing soil was placed in a metal canister, returned to the laboratory and dried at 105 °C to constant mass. All material was analyzed for C and N on a Perkin-Elmer 2400 CHN analyzer (Perkin-Elmer, Norwalk, CT).

Soil respiration

Permanent chambers (PVC pipe; 10-cm ID) were installed at each site for the direct measurement of [CO_2] (12 pipes each at the 20- and 40-year sites, and 16 at the old-growth site). Cham-

bers, which were 7.5 cm high, were inserted through the forest floor material and duff layer to the top of the soil surface. A visual examination showed that no fine roots were cut. Soil CO_2 efflux was measured with an LI-6250 infrared gas analyzer (Li-Cor, Lincoln, NE) equipped with a Li-Cor LI-6100-09 chamber. Litter was allowed to fall into the collars, but lichens, mosses and seedlings were removed before measurement. Based on measurements at the WRCCRF conducted every 4 h over several 24-h periods, it was determined that averaging an early morning and a late afternoon measurement captured the mean daily soil CO_2 efflux. Soil respiration at the sites was measured on a monthly basis, snow depth permitting. The snow layer traps the soil CO_2 because of its high water content and reduces or blocks CO_2 efflux from the forest floor. Temperature measurements were monitored continuously with HOBO data loggers (Onset Computers, Bourne, MA) using thermocouples located in air at 1 m above ground and buried at a depth of 15 cm at two locations per site. Measurements were recorded every 15 min. Temperatures at the old-growth stand were consistently higher than at the other stands, presumably because of lower elevation. Soil temperatures at the 20- and 40-year sites were comparable, with the exception of earlier snowmelt and a subsequent earlier temperature increase at the 20-year site. Soil water (w/w) was measured at the 20- and 40-year sites by taking replicate bulk soil samples from the 0–10 cm and 10–20 cm depths and weighing the samples before and after drying at 85 °C. For the old-growth site, soil water data were obtained from temporary microclimate recording stations (Tim Link, Oregon State University, Corvallis, OR, personal communication).

Soil bag experiment

Measurements of changes in soil C pools offer the simplest means of estimating soil C sequestration, but the inherent variability in soils makes it difficult to interpret the changes statistically (e.g., Paul et al. 1995). As an alternative to measuring changes in soil C pools, David et al. (1990) developed the buried bag technique, where soil samples from a site are homogenized to reduce variability, placed in mesh bags, and buried for later retrieval. On an annual basis, roots can input as much carbon as litterfall (Vogt et al. 1983, 1996, Gower et al. 1992). Helmisaari and Hallbäcken (1999) compared results of root ingrowth bags with that of soil cores and found that, during the first 2 years, roots growing into the ingrowth bags represented current growth potential rather than absolute fine-root production. However, results were comparable with standing crop values obtained with soil cores after 3 years (Makkonen and Helmisaari 1999).

For each stand, A horizon soil was collected, coarse-sieved (1.25 cm), homogenized to reduce variability, and about 750 g was placed in each nylon 1-mm mesh soil bag (7.5 cm in diameter and 20 cm high and cylindrical when filled). The soil bags were buried vertically in the soil at their respective sites with 192 bags placed at the old-growth site and 36 bags at each of the sites supporting the young stands. After 1 year, 16 bags were extracted from the old-growth site and 12 each from the young stands. After removal, the bags were transported under ice to the laboratory where they were divided into upper and lower 10-cm sections. The soils from the bags were sieved and all roots were separated from the soil by hand, dried and weighed. Because the fine root samples were too small to undergo washing, a subsample of roots was ashed at 550 °C for 4 h to determine ash-free biomass and to correct the C and N concentrations for contamination by soil as described by Blair (1988) for litter. Soil samples from each bag were analyzed with a Perkin-Elmer 2400 CHN analyzer to determine C and N contents.

Litterfall

Litterfall was collected on 40 × 40 cm frames covered with nylon-mesh netting. Twenty collectors were placed randomly in the old-growth stand and eight collectors were placed in each of the young stands. Litter was collected monthly when snow depth permitted. Litter was returned to the laboratory, dried, sorted into categories based on plant type and part, and weighed. Litterfall data were obtained for 2 years (1999–2001), but only the data for 1999–2000 are reported.

Statistical analysis

A limitation of the experimental design was that only one stand of each age was sampled because comparable stands of similar age and site conditions were unavailable. Therefore, to avoid a statistical comparison based on pseudo-replication, we did not analyze differences between stands. Instead, we used the stand data (e.g., soil nutrients), which were obtained from an extensive sampling of the combination of site and age differences, to characterize the belowground processes at each site. Analysis of variance for unequal sample sizes was performed on the soils in the soil bags. All statistical analyses were made with SAS software (1999; SAS Institute, Cary, NC). The CO_2 efflux data from the four points surrounding the temperature data loggers were pooled and used with the 24-h mean temperatures during the period that soil respiration was measured to determine Arrhenius plots (logarithm of efflux against the inverse of absolute soil temperature). The data were then subjected to linear regression analysis to determine the slopes of the soil temperature–efflux relationships. The data were scaled to an annual value by summing the regression results of the mean daily soil temperature for each stand.

Results

Nutrient pools

Concentrations and pool sizes of C and N in the forest floor and upper 20 cm of soil at the three sites are listed in Tables 1 and 2, respectively. Concentrations of C and N in the forest floor and soils differed depending on the component and element. Both young stands had relatively high concentrations of C in the upper soil layer compared with the lower soil layer (Table 2). The C pool (111 Mg C ha^{-1}) in the forest floor plus the top 20 cm of soil at the old-growth site was comparable

Table 1. Concentrations (g kg^{-1}) of carbon and nitrogen and C/N ratios in the forest floor and soils of three stands at and near the Wind River Canopy Crane Research Site. Values are means with standard errors in parentheses.

Component	Carbon	Nitrogen	C/N
Forest floor of 20-year-old stand			
O_a and O_e layers	464.3 (10.3)	9.8 (0.7)	49.4 (2.9)
O_i layer	348.8 (39.1)	8.8 (0.8)	40.2 (3.9)
Soil of 20-year-old stand			
0–10 cm	76.8 (10.3)	2.0 (0.3)	39.2 (2.9)
10–20 cm	70.0 (17.9)	1.6 (0.3)	39.2 (4.3)
Forest floor of 40-year-old stand			
O_a and O_e layers	477.4 (9.0)	11.7 (1.0)	43.6 (3.6)
O_i layer	358.5 (23.2)	12.4 (0.6)	29.1 (2.2)
Soil of 40-year-old stand			
0–10 cm	102.3 (14.7)	4.2 (0.6)	24.9 (1.8)
10–20 cm	76.1 (10.6)	3.4 (0.3)	21.9 (1.5)
Forest floor of old-growth stand			
O_a and O_e layers	452.9 (10.2)	8.0 (0.4)	59.7 (3.5)
O_i layer	436.6 (11.8)	9.4 (0.4)	48.6 (2.6)
Soil of old-growth stand			
0–10 cm	52.6 (3.7)	1.9 (0.1)	28.0 (1.2)
10–20 cm	33.8 (2.1)	1.4 (0.1)	24.6 (1.1)

with published values for old-growth forests in the region (Homann et al. 1998). This value includes neither the 93.5 Mg C ha^{-1} of coarse woody debris in the old-growth stand nor dead roots (M.E. Harmon et al., Oregon State University, Corvallis, OR, unpublished observations). The amount of C in aboveground coarse woody debris (stumps, logs) at the 40-year site was not quantified, nor that in the numerous buried stumps and logs at the 20-year site, which probably contributed to the higher soil C concentrations as observed in other logged stands (Edmonds 1991).

Table 2. Pools (Mg ha^{-1}) of carbon and nitrogen in the forest floor and soils of three stands at and near the Wind River Canopy Crane Research Site. Values are means with standard errors in parentheses.

Component	Carbon	Nitrogen
Forest floor of 20-year-old stand		
O_a and O_e layers	4.6 (0.51)	0.09 (0.01)
O_i layer	7.4 (1.47)	0.18 (0.03)
Soil of 20-year-old stand		
0–10 cm	73.0 (9.31)	1.9 (0.14)
10–20 cm	84.0 (15.6)	1.6 (0.02)
Total for 20-year-old stand	169.0	3.77
Forest floor of 40-year-old stand		
O_a and O_e layers	8.0 (1.07)	0.19 (0.02)
O_i layer	8.1 (1.06)	0.26 (0.03)
Soil of 40-year-old stand		
0–10 cm	94.2 (9.75)	3.9 (0.54)
10–20 cm	80.3 (11.3)	3.6 (0.31)
Total for 40-year-old stand	190.6	7.95
Forest floor of old-growth stand		
O_a and O_e layers	7.3 (1.07)	0.13 (0.03)
O_i layer	6.3 (1.06)	0.15 (0.02)
Soil of old-growth stand		
0–10 cm	56.8 (4.02)	2.1 (0.14)
10–20 cm	40.6 (2.58)	1.7 (0.02)
Total for old-growth stand	111.0	4.08

The higher N concentrations in the soil and forest floor at the 40-year site compared with the other sites (Tables 1 and 2) were attributed to the presence of red alder, an N-fixer (Cole et al. 1990, Binkley et al. 1992, Bormann et al. 1994). The low N concentrations and high C/N ratios at the old-growth site are comparable with other Andisols in the region (e.g., Homann et al. 1998).

Soil respiration

Soil respiration rates are dependent on soil temperature and soil water (e.g., Raich and Schlesinger 1992, Conant et al. 1998, Law et al. 1999, Raich and Tufekcioglu 2000, Rayment and Jarvis 2000). During 1999, the pattern of soil CO_2 efflux from the three sites followed the seasonal pattern of temperature (Figure 1). The CO_2 efflux rates from the 40-year site were significantly less than from the other sites during the growing season. Values for the 20-year and old-growth sites differed between sampling times, but showed no consistent differences. Regressing the results of Arrhenius plots between soil temperature and soil respiration resulted in r^2 values of 0.92, 0.88 and 0.84 ($P < 0.01$ in all cases) for the 20- and 40-year and old-growth sites, respectively. The addition of soil water content in the regression equations reduced r^2 values. Soil water content at the 40-year site was statistically greater during the growing season than at the other stands. Estimates of annual C released through soil efflux, determined by regression, were 1367, 883 and 1194 g m^{-2} $year^{-1}$ for the 20-year, 40-year and old-growth sites, respectively.

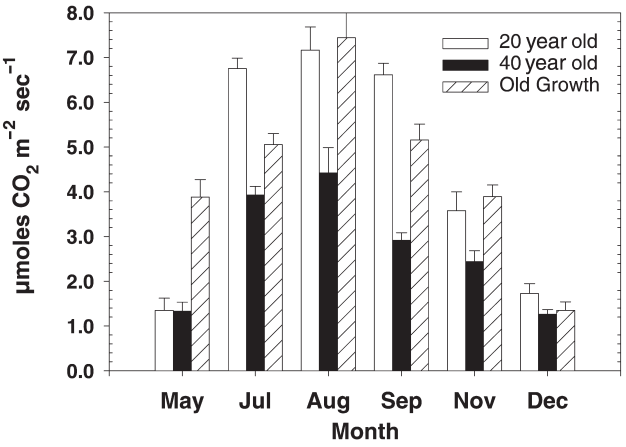

Figure 1. Soil respiration during 1999 in a 20-year-old, 40-year-old and an old-growth Douglas-fir stand at the Wind River Canopy Crane Research Facility in south-central Washington. Bars represent the means and standard errors of combined morning and late afternoon measurements.

Soil bag experiment

The mean (± SE) biomass (ash-free biomass) of live fine roots measured in the bags after one year was 172.6 ± 14.5, 120.5 ± 12.4 and 387.8 ± 24.0 g m^{-2} for the 20-year-old, 40-year-old and old-growth stands, respectively. The amount of fine root biomass within the soil bags after 1 year is undoubtedly an underestimate of actual fine root production because some root pruning occurred when the bags were buried. However, the data provide a relative comparison of the productivity of the fine roots at the three sites (Persson 1990). The lower amount of fine-root biomass measured in the 40-year-old stand compared with the other stands supports the hypothesis that belowground allocation of C decreases with increasing fertility. However, total production, manifested in aboveground growth, increased in the 40-year-old stand compared with that in Douglas-fir stands without N-fixers (Cole et al. 1990, 1995, Binkley et al. 1992, Kromack et al. 1999). The high N tissue concentrations in needles and litterfall at the 40-year site were also a reflection of the presence of N fixers in the stand.

Significant differences were noted between the initial soil C and N concentrations of the soil bags and those in soil samples extracted after 1 year. In general, the soil in the bags at the 20- and 40-year-old stands lost C and N, whereas C and N concentrations of soil in the bags at the old growth stand increased (Table 3). Although based on only 1 year of data, it appears that, following a disturbance (i.e., sieving and placing the soil in soil bags), the soils of the younger stands lost C, whereas the old-growth soils gained C.

Table 3. Changes in C and N concentrations (g kg^{-1}) in the soil bags after a 12-month period at three stands at and near the Wind River Canopy Crane Research Facility. Initial = homogenized soil in bags at the beginning of the experiment. Values for the initial soil bags are the means of five random samples from the homogenized soil from each stand. Values for the 1-year soil bags are the means of 12 bags from the 20- and 40-year-old stands and 16 bags from the old-growth stand. An asterisk (*) denotes a statistical difference ($P < 0.05$) between the concentrations at the beginning of the experiment and after 1 year.

Stand/soil depth	Element	Initial	One year
20-Year-old stand			
0–10 cm	C	54.3 (3.9)	45.7 (0.9)*
	N	1.75 (0.11)	1.50 (0.04)*
10–20 cm	C	54.3 (3.9)	45.4 (1.8)*
	N	1.75 (0.11)	1.38 (0.04)*
40-Year-old stand			
0–10 cm	C	75.3 (2.8)	71.8 (1.1)
	N	3.78 (0.10)	3.63 (0.07)
10–20 cm	C	75.3 (2.8)	70.9 (1.2)*
	N	3.78 (0.10)	3.48 (0.05)*
Old-growth stand			
0–10 cm	C	31.8 (1.7)	38.3 (1.1)*
	N	1.14 (0.07)	1.47(0.04)*
10–20 cm	C	31.8 (1.7)	36.0 (0.05)*
	N	1.14 (0.07)	1.22 (0.02)

Litterfall

Figure 2 depicts the annual litterfall at the three sites and the turnover times (forest floor mass/annual litterfall) for 1999–2000. Data for 2000–2001 showed statistically similar results, but long-term data from the H.J. Andrews Experimental Forest show that litterfall can vary by a factor of two from year to year (J. Means, Oregon State University, Corvallis, OR, personal communication). Although variability was high, because of the limited number of samples at the 20- and 40-year-old stands, there were significant differences in the proportions of needle/leaf, twig and branch, and reproductive structures in the litterfall among stands.

Discussion

The lack of replication of the different age stands limited statistical comparison; however, differences in forest floor and soil C and N were apparent among the three stands. The rapid turnover times of forest floor organic matter combined with the small amount of forest floor biomass are responses to the relatively warm and wet environment. Data taken from a study by Edmonds (1979) on a chronosequence of Douglas-fir stands showed similar forest floor organic matter turnover times to the 20-year-old stand, but significantly longer turnover times than estimated for the 40-year-old stand. Nitrogen fertility of the 40-year-old stand as indicated by soil and foliar N concentrations (N. McDowell, University of Oregon, Corvallis, OR, unpublished observations) distinguished this stand from the other stands. Compared with the 20-year-old and old-growth stands, the 40-year-old stand showed increased aboveground productivity (Johnson and Curtis 2001)

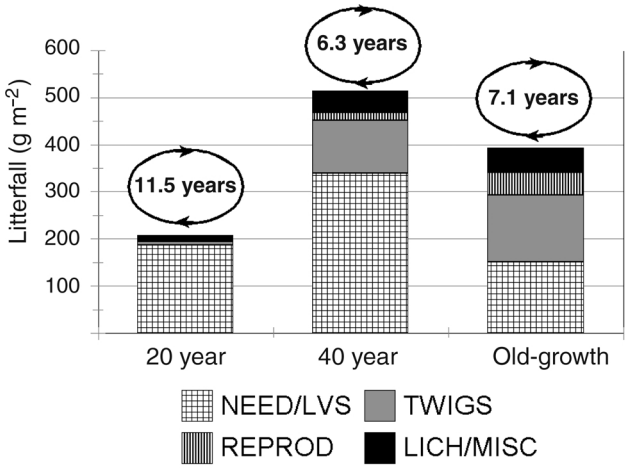

Figure 2. Annual litterfall measured at a 20-year-old, 40-year-old and an old-growth Douglas-fir stand at the Wind River Canopy Crane Research Facility in south-central Washington State from fall 1999 to fall 2000. Values in circles above bars indicate the calculated turnover time for forest floor organic matter (Oe, Oi and Oa layers). Abbreviations: NEED/LVS = needles and leaves; TWIGS = twigs and branches < 1.0 cm in diameter; REPROD = reproductive structures; and LICH/MISC = lichens, mosses and miscellaneous and unidentified plant parts.

that was manifested in increased litterfall and decreased partitioning of production to belowground biomass (Perry 1994), and a greater concentration and pool size of C in the upper soil layer.

Annual soil CO_2 efflux at the three sites was higher than the values summarized by Raich and Schlesinger (1992) from published studies; however, the data from many of those studies were based on the alkali absorption technique that tends to underestimate CO_2 efflux. Rayment and Jarvis (2000) recently estimated soil CO_2 efflux rates of 896 g C m^{-2} $year^{-1}$ for a southern expanse of boreal black spruce (*Picea mariana* (Mill.)) forest. Law et al. (1999) estimated a soil CO_2 efflux rate of 683 g C m^{-2} $year^{-1}$ for an old-growth ponderosa pine (*Pinus Ponderosa* Dougl. ex Laws.) stand that had less than a third of the C storage in its belowground system than the old-growth Douglas-fir stand. Knapp et al. (1998) reported soil CO_2 efflux rates of between 1279 and 2141 g C m^{-2} $year^{-1}$ for tall-grass prairie.

To determine whether the belowground component of a forest stand is a C source or sink, the live root contribution (autotrophic respiration) to total soil CO_2 efflux rates must be determined before measurements of soil respiration can be used to infer rates of long-term soil C storage (Hanson et al. 2000). Estimates of the contribution of live root respiration to total soil efflux vary from 30 to 70% (Schlesinger 1977, Raich and Schlesinger 1992). Ryan et al. (1997) reported that live root respiration accounted for 52 to 70% of total autotrophic respiration. Based on an earlier study, I estimated that root (and mycorrhizal) respiration in the old-growth stand comprised 60% of total soil CO_2 efflux (J.M. Klopatek, unpublished observations) (cf. Ryan et al. 1997, Hanson et al. 2000, Raich and Tufekcioglu 2000).

Fine-root biomass is linearly related to soil respiration (Pregitzer et al. 2000). The relatively low soil CO_2 efflux in the 40-year-old stand reflects its lower fine root production as a result of increased site fertility. Among the three stands, the old-growth stand had the highest fine-root biomass, whereas the 20-year-old stand had the highest annual soil CO_2 efflux but a lower fine-root biomass and presumably a higher decomposition rate of the organic C pool.

The litterfall data reflect differences in the proportion of biomass allocated to different structures and the effect of a closed canopy on needle maintenance in Douglas-fir. The age of the old-growth stand at the WRCCRF suggests that litterfall and decomposition of the forest floor are in steady state. The data indicate that the forest floor organic matter of the old-growth site had a turnover time of 6.6 to 7.1 years, which corresponds with that found for an old-growth forest in Oregon (Fogel and Hunt 1979), but is higher than that (12.1 years) at Watershed 10 of the H.J. Andrews (Grier and Logan 1977).

It is not known how much of total annual net primary productivity (NPP) is allocated to belowground biomass. The ingrowth data for the first year of the experiment provide only a relative comparison of the three stands and cannot be compared to published values for similar stands (Keyes and Grier 1981, Vogt et al. 1987). Fogel and Hunt (1983) determined that belowground production contributed more than 70% of the total NPP of a 35–50-year-old Douglas-fir stand, which is comparable with that found by Vogt et al. (1983) for Pacific silver fir stands (60.4 and 71.8% for a 23- and 180-year-old stands, respectively).

Many investigators have used the method developed by Raich and Nadelhoffer (1989) to determine total root carbon allocation (TRCA). The TRCA is largely a function of the magnitude of soil CO_2 efflux because fine-root biomass is linearly related to soil respiration (Pregitzer et al. 2000). Thus, TRCA = soil respiration – litterfall + export + $C_{root} - C_{soil}$. The TRCA was calculated only for the old-growth stand because the method is limited to mature forests that are at steady state relative to their C fluxes (Nadelhoffer et al. (1998). For the old-growth site at the WRCCRF a TRCA of ~1300 g C m^{-2} $year^{-1}$ was determined. This value approximates the value of 1100 g C m^{-2} $year^{-1}$ estimated from unpublished data; however, both estimates are based on samples collected over a limited time. Bosquet et al. (2000) has argued that steady-state carbon balances of forests is a relative term. Thus, the TRCA method should perhaps only be used for long-term averaging of litterfall and soil CO_2 efflux rates.

The data presented here suggest that the belowground components of the 20- and 40-year-old stands are sources of atmospheric C, yet all three stands are sinks during the summer season. Similarly, Chen et al. (2002) report that all three stands are net sinks of C during the summers of 1998 and 1999. It is concluded that a more intensive and extensive investigation of successional stands in the region is needed to obtain an approximation of when these stands switch from a C source to a C sink and how cutting or other disturbances affect the timing of this switch.

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