Ecosystems (2004) 7: 498–512
DOI: 10.1007/s10021-004-0140-9

ECOSYSTEMS

Production, Respiration, and Overall Carbon Balance in an Old-growth *Pseudotsuga-Tsuga* Forest Ecosystem

Mark E. Harmon,[1]* Ken Bible,[2] Michael G. Ryan,[3] David C. Shaw,[2] H. Chen,[1] Jeffrey Klopatek,[4] and Xia Li[5]

[1]*Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, USA;* [2]*College of Forest Resources, University of Washington, Seattle, Washington 98195, USA;* [3]*Rocky Mountain Research Station, USDA Forest Service, Fort Collins, Colorado 80526, USA;* [4]*Department of Plant Biology, Arizona State University, Tempe, Arizona 85287, USA;* [5]*Department of Biology, Stanford University, Stanford, California 94305, USA*

Abstract

Ground-based measurements of stores, growth, mortality, litterfall, respiration, and decomposition were conducted in an old-growth forest at Wind River Experimental Forest, Washington, USA. These measurements were used to estimate gross primary production (GPP) and net primary production (NPP); autotrophic respiration (R_a) and heterotrophic (R_h) respiration; and net ecosystem production (NEP). Monte Carlo methods were used to calculate uncertainty (expressed as ± 2 standard deviations of 200–400 calculations). Live carbon (C) stores were 39,800 g C m^{-2} (34,800–44,800 g C m^{-2}). The store of C in detritus and mineral soil was 22,092 g C m^{-2} (20,600–23,600 g C m^{-2}), and the total C stores were 61,899 g C m^{-2} (56,600–67,700 g C m^{-2}). Total NPP was 597 g C m^{-2} y^{-1} (453 to 741 g C m^{-2} y^{-1}). R_a was 1309 g C m^{-2} y^{-1} (845–1773 g C m^{-2} y^{-1}), indicating a GPP of 1906 g C m^{-2} y^{-1} (1444–2368 g C m^{-2} y^{-1}). R_h, including the respiration of heart rots in tree boles, was 577 g C m^{-2} y^{-1} (479–675 g C m^{-2} y^{-1}). Long-term NEP was estimated to be +20 g C m^{-2} y^{-1} (−116 to +156 g C m^{-2} y^{-1}), indicating this stand might be a small sink. These estimates contrast with the larger sink estimated at the same site using eddy-flux methods. Several hypotheses to explain this discrepancy were explored, including (a) undetected biomass increases, (b) underestimates of NPP, (c) unmeasured losses, and (d) a temporal mismatch between the two sets of measurements. The last hypothesis appears the most likely.

Key words: autotrophic respiration; carbon flux; carbon stores; decomposition; gross primary production (GPP); heterotrophic respiration; net ecosystem production (NEP); net primary production (NPP).

Introduction

Net ecosystem production (NEP) of terrestrial ecosystems is a key process to understand when actively managing the carbon (C) cycle. Despite the need to understand how and why this rate varies in space and time, most ecosystem studies have focused on net primary productivity (NPP). While knowledge of controls of NPP is important, several other processes including heterotrophic respiration (R_h) and disturbance also have to be understood before NEP can be determined (Randerson and others 2002).

Received 15 February 2002; accepted 28 August 2002; published online 12 May 2004.
*Corresponding author; e-mail: mark.harmon@oregonstate.edu

There are several approaches to estimating NEP in forests. Long-term observations of growth, mortality, litterfall, harvest, and decomposition, coupled with detritus and soil stores, as well as short-term measurements of respiration can be used in the "aggregated" flux method (Grier and Logan 1977; Law and others 2000). Alternatively, NEP can be estimated by measuring the change in total C stores over time by using the delta-stores method (Turner and others 1999). Simulation models have also been used to predict changes in NEP, either in response to climate change, carbon dioxide (CO_2) increases, and increased nitrogen deposition [for example, see Lloyd (1999)] or disturbance, including timber harvest [for example, see Harmon and others (1990)]. These models are largely based on a synthesis of ground-based measurements similar to the aggregated-flux method. Most recently, estimates of NEP for entire ecosystems (that is, not one part at a time) have been derived from micrometerologic methods such as eddy covariance (Wofsey and others 1993; Goulden and others 1996). Given that each of these methods has developed at different times and places, there have been very few comparisons of all methods at one place and time. Research currently being conducted at the Wind River Experimental Forest, Washington, USA, provides such an opportunity.

Our objectives in this report are (a) to use the ground-based, aggregated-flux method to estimate gross primary production (GPP) and net primary production (NPP), respiration of autotrophs (R_a) and heterotrophs (R_h) of an old-growth forest at Wind River; (b) to use these numbers to estimate the net ecosystem production (NEP) of this forest; and (c) to compare our long-term, ground-based estimates of NEP with those derived by eddy covariance (Paw U and others 2004) and simulation models [that is, the Soil–Plant–Atmosphere model (Winner and others 2004)]. We then evaluate alternative hypotheses that might resolve the differences (if any) in the estimates derived from these three independent methods.

Study Area

This study was conducted at the Wind River Canopy Crane Research Facility (WRCCRF). The site is typical of old-growth forests west of the Cascades (Shaw and others 2004). A detailed description of this old-growth stand is presented by Parker and colleagues (2004). The forest is classified as a western hemlock–salal cover type and is estimated to be approximately 500 years old. Dominant tree species are Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Dominant understory shrub species are vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), and dwarf Oregon grape (*Berberis nervosa*). The climate is characteristic of a temperate winter-wet, summer-dry climate. Annual precipitation totals 2467 mm, with less than 10% occurring between June and September. Mean annual temperature is 8.7°C. Soils are of the Stabler series, coarse textured and developed on 2–3 m of volcanic ejecta over basalt bedrock. Texture ranges from shotty loam to clay with coarse particles in the top 1 m averaging 3% of the soil volume.

Methods

Live Biomass

Tree Biomass. Tree biomass, mortality, and ingrowth were estimated around the Wind River canopy crane in a 4-ha plot (hereafter, the *crane plot*) that was established in 1994 and divided into four 1-ha quadrants, each of which were further divided into 16 numbered 25-m × 25-m subplots. All trees larger than 5-cm DBH (diameter at breast height) were measured for diameter and height as well as tagged with aluminum tags at breast height (1.3 m). Diameter was measured with a tape to the nearest 0.1 cm. Annual surveys were conducted between 1995 and 1999 to determine the trees that died. All surviving trees and those that grew into the minimum diameter class (that is, ingrowth) were measured in summer 1999. Biomass of all live tree parts and volume for the bole were calculated using allometric equations (Gholz and others 1979; Means and others 1994). Species-specific allometric equations were used when available, and substitutions for some minor species (for example, *Abies grandifolia* and *Taxus brevifolia*) were used. Coarse-root allometric equations were used for roots larger than 5 mm in diameter. The mass of roots 2–5 mm in diameter from fine-root cores (see below) was added to the allometric equation estimates to calculate the total mass of coarse roots. Leaf mass was estimated using a sapwood area-based estimate using DBH-sapwood thickness and leaf-area relationships developed for the H. J. Andrews Experimental Forest in the central Cascades of Oregon (Gholz and others 1976; Waring and others 1982; Means and others 1999). Sapwood volume was estimated from equations developed by Harcombe and colleagues (1990) that predict the proportion of the total bole in sapwood from DBH.

Table 1. Estimated Stores of Carbon and Rates of Production Associated with Live Biomass; Mean (Standard Error)

Pool	Store	Δ Stores	Mortality/Litterfall	NPP
	g C m^{-2}		g C m^{-2} y^{-1}	
Stem sapwood	6567 (198)	2 (1)	30 (9)	32 (9)
Stem heartwood	15,351 (1151)	26 (2)	50 (13)	76 (13)[d]
Stem bark	3337 (263)	2 (4)	12 (2)	14 (3)
Live branches	4489 (112)	8 (10)	100 (34)	108 (34)
Dead branches	318 (20)	0 (0)[a]	3 (1)	3 (1)
Tree foliage	941 (322)	0 (0)[a]	135 (12)	150 (14)[e]
Coarse roots	8122 (639)	21 (7)	30 (5)	51 (7)
Fine roots	362 (26)	0 (0)[a]	91 (16)[f]	91 (16)
Understory shrubs	144 (37)	0 (0)[a]	26 (5)[b]	26 (5)
Understory herbs	76 (8)	0 (0)[a]	40 (8)[c]	40 (8)
Epiphytes	100 (25)	0 (0)[a]	6 (1)	6 (1)
Total	39,807 (2479)	59 (24)	523 (69)	597 (72)[e]

[a]*The net change in stores in these pools was assumed to be zero.*
[b]*Assumed that all leaves were from shrubs that died each year and that 0.5%–1.0% of the stems died. Litter traps indicate that the value of shrub litterfall may be as low as 1 g C m^{-2} y^{-1}.*
[c]*Assumed that litterfall from herbs was 40%–60% of live stores to account for the fact some small woody-stemmed, evergreen plants are included in the herb category.*
[d]*Assumes no heart rot is present.*
[e]*Includes grazing of 15 g C m^{-2} y^{-1}.*
[f]*Assumes 20%–30% of fine roots die annually.*
C. carbon; and NPP, net primary production.

Fine Roots. In October 2000, 20 soil cores of 5-cm diameter to a depth of 1 m were removed to estimate biomass of fine roots less than 2 mm in diameter. In each 1-ha quadrant of the crane plot, five cores were sampled at random distances along transects placed diagonally across the quadrant. Organic horizons were sorted by hand to remove live and dead fine roots. Mineral soil was subdivided into 20-cm depths and then washed using a root elutor to separate roots. Roots were sorted into size classes and live versus dead, oven dried at 55°C, and weighed. Subsamples of root material were placed in an oven at 550°C for 4 h to determine ash-free dry weights. Means and standard errors were calculated using all 20 samples as a basis.

Understory Plants. The aboveground biomass of understory shrubs and trees larger than 5-cm DBH was estimated at 21 locations within the T. T. Munger Research Natural Area (RNA) by recording their diameter at the base (except salal and Oregon grape, which were treated as herbs) within a 25 × 1-m belt transect at each location. This RNA surrounds the crane plot (Shaw and others 2004). These sampling locations were in existing plots systematically placed throughout the RNA at 100-m spacing (Smithwick and others 2002). The cover of mosses, herbs, salal, and Oregon grape was determined in 25-, 20-, by 50-cm microplots systematically placed along each of the 25-m belt transects. The biomass of understory plants was calculated using allometric equations (Means and others 1994). In cases where equations for a species (particularly herbaceous ones) did not exist, equations from similar species were used.

Epiphytes. The biomass of epiphytes was based on work by McCune (1993) and McCune and colleagues (1997) from aerial and ground-based surveys conducted at the Wind River site and other old-growth Douglas-fir forests in the Pacific Northwest region. The most precise estimates of epiphyte biomass were for lichens. We therefore multiplied the estimated biomass of lichens by 2, given bryophytes and lichens are of approximately equal abundance (McCune 1993).

Net Primary Production

NPP estimates of the woody parts of trees (that is, sapwood, heartwood, bark, branches, and coarse roots) were assumed equivalent to the change in live stores, the losses from mortality (that is, entire death of trees), and ingrowth gains from trees that grew into the minimum size class:

$$NPP_w = \Delta stores_w + mortality_w + ingrowth_w$$

Where w represents a woody tree part (Clark and others 2001). Note that Δstores for heartwood did not account for the possible loss from heart-rot decomposition. We accounted for those losses under heterotrophic respiration (see below). For nonwoody, aboveground components, NPP was

Table 2. Estimated Rates of Production and Respiration Associated with Live Biomass; Mean (Standard Error)

Pool	R_a	NPP	GPP
		g C m^{-2} y^{-1}	
Stem sapwood	153 (11)	32 (9)	185 (13)
Stem heartwood	NA[a]	76 (13)[a]	76 (11)
Stem bark	NA[b]	14 (3)	14 (3)
Live branches	7 (0.5)	108 (34)	115 (32)
Dead branches	NA[c]	3 (1)	3 (1)
Tree foliage	577 (233)	150 (14)[d]	727 (218)
Coarse roots	167 (21)	51 (7)	218 (20)
Fine roots	274 (30)	91 (16)	365 (32)
Understory shrubs	10 (4)	26 (5)	36 (6)
Understory herbs	57 (15)	40 (8)	97 (16)
Epiphytes	64 (19)	6 (1)	70 (17)
Total	1309 (232)	597 (72)	1906 (231)

[a] *Does not account for possible losses from heart rot in range of 0–46 g C m^{-2} y^{-1}.*
[b] *Inner bark accounted for in sapwood calculation.*
[c] *Accounted for under detritus in Table 3.*
[d] *Includes aboveground grazing of 15 g C m^{-2} y^{-1}; the litterfall portion was 135 (12) g C m^{-2} y^{-1}, mean (standard error).C, carbon; GPP, gross primary production; NPP, net primary production; and R_a, autotrophic respiration.*

estimated from litterfall and tree foliage grazing estimates. A total of 20 litter traps, 40 × 40-cm squares lined with fine mesh, were used to collect fine litterfall between June 1997 and December 1999. The 0.5-m-tall traps were placed randomly at five fixed locations in each of the 1-ha quadrants of the 4-ha crane plot. Samples were collected monthly (except when snow depth exceeded trap depth) and then oven-dried and weighed to the nearest 0.001 g, and sorted into nine categories: green conifer needles; brown conifer needles; nonconifer leaves; twigs (woody); cones, seeds, other reproductive parts; cyanolichens; other lichens; moss; and miscellaneous materials. Woody material larger than 1 cm in diameter was excluded, and accounted for under mortality. To estimate spatial variance, the mean litterfall from each of the 20 traps was used for the 2.5-year period of observation. For understory herbs, we estimated aboveground NPP assuming Δstores was 0 and that 40%–60% of the aboveground biomass died annually. A portion less than unity was used because approximately 50% of the herb layer was comprised of woody evergreen shrubs with a leaf life span of 2 years. For shrubs, we assumed the litterfall portion of NPP was captured in litter traps and was represented by nonconifer leaves. The mortality of woody shrubs was not measured, but was estimated by assuming 1% of the stems died annually. Fine-root production was estimated by assuming fine-root biomass was not increasing and that annual fine-root mortality was 20%–30%. This preliminary mortality estimate was from 40 minirrhizotron tubes in the crane plot that were visited monthly over 1999 and based on standard methods (Fahey and others 1999).

We estimated aboveground grazing of trees from visual surveys of foliage damage in the canopy crane plot conducted in 1995, 1996, and 1999. We did not account for belowground herbivory (other than that associated with fine-root mortality) and assumed the belowground herbivory flux to be zero. In 1995 and 1996, the fraction of the current-year foliage that was damaged by herbivory and other unknown causes was noted in a systematic survey of the lower, middle, and upper canopy by using the canopy crane for access. We assumed that all this damage was from herbivory. In 1999, herbivory damage to all age classes of foliage was visually estimated using a similar survey method as earlier. To estimate the mass of herbivory, we multiplied the fraction damaged by the appropriate foliage mass (that is, current-year mass for 1995 and 1996 and total mass for 1999). We assumed that all herbivory resulted in respiration, either directly or in the death and decomposition of herbivores. Because the majority of aboveground herbivory is probably from insects, this assumption is quite reasonable.

Autotrophic Respiration

Autotrophic respiration was estimated as a rate constant times the biomass times a temperature

Table 3. Estimated Stores of Carbon, Rate Constants, and Fluxes Associated with Grazers, Heart Rot, Detritus and Soil Pools; Mean (Standard Error)

Pool	Store	Rate Constant[j]	R_h
	$g\ C\ m^{-2}$	y^{-1}	$g\ C\ m^{-2}\ y^{-1}$
Logs *Pseudotsuga*	1920 (170)	0.014 (0.006)	27 (11)
Thuja	50 (20)	0.007 (0.003)[h]	0.3 (0.2)
Other	2220 (210)	0.018 (0.003)	40 (7)
Subtotal	4190 (310)	0.016	67 (12)
Snags *Pseudotsuga*	2170 (390)	0.021 (0.009[c])	46 (19)
Thuja	10 (1)	0.011 (0.005)[h]	0.1 (0.1)
Other	710 (140)	0.028 (0.004)[c]	20 (4)
Subtotal	2890 (430)	0.023	66 (19)
Fine woody debris Downed	450 (70)	0.064 (0.010)	29 (5)
Dead on snags	150 (40)[a]	0.050 (0.001)[d]	8 (2)
Dead attached	320 (20)	0.050 (0.001)[d]	16 (1)
Subtotal	920 (82)	0.058	53 (7)
Litter	1780 (40)	0.105 (0.020)[e]	187 (37)
Dead fine roots	476 (112)	0.191 (0.013)[e]	91 (21)
Decomposed wood	940 (120)	0.007 (0.003)[f]	7 (3)
Dead coarse roots *Pseudotsuga*	927 (80)[b]	0.011 (0.003)	10 (3)
Thuja	10 (0)[b]	0.019 (0.002)[g]	0.2 (0.1)
Other	659 (60)[b]	0.019 (0.002)	12 (1)
Subtotal	1596 (103)	0.014	22 (1)
Mineral soil C to 100 cm	9300 (530)	0.005 (0.0013)	46 (12)
Grazer respiration			15 (2)[i]
Stem heart rot			23 (13)
Total	22,092 (750)	0.026	577 (49)

[a] *Estimated from a ratio of dead branches to dead boles. Only class 1 and 2 snags were considered to have dead branches.*
[b] *Estimated from the ratio of dead roots to snag and log mass.*
[c] *Based on rate constants for logs adjusted upward to match the mean difference measured by Graham (1982).*
[d] *Based on rate constants for downed fine woody debris and adjusted according to difference between downed and suspended branches in time series experiments.*
[e] *Determined through extrapolation of long-term data on decomposition.*
[f] *Based on changes in density of class 5 logs over a 19-year period.*
[g] *Assumed to be the same as Tsuga.*
[h] *Assumed to be half the rate of Pseudotsuga.*
[i] *All grazing consumption assumed to be respired.*
[j] *A rate constant is the proportion of each pool turning over each year.* R_h, *heterotrophic respiration.*

adjustment. Measurements of foliar respiration, taken at daytime after shading, were the only autotrophic respiration measurements made at the WRCCRF. Therefore, our estimates of R_a are preliminary and rely on measurements of the same species at other locations. The effect of temperature on diurnal and annual respiration totals was estimated (Ågren and Axelsson 1980), with a mean annual temperature of 8.7°C; diurnal temperature amplitudes of 5°C for air and foliage temperature and 1°C for soil temperature; and 15°C for annual temperature amplitude. The measured response of respiration to temperature was used when available, but a Q_{10} of 2 was assumed otherwise (Amthor 1989). We estimated both maintenance (R_m) and construction (R_c) respiration (Ryan 1991a). For woody R_m, we used rates per unit sapwood C and assumed that branches, coarse roots, and shrubs were 100% sapwood. Large branches and coarse roots likely have heartwood for these large trees, so this assumption may overestimate sapwood biomass. However, this is offset by the fact that respiration rates for branches and coarse roots are likely to be greater than for stems (Sprugel 1990; Ryan and others 1995, 1996). We used respiration rates measured in the autumn after growth had ceased, and we assumed such rates apply for the entire year. We estimated foliage maintenance respiration for night only, assuming night temperatures averaged 3.7°C (mean annual temperature minus diurnal amplitude) and that yearly foliar respiration rates were the average of rates measured in summer and autumn. We assumed that respiration rates per mass of herbs and epiphytes were the same as conifer foliage. We estimated construction respiration as 25% of NPP for all live components (Ryan 1991b). For all these terms, we assumed that the respiration rates were accurate to

within ±10% of the actual number. This variation, and that caused by variation in the pool sizes, were used to determine a standard error for all R_a fluxes.

Gross Primary Production

GPP was estimated by adding the autotrophic respiration fluxes to the net primary production (NPP) fluxes:

$$GPP = NPP + R_a$$

Respiration losses associated with heart rot within living trees was assumed to be part of heterotrophic respiration (see below).

Detritus and Mineral Soil: Stores and Decomposition

Coarse Woody Detritus. Downed coarse woody detritus (larger than 10 cm in diameter at the large end) was measured using the line-intercept method (Harmon and Sexton 1996). The diameter, species, and decay class of all downed wood crossing the boundaries between all the 25 × 25-m subplots was measured within the 4 ha that was inventoried for live trees and in another 8 ha of plots that had been established next to the crane plot. All the plots are contiguous, forming a 12-ha sample. All standing dead trees larger than 10-cm DBH and more than 1 m tall (snags) were inventoried on the entire 12-ha set of plots by measuring the basal and top diameters and height as well as assigning them to decay classes. Volume was determined for each species and decay class of logs and snags, and these were converted to mass by multiplying by species and decay class specific density values (Harmon and Sexton 1996). To determine variation at the scale of 1.0 ha, we computed the mean mass of logs and snags separately for each of the 12 ha that was sampled. Decomposition rate constants of logs were based on resampling 50 logs in 1998 originally sampled by Sollins (1982). The location of the logs was in the T. T. Munger RNA. At both times, a single cross section was removed from each log by using a chainsaw. The diameter and thickness of the cross section were used to calculate the volume (including any hollows). Dry mass was determined by weighing entire cross sections in the field and determining the moisture content from a subsample oven dried at 55°C. Density was calculated as dry mass divided by moist volume. The mean density of Douglas-fir and all other species was calculated for each sample time, and the ratio of the 1998 to 1979 values was used to calculate the decomposition rate constant. We assumed that changes in density equaled losses of C, although a very small fraction (less than 1%) of the dissolved organic carbon (DOC) leached from logs over this period may have accumulated in soil underlying the logs (J. Spears personal communication). Moreover, because fragmentation was not estimated, we assumed that the rate of C loss from fragments was the same as from logs. This assumption likely underestimates losses because smaller fragments probably decompose faster than the logs. The upper bound of the decomposition rate constant was estimated by adding 1 standard error (SE) to the 1979 mean density and then subtracting 1 SE from the 1998 mean density before recomputing the decomposition rate constant. The lower bound was estimated by the inverse process. This range was then converted to a standard error by dividing the range by 4. The decomposition rate constants of snags could not be measured directly. We therefore used the mean ratio of snag to log decomposition rate constants determined by Graham (1982) to adjust snag decomposition rate constants upward. The mean ratio was 1.52, indicating snags at this site decompose 1.5 times faster than logs. Based on the variation in this ratio, however, the value is expected to range between 1.12 and 1.92. This source of variation was included in our estimate of the standard errors of respiration for snags.

Fine Woody Detritus. The mass of downed fine wood (less than 10 cm in diameter) was measured by harvesting all the wood in one hundred 1 × 1-m quadrats placed systematically at 21 locations throughout the T. T. Munger RNA (Remillard 1999) and randomly within the crane plot. Samples were weighed in the field, and subsamples were dried at 55°C to determine moisture content. Stores in several other fine woody-detritus pools were estimated using assumptions based on the ratios of live parts, the relative decomposition rate of the parts, and their retention on dead boles. Dead coarse roots were estimated assuming they equaled 18%–26% of snag and log mass. This range was calculated by assuming that belowground woody tissues were the equivalent of 15%–20% of the aboveground woody biomass and then simulating the decomposition of the boles and roots at rates indicated by the field data for a 100-year period. The ratio for dead trees was then computed as the ratio of dead coarse roots and dead boles for this entire period. Suspended fine woody debris on snags was estimated using a similar set of calculations. In this case, dead attached branches were estimated to equal 10%–13% of the snag mass. As branches fall off of snags, we assumed that they were only attached to decay class 1 and 2 snags.

The decomposition of fine woody debris on the forest floor was measured by placing fresh branches of Douglas-fir and western hemlock on the forest floor and retrieving four branches of each species after 1, 2, and 3 years. Initial dry mass was determined by weighing the fresh branches and taking subsamples. Final dry mass was determined by removing the entire branches and oven drying them at 55°C. The decomposition rate constant of attached dead branches was estimated from the decomposition of four fresh branches each of Douglas-fir and western hemlock that had been suspended 1–2 m off the forest floor for 2 years in a similar experiment. The decomposition rate constant of dead coarse woody roots was estimated by excavating roots attached to stumps from trees that had been cut 4–50 years prior to excavation (Janisch 2001). A total of 21 Douglas-fir and 21 western hemlock stumps were sampled, with 8–24 roots excavated from each stump. The diameter and length of each root were measured to determine volume, and the dry mass was then determined after drying at 55°C (Chen and others 2001). The decomposition rate constant of each species was calculated using linear regression with a natural logarithmic transformation of root density against time since the tree was cut. The standard error used in uncertainty calculations was that of the regression model.

Forest Floor. The store of C in the forest floor [that is, excluding highly decomposed, buried coarse woody debris (CWD), but including partially and highly decomposed leaves, cones, and wood less than 1 cm in diameter] was determined by two methods. The first used a 5-cm-diameter, stainless-steel corer that was driven into the soil. The core was then extracted, and decomposed wood was separated from the other material. A total of 105 cores grouped in sets of five were taken throughout the T. T. Munger RNA systematically along the 21 transects used for understory biomass sampling. The second method sampled forest floor at the locations of the 10 soil pits by using five similar-sized cores. The forest-floor cores were taken above the sampling face of the soil pit and were pooled for each soil pit. In both cases, the samples were oven dried at 55°C and the ash content determined on a subsample by using a muffle furnace. The decomposition rate constant of the forest floor derived from fine litter and fine roots was estimated from 6-year-long litter decomposition experiments conducted at the H. J. Andrews Experimental Forest. Samples were removed after 1, 2, 4, and 6 years of decomposition. Litterbags were 20 × 20 cm and filled with 10 g of litter. At each sample time, four litterbags of each four species [Douglas-fir, western white pine (*Pinus monticola*), Pacific rhododendron (*Rhododendron macrophyllum*), and vine maple] were harvested and dried to constant mass at 55°C. To estimate the average rate of litter decomposition, we used long-term data to give year-specific decomposition rate constants. We extrapolated the decomposition rate between years 4 and 6 to estimate the long-term pattern of mass loss. We then simulated the accumulation of forest floor that would be expected if the inputs of fine litter were constant for a period of 50 years, and the ratio of input and this simulated store was used as an estimate of the average decomposition rate constant of the forest floor, excluding highly decomposed wood. We used the range of the four species to estimate the range of this parameter

We also measured the amount of decomposed, brown-rotted wood buried within the forest floor. The methods used were as described above for the nonwoody material. Brownish red and highly decomposed wood was separated from the other types of forest-floor material. The decomposition rate constant of this extensively decomposed wood was not measured directly but assumed to encompass the range in decomposition rate constants observed for class 5 logs (that is, the most decayed).

Dead Fine Roots. We measured dead fine roots at the site by using the methods described for live fine roots; however, the recovery of dead fine roots less than 2 mm in diameter was very low (0.2 Mg C ha^{-1} y^{-1}). This may have been caused by a misclassification of dead roots as live or fragmentation during the washing process. Regardless, if this was the correct mass of dead roots, the decomposition rate would have to be 20-fold higher than observed in temperate forests (Chen and others 2002). Although root bags probably underestimate decomposition rates, it is unlikely they do so by this amount. We therefore used the decomposition rate constant for dead fine roots and the mortality of fine roots to estimate the store in dead fine roots. The average decomposition rate constant for dead fine roots was estimated using results from a 4-year-long study from the H. J. Andrews Experimental Forest (Chen 1999). We used a procedure similar to that used for litter, extrapolating the decomposition rate constant for year 4 of the study. The results of four species [Douglas-fir, western hemlock, ponderosa pine (*Pinus ponderosa*), and red alder (*Alnus rubra*)] were used to give a range of possible values. It is highly likely that the rate constants for the Wind River will be similar to that found at the H. J. Andrews Experimental Forest, given that Chen and colleagues (2002) found very

little site-level variation within the forests of the Pacific Northwest.

Mineral Soil. The estimates of C stores in mineral soil are from Remillard (1999). Soil texture, the faction of particles larger than 2 mm in diameter, bulk density, and C content were determined in 10 soil pits that were at least 1 m deep. The latter three variables were determined for three depths: (a) 0–20 cm, (b) 20–40 cm, and (c) 40–100 cm. The fraction of particles larger than 2 mm in diameter was estimated for each sample depth. Bulk density was determined from three 5-cm-diameter cores per depth. C content was determined from a well-mixed bulk sample of approximately 1000 mL taken from the entire depth of each sample zone. Although the lower depth of 100 cm is arbitrary, it represents the zone where most roots occur at this site; sampling to bedrock would have increased the total mineral soil store less than 25% (based on the observed decrease in C content with depth). Samples were air dried and sieved to remove organic as well as mineral particles larger than 2 mm in diameter. Aggregates larger than 2 mm were crushed and also analyzed. C content was determined by using a Leco 2000 C/N/S analyzer (Leco, St. Joseph, MI, USA). Soil C was then calculated based on the C content of all fractions, the bulk density, fraction of coarse particles, and depth. The integrated value to 100-cm depth for each of the soil pits was used to calculate the mean and standard error of soil C stores. We estimated the decomposition rate constant of mineral soil C by two methods. First, an upper bound was set by dividing mineral soil respiration by the mineral soil stores of C. Mineral soil respiration rates were calculated as the difference between total soil respiration and the sum of respiration associated with decomposing dead fine and coarse roots as well as that of the litter and rotten wood in the forest floor. Total soil respiration was determined from the mean efflux of soil CO_2 at eight locations near the canopy crane where a PVC (polyvinyl chloride)-pipe (5 cm deep and 10 cm in diameter) was installed 2 cm deep into the forest floor. CO_2 -flux measurements were made in April, June, August, and October 1997 and January 1998 using a Li-Cor 6250 infrared gas analyzer (Li-Cor Biosciences, Lincoln, NE, USA) equipped with a soil respirometer. Second, a lower bound was set to 0.0025 y^{-1}, based on the results of a long-term laboratory incubation experiment [for example, see Hart and others (1994)] that were adjusted for temperature differences using a Q_{10} of 2.

Heart Rot. In addition to the traditional components of heterotrophic respiration, we included an estimate of losses from heart rot within living trees. This respiration term was important to include, given 16.5% of the Douglas-fir trees at the site had fruiting bodies on their upper boles and many trees had dead tops, swellings at branch nodes, and other indications of heart rot and butt rot. Respiration associated with these rots was not measured directly. We used literature values from forests in the region to set an upper limit (25%) of stem wood volume being attacked by heart rot (Harmon and others 1996). The mass of heart rot was calculated as this fraction of bole wood, adjusted for past decomposition losses (heart rot was assumed to have half the density of sound wood). The lower limit was set at zero even though there is evidence to counter this assumption. We assumed that the rate constant of heart-rot decomposition was equal to the mean of logs.

Carbon Content

The C content of all pools except mineral soil was assumed to be 50%. For mineral soil, the values from the Leco 2000 C/N/S analyzer were used. For the forest floor, the C content of the non-ash portion of samples was assumed to be 50%. The majority of other tissues were woody, and a 50% C content is consistent with values found by Sollins and colleagues (1987) for sound and decayed wood.

Heterotrophic Respiration (R_h)

Heterotrophic respiration for each pool was calculated as the product of the store of detritus or mineral soil (D) and the decomposition rate constant (k):

$$R_h = kD$$

Net Ecosystem Production (NEP)

The net C flux at the site or NEP was calculated as the difference between NPP and R_h:

$$NEP = NPP - R_h$$

Because our method was based on multiple flux terms (some of which involve changes in stores), it should be considered an aggregated-flux approach. This was necessary because we did not have multiple measurements of the various C pools (aside from the live trees) required for the delta-stores approach.

Uncertainty Analysis

Rather than present one estimate of rates, we determined the uncertainty associated with these estimates. Given that our estimates represent long-term average rates and stores, we focused on uncertainty associated with spatial variation at the

approximate spatial scale measured by eddy-flux methods. Hence, our estimates of pool sizes and rate constants included an estimate of spatial variation at the level of multiple hectares, if possible. We also included uncertainty associated with measurements or estimates of pools or rate constants.

A Monte Carlo method was used to calculate the uncertainty of C stores, GPP, NPP, R_a, R_h, and NEP estimates. Here, the values of each flux, store, and each associated rate constant involved in calculations were varied from the mean ±2 SE. We assumed a normal distribution (that is, standard errors of the mean have a normal distribution). The standard error of the mean was used because it reflected the variation in the estimate of the mean at the scale of a hectare. The standard deviation, in contrast, would have represented the variation of individual samples, many with spatial extents far smaller than 1 ha. If the pools or the fluxes were estimated independently, then the value used for a pool or flux was selected independently for each round of calculations. If sizes or rate constants of one pool were used to derive the values of other pools, then variation in the former pool was directly linked to that of the latter. In the case of NEP, uncertainty calculations were done several ways. First, we assumed variation in NPP was independent of R_h. Second, we assumed that part of the variation in R_h was associated with variation in NPP. This is because a major portion (more than 90%) of NPP for this stand was in the form of litterfall and mortality. When these fluxes vary, the store of detritus or soil C also varies and this influences R_h. We therefore linked a portion of the variation in detritus stores (equal to the fraction of NPP that was allocated to litterfall and mortality) to the variation in NPP. The remaining variation in detritus and soil stores varied randomly. Replicate Monte Carlo calculations were conducted, and the mean and standard deviation were computed using an Excel spreadsheet. The standard deviation was used in the final presentation of uncertainty, as it reflected the variation more liberally than did the standard error (which would have been 14–20 times lower, given the sample sizes used). In addition, as the Monte Carlo estimates were for the mean at the scale of a hectare, the standard deviation of these estimates is equivalent to the standard error at this scale (one can think of the standard error as the standard deviation of estimates of the mean). Uncertainty of each estimate was expressed as ±2 SD of 200–400 calculations, depending on the number required for the variance to stabilize.

Results

Biomass

The total store of C in living plants at the Wind River site was 39,800 g C m^{-2} (34,800–44,800 g C m^{-2}) (Table 1). Trees form the majority of this store, comprising 99.2% of the total. Within trees, heartwood is the largest pool, and it comprises 39% of the site store in live plants.

Net Primary Production

The total change in live plant stores (that is, Δ stores) was 59 g C m^{-2} y^{-1} (11–107 g C m^{-2} y^{-1}). Therefore, live stores might have increased over the period of observation as long as heart-rot losses were zero. Given that heart rot is present in the stand, this increase in live stores is likely to be overestimated by up to 46 g C m^{-2} y^{-1}. The differences in change in C stores of live pools is similar to the distribution of live C stores. This observation must be tempered in that we assumed that fine-root, herb, shrub, and epiphyte C was not accumulating (that is, Δ stores was zero). If these other pools increased by the amount observed for trees (0.2% y^{-1}), then live stores would have increased an additional 0.5 g C m^{-2} y^{-1}. Viewed another way, a 10% underestimate in the total change in Δ stores would occur only if nontree pools increased at a rate 10 times that of the tree pools (that is, 2% y^{-1}).

Mortality of plant parts was a major flux (Table 1), and at 523 g C m^{-2} y^{-1} (385–661 g C m^{-2} y^{-1}) was approximately 10-fold larger than Δ stores and 25–50 times larger than grazing. The largest source of mortality was leaf fall, with 135, 26, and 40 g C m^{-2} y^{-1} for tree, shrubs, and herbs, respectively. The contribution from live branches, primarily in the form of twigs and cones, was 100 g C m^{-2} y^{-1}. This high contribution of fine woody litter (32%) to total aboveground fine litterfall is quite typical of coniferous forest ecosystems in this region (Grier 1976; Grier and Logan 1977; Grier and others 1981). Fine-root mortality was 91 g C m^{-2} y^{-1}, based on the observation that 25% of the fine roots were dying annually.

Grazing of tree foliage was low in 1995–96, amounting to 1%–8% of the current year's foliage. Assuming an average damage value of 5%, and that all of this damage was due to herbivory, gives a grazing loss of approximately 10 g C m^{-2} y^{-1}. Data from the visual survey of foliage damage at the site in 1999 indicated that 2% of the conifer foliage and 10% of the understory *Acer circinatum* leaves had damage. Assuming this fraction of all leaves was

eaten indicates the aboveground grazing flux was approximately 20 g C m^{-2} y^{-1}. This range of values, equivalent of between 2% and 4% of total NPP, is typical of past estimates for conifer forests (Schowalter 1989).

Total NPP, including grazing, was estimated to be 597 g C m^{-2} y^{-1} (453–741 g C m^{-2} y^{-1}). Unlike Δ stores, NPP was not related to the biomass distribution, with approximately 4% of the live C pools accounting for approximately 50% of the total NPP.

Autotrophic Respiration and Gross Primary Production

Annual R_a was estimated to be 1309 g C m^{-2} y^{-1} (845–1773 g C m^{-2} y^{-1}) (Table 2). This estimate does not include estimates for foliage "dark" respiration during the day. Aboveground parts accounted for 868 Mg g C m^{-2} y^{-1} or 66% of the total, and coarse and fine roots accounted for the other 441 g C m^{-2} y^{-1}. The net assimilation (A) of foliage of conifers would have to have been 1123 Mg g C m^{-2} y^{-1} if the R_a associated with all tree components except leaves is added to tree NPP terms. Based on NPP and R_a, GPP for this stand would have been 1906 g C m^{-2} y^{-1} (1444–2368 g C m^{-2} y^{-1}). This indicates that NPP is equivalent to approximately 31% of GPP.

Detritus and Soil Pool Stores and Decomposition

The total store of C in detritus and mineral soil was 22,100 g C m^{-2} (20,600–23,600 g C m^{-2}) (Table 3). Adding this store to the live C stores indicates that the Wind River old-growth forest stores a total of 61,899 g C m^{-2} (56,600–67,700 g C m^{-2}), with 36% of that comprised of detritus and mineral soil stores. The two largest pools were mineral soil and woody detritus, which stored 9300 and 9550 g C m^{-2}, respectively. Fine, nonwoody litter was the smallest pool, storing 3180 g C m^{-2} or 14% of the total "dead" stores.

Decomposition rate constants for the detritus and mineral soil pools were highly variable, ranging from 0.005 y^{-1} for mineral soil to 0.191 y^{-1} for fine roots. Dividing the estimate of total R_h by the total soil and detritus store indicates an average decomposition rate constant of 0.026 y^{-1}, which would correspond to a turnover time of 38 years.

Heterotrophic Respiration

Total R_h, including respiration of grazers and heart rot, was estimated to be 577 g C m^{-2} y^{-1} (479–675 g C m^{-2} y^{-1}). The majority of the R_h flux was associated with the forest-floor litter, which, with a value of 187 g C m^{-2} y^{-1}, accounted for 32% of the total flux with 8% of the C store. The next largest R_h flux was from woody detritus of all forms, with a value of 215 g C m^{-2} y^{-1} accounting for 37% of the total flux and slightly less than their proportion of C store (48% of total). Respiration of grazers, though not measured directly, was assumed to be equal to consumption, meaning 10–20 g C m^{-2} y^{-1} is respired by grazers. In our calculations of R_h, we accounted for a heart-rot flux ranging from 0 to 46 g C m^{-2} y^{-1}. This is small relative to the total estimated flux of R_h, but is equivalent to 88%–176% of the estimated heartwood Δ stores and indicates heartwood may not be accumulating in the stand as indicated by our NPP calculations.

Net Ecosystem Production

Using the NPP flux and R_h not corrected for heart-rot respiration indicates that the old-growth forest at Wind River is a C sink of +43 g C m^{-2} y^{-1} (since NEP is referenced to the ecosystem, a positive value indicates a sink and negative value indicates a source). Deducting the estimated range of losses from heart rot would make the stand either a slight source of −3 g C m^{-2} y^{-1} or a slight sink of +20 g C m^{-2} y^{-1}. These results indicate that the Wind River old-growth stand is a slight sink for atmospheric C if heart rot in the stand is not too extensive. The maximum possible range in NEP including heart-rot losses, estimated by adding the lowest possible value of NPP to the highest possible of R_h, is quite wide, bracketing a very moderate source to a very large sink (−222 to +262 g C m^{-2} y^{-1}). Monte Carlo-based estimates including heart-rot losses and assuming independent variation in NPP and R_h are more constrained, indicating −170 to +216 g C m^{-2} y^{-1} would be the most likely range. Partial dependence of NPP and R_h (reflecting the fact that 90% of NPP is in the form of mortality and litterfall) gives an even narrower range of −116 to +156 g C m^{-2} y^{-1}. The latter range is the most likely, given the known dependence of detritus and soil stores on NPP and observation that most NPP at this site offsets losses to mortality.

Discussion

Carbon Stores

Our estimate of total live biomass (39,807 g C m^{-2}) was slightly lower than the 43,500 g C m^{-2} found by Grier and Logan (1977) and considerably lower

than the approximately 73,500 g C m^{-2} reported by Means and colleagues (1992) for *Pseudotsuga*-dominated forests. Within the Pacific Northwest region, Smithwick and colleagues (2002) reported a range between 14,700 g C m^{-2} for eastside *Pinus*-dominated forests and 60,600 g C m^{-2} for coastal *Picea sitchensis–Tsuga heterophylla* forests, with a regional mean of 45,500 g C m^{-2}. Boone and colleagues (1988) reported a live store of approximately 20,000 g C m^{-2} for a mature *Tsuga mertensiana* stand at high elevation, whereas Krumlik and Kimmins (1976) reported approximately 29,000 g C m^{-2} for an old-growth *Abies amabilis–Tsuga mertensiana* stand in British Columbia. Thus, our estimates lie within the range expected in this region.

Our estimates of detritus and mineral soil C stores (22,092 g C m^{-2}) also lie well within the range reported for the Pacific Northwest region. In *Pseudotsuga*-dominated forests, Grier and Logan (1977) and Means and colleagues (1992) reported 19,000 and 39,600 g C m^{-2}, respectively, in detritus and soils. The range reported for the entire Pacific Northwest region by Smithwick and colleagues (2002) was from 7500 g C m^{-2} for east-side *Pinus*-dominated stands to 50,000 g C m^{-2} for coastal *Picea–Tsuga*-dominated forests. The regional mean detritus and mineral soil store from this study is 27,500 g C m^{-2}. High-elevation *Tsuga mertensiana* forests were estimated to store 10,000 g C m^{-2} in detritus and mineral soil (Boone and others 1988). The proportion of total C stored in detritus and mineral soils at Wind River is close to the regional mean of 38%; however, there is considerable range in this proportion, with the highest proportions at coastal sites (45%) and high elevation (47%) (Boone and others 1988; Smithwick and others 2002).

Our estimates of total C stores (61,899 g C m^{-2}) also lie within the range reported in the Pacific Northwest. Grier and Logan (1977) and Means and colleagues (1992) report a total C store of 62,400 and 111,000 g C m^{-2}, respectively, with the value from Means and colleagues being just below the absolute upper limit of 122,400 g C m^{-2} found by Smithwick and coworkers (2002). The regional mean from Smithwick and colleagues was 73,300 g C m^{-2}, with the regional maximum of 110,700 g C m^{-2} found in coastal *Picea–Tsuga* forests and the regional minimum of 22,200 g C m^{-2} found in *Pinus*-dominated east-side forest. Total C stores at Wind River are considerably higher than the 21,500 g C m^{-2} found in high-elevation *Tsuga mertensiana* forests (Boone and others 1988).

Net Primary Production, Autotrophic Respiration, and Gross Primary Production

There are few ecosystem estimates of total NPP in the Pacific Northwest region to compare with our estimates; however, values for the most similar ecosystem are 544 g C m^{-2} y^{-1} (Grier and Logan 1977) and within our estimated range (453–741 g C m^{-2} y^{-1}). Both estimates are well below the 891 g C m^{-2} y^{-1} reported by Gower and colleagues (1992) for a 50-year-old *Pseudotsuga* forest in New Mexico. This difference might be caused by differences in forest age, as NPP is known to decrease once forest canopies have closed (Ryan and others 1997; Acker and others 2000, 2002), or alternatively it may be caused by different methods of estimating the belowground NPP. For example, the root mortality rates reported by Gower and coworkers (1992) indicate that roots have a mean life time of 0.75 years, whereas our estimates indicate a mean lifetime of 3–5 years. Total NPP at Wind River was also lower than the 840 g C m^{-2} y^{-1} found at a 180-year-old *Abies amabilis* stand in Washington (Grier and others 1981) or the 650 g C m^{-2} y^{-1} for aboveground NPP of coastal *Picea–Tsuga* forests (Grier 1976). Although the latter is an underestimate of total NPP, the difference in aboveground NPP with the Wind River site (444 g C m^{-2} y^{-1}) is consistent with the 1.5-fold greater store in live biomass at the coastal site. The lower value of total NPP than at the high-elevation *Abies*-dominated site is most likely due to the lower fine-root NPP estimates at Wind River, as indicated by the mean lifetime of fine roots of 1.1 years at the *Abies* stand. Aboveground NPP at the high-elevation *Abies*-dominated site was 228 g C m^{-2} y^{-1} and is more in line with the difference in live C stores found between the sites.

Our estimate of R_a for Wind River of 1309 g C m^{-2} y^{-1} is very preliminary. It is far lower than the 7500 g C m^{-2} y^{-1} reported by Grier and Logan (1977) and roughly twice the 765 g C m^{-2} y^{-1} predicted by Kaduk and colleagues using a model. Measurements of live pools other than leaves at the site would help resolve the latter difference. Because of the vast differences in R_a between our study and that of Grier and Logan (1977), our estimate of GPP is 7.7-fold smaller than theirs. Our estimate of GPP is lower than the annual value of 2200–2460 g C m^{-2} y^{-1} estimated by Winner and colleagues (2004) using the Soil–Plant–Atmosphere model, but larger than the 1300 g C m^{-2} y^{-1} modeled by Kaduk and colleagues (2004) and the 1570 g C m^{-2} y^{-1} estimated by Paw U and colleagues (2004) from eddy flux.

Net Ecosystem Production

The only other published ground-based estimates of old-growth *Pseudotsuga* forest NEP are by Grier and Logan (1977), who reported a C sink of 166 g C m^{-2} y^{-1}. However, this estimate must be interpreted in light of uncertainties in R_h (identified by Grier and Logan) that have been resolved (Franklin and others 1987; Harmon and Chen 1991; Chen and others 2001; Harmon and others 2001). The most significant improvement has been information on the rate that woody detritus decomposes. Grier and Logan assumed a decomposition rate constant for this material of 0.0067 y^{-1}, based on the ages of trees found growing on several logs. Since that time, higher rate constants, similar to the ones we used, have been measured by a variety of studies (Harmon and others 2001). This indicates that the Grier and Logan (1977) estimate of R_h needs to be increased by 120 g C m^{-2} y^{-1}, and thus their overall estimate of NEP would be 44 g C m^{-2} y^{-1}. Grier and Logan also assumed, given the lack of root decomposition data at the time, that R_h associated with dead roots would equal 50% of root mortality. Subsequent work on fine-root and coarse-root decomposition has found no basis for this assumption (Chen and others 2001, 2002). Other factors might also decrease the Grier and Logan (1977) NEP estimate. For example, they noted that heart rot was present in the stand but did not include these respiration losses. As little as 10% of heart rot in stems of their forest could completely offset the gains in stem stores they estimated. These values of heart rot are within the range typical for old-growth *Pseudotsuga* forests (Harmon and others 1996).

Unless some form of long-term production or removal from the forest has been neglected by our measurements, the uncertainty analysis of long-term ground-based measurements indicates that it is unlikely that the stand at Wind River is as strong a long-term sink as estimated by the eddy-covariance method in 1998–99 [150–220 g C m^{-2} y^{-1} (Paw U and others 2004)]. The error in ground-based measurements would have to be at least 100 and possibly as large as 200 g C m^{-2} y^{-1}. Our uncertainty analysis indicates that approximately 95% of the long-term ground-based estimated values lie below +150 g C m^{-2} y^{-1}.

Assuming that the eddy-flux tower system and related calculations are not resulting in underestimates in respiration terms, there are several hypotheses that might explain the differences between our ground-based and eddy-covariance-based estimates, including (a) undetected biomass increases, (b) underestimates of NPP, and (c) unmeasured C losses from the system in the ground-based system, as well as (d) a temporal mismatch between the long-term ground-based versus short-term flux tower measurements. Each hypothesis is addressed below.

The first hypothesis is that biomass increases were not detected by our measurements. However, measurements of diameters and heights in nearby permanent plots by using individually tagged trees indicate that live C stores have steadily increased by 920 g C m^{-2} over the last 50 years, giving an annual increase of 18 g C m^{-2} y^{-1} (Bible 2001). These increases do not account for losses from heart rot, however, and therefore are likely to be overestimated. Although our estimates include root biomass, it is possible that more C is being allocated to coarse roots than in the past. If the relationship between aboveground parts and coarse roots has changed since the 1970s, this difference should be evident from a comparison of root to shoot ratios of trees sampled in the 1970s and today. Unfortunately, data for such a comparison do not currently exist. Another possibility is an increase in CWD stores; however, a comparison with the data collected 20 years earlier at the Wind River old-growth stand by Sollins (1982) does not support this hypothesis. Sollins estimated a mean C store of 6750 g C m^{-2}, whereas our mean estimate was 7080 g C m^{-2}. Although these measurements were not taken on the same plots, they were in very close proximity and differed by less than 0.5 SE. Using current estimates of decomposition rate constants and long-term mortality records from plots near the stand we examined (Bible 2001) indicates that even if CWD C stores were zero 50 years ago, CWD could only account for a sink of 50 g C m^{-2} y^{-1}. A more reasonable initial CWD store of 75% of the current value yields a current potential sink of 16 g C m^{-2} y^{-1}. C stores in mineral soil could also be increasing, but difficult to detect. By only sampling to 1-m depth, we probably underestimated the mineral soil C store by 25%, based on decreases in C content with soil depth. This would underestimate the total C store of the site by 3.7%, but assuming these deeper layers respired at the same rate constant as the shallower soil would also underestimate R_h by 2% and, hence, increase the difference between the eddy-flux and the ground-based estimates. Our estimates of the decomposition in the mineral soil C pool are highly uncertain; if they are high, this could lead to an increased NEP estimate. C increase in mineral soil with sandy texture during old-field succession was approximately 4 g C m^{-2} y^{-1} (Richter and others

1999), although this rate should be higher on soils with more clay content, as found at Wind River (Hassink and Whitmore 1997). Globally, Schlesinger (1990) considered an increase of 20 g C m^{-2} y^{-1} to represent the upper limit of soil C increases. With the higher of these two rates, most of the current C store in mineral soil could have accumulated since the last major disturbance approximately 450 years ago. Given that disturbance is thought to have a minimal effects on C in mineral horizons of forests (Johnson and Curtis 2001), it seems unlikely that C accumulation in the mineral soils is causing a major underestimate in NEP.

The second hypothesis is that NPP was underestimated. Grazing losses are difficult to measure, but because grazing increases both NPP and R_h it should not influence the NEP estimate unless grazer C is increasing. Our estimates of grazing losses and respiration of consumers are admittedly crude, but within the range observed by others (Schowalter 1989). For grazing to account for a systematic underestimate of NEP large enough to explain the eddy-flux versus ground-based discrepancy, an amount equivalent to 20% of the foliage would have been grazed, and most of that C would have to be accumulating in grazers each year. The most likely grazers are insects and, because these are short-lived organisms, they store very little C, with a range of 190–210 g C m^{-2} in Pacific Northwest forests (Schowalter 1989). The required accumulation of insect C implies that insect C is increasing several fold annually. This increase is also unlikely for large, longer-lived vertebrates such as deer and elk. Another component of NPP that we did not measure was in DOC associated with throughfall and stem flow. Grier and Logan (1977) estimated this flux to be 30 g C m^{-2} y^{-1}, and a similar value would be expected at Wind River. These are likely to be highly decomposable materials, however, and the majority should be respired within a year of deposition. This flux is likely to increase both NPP and R_h and have little net effect on the NEP estimate. Losses via biogenic hydrocarbon emissions could also lead to underestimates of NPP, although given the small size of this flux [that is, 0.5%–2% of CO_2 fluxes (Winner and others 2004)] it would also have little effect on our NEP estimate.

The third hypothesis is that we failed to measure a C export from the ecosystem. As we did not measure DOC losses from the stand at Wind River, this is one logical source of bias. These losses have been measured at the H. J. Andrews Experimental Forest as 3 g C m^{-2} y^{-1} (Grier and Logan 1977; Swanson and others 1982). Typical concentrations of DOC extracted from mineral soil in the region by tension and tension-free lysimeters are 1–10 Mg C L^{-1} (K. Lajtha personal communication). Assuming Wind River old-growth evapotranspires the same as basins in the H. J. Andrews Experimental Forest means that 1.6×10^4 m^3 ha^{-1} of water leaves the Wind River stand via groundwater, and using the mineral soil DOC values observed by Lajtha yields an annual export of DOC of 1–10 g C m^{-2} y^{-1}, similar to the magnitude reported by Grier and Logan (1977). It is also possible that particulate organic C (POC) is leaving via erosion and fluvial transport. Estimates of POC exports via litterfall and an assortment of geomorphic processes in steep slopes in Pacific Northwest are approximately 2 g C m^{-2} y^{-1} (Swanson and others 1982). It is likely that on the flat terrain at Wind River rates of POC export would be lower, indicating omitting this flux would cause minimal underestimates in NEP. Transport of larger material such as logs in the seasonal stream running through the crane plot is also highly unlikely and has not been observed since the plot was established.

The final hypothesis involves the fact that the flux tower measured a single year, whereas we calculated a long-term average. For the most part, our estimates of NPP and R_h are based on long-term measurements with no estimate of annual variation. There are, however, two exceptions. Wind River site litterfall has a year-to-year variation of ±30%. Litter decomposition rate constants between the driest and wettest year at H. J. Andrews Experimental Forest vary by ±35% (M. Harmon unpublished data). Assuming that all NPP components vary the same as litterfall, NPP is likely to vary within a range of 418–776 g C m^{-2} y^{-1}. Similarly, by assuming that R_h varies as much as short-term litter decomposition, this flux is likely to vary from 404 to 750 g C m^{-2} y^{-1}. Using Monte Carlo methods to vary these two fluxes and assuming these two fluxes vary independently of each other yields an approximate NEP range of −227 to +267 g C m^{-2} y^{-1}. Thus, annual variation is the hypothesis most consistent with the value estimated by the eddy-flux method and therefore warrants additional examination.

ACKNOWLEDGEMENT

We thank Mr. Jay Sexton and Ms. Becky Fasth for helping to collect much of the data used in this study. This research was funded in part by the Pacific Northwest Research Station and the H. J. Andrews Long-term Ecological Research Program (DEB-9632921). This research was also supported

in part by the Office of Science, Biological and Environmental Research Program (BER), US Department of Energy (DOE), through the Western Regional Center (WESTGEC) of the National Institute for Global Environmental Change (NIGEC) under Cooperative Agreement DE-FC03-90ER61010. Any opinions, findings, and conclusions or recommendations expressed herein are those of the authors and do not necessarily reflect the view of the DOE.

REFERENCES

Acker SA, Halpern CB, Harmon ME, Dyrness CT. 2002. Trends in bole biomass accumulation, net primary production, and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiol 22:213–7.

Acker SA, Harcombe PA, Harmon ME, Greene SE. 2000. Biomass accumulation over the first 150 years in coastal Oregon *Picea–Tsuga* forest. J Veg Sci 11:725–38.

Ågren GI, Axelsson B. 1980. Population respiration: a theoretical approach. Ecol Modell 11:39–54.

Amthor JS. 1989. Respiration and crop productivity. New York: Springer-Verlag.

Bible K. 2001. Long-term patterns of Douglas-fir and western hemlock mortality in the western Cascades of Washington and Oregon [PhD dissertation]. Seattle: University of Washington.

Boone RD, Sollins P, Cromack K Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. Ecology 69:714–22.

Chen H. 1999. Root decomposition in three coniferous forests: effects of substrate quality, temperature, and moisture [PhD dissertation]. Corvallis: Oregon State University.

Chen H, Harmon ME, Griffiths RP. 2001. Decomposition and nitrogen release from woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. Can J For Res 31:246–60.

Chen H, Harmon ME, Sexton J, Fasth B. 2002. Fine root decomposition and N dynamics in coniferous forests of the Pacific Northwest of USA. Can J For Res 32:320–31.

Clark DA, Brown S, Kicklighter DK, Chambers JQ, Thomlinson JR, Ni J. 2001. Measuring net primary production in forests: concepts and field methods. Ecol Appl 11:356–70.

Fahey TJ, Bledsoe CS, Day FP, Ruess RW, Smucker AJM. 1999. Fine root production and demography. In: Robertson GP, Coleman DC, Bledsoe CS, Sollins P, editors. Standard soil methods for long-term ecological research. New York: Oxford University Press. p 437–55.

Franklin JF, Shugart HH, Harmon ME. 1987. Tree death as an ecological process. BioScience 37:550–6.

Gholz HL, Fitz FK, Waring RH. 1976. Leaf area differences associated with old-growth forest communities in the western Oregon Cascades. Can J For Res 6:49–57.

Gholz HL, Grier CC, Campbell AG, Brown AT. 1979. Equations for estimating biomass and leaf area for plants in the Pacific Northwest. Research paper 41. College of Forestry Organ State University: Corvallis, 39 p.

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsey SC. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271:1576–8.

Gower ST, Vogt KA, Grier CC. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecol Monogr 62:43–65.

Graham RL. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascades Range [PhD dissertation]. Corvallis: Oregon State University.

Grier CC. 1976. Biomass, productivity and nitrogen–phosphorus cycles in hemlock–spruce stands of the central Oregon coast. In: Atkinson WA, Zasoski RJ editors. Western hemlock management. Seattle: College of Forest Resources, University of Washington. p 71–81.

Grier CC, Logan RS. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol Monogr 47:373–400.

Grier CC, Vogt KA, Keyes MR, Edmonds RL. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can J For Res 11:155–67.

Harcombe PA, Harmon ME, Greene SE. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis–Tsuga heterophylla* forest approaching maturity. Can J For Res 20:1602–10.

Harmon ME, Chen H. 1991. Coarse woody debris dynamics in two old-growth ecosystems: Changbai Mountain Biosphere Reserve, People's Republic of China and H. J. Andrews Experimental Forest, USA. BioScience 41:604–10.

Harmon ME, Ferrell WK, Franklin JF. 1990. Effects on carbon storage of conversion of oldgrowth to young forests. Science 247:699–702.

Harmon ME, Garman SL, Ferrell WK. 1996. Modeling historical patterns of tree utilization in the Pacific Northwest: carbon sequestration implications. Ecol Appl 6:641–52.

Harmon ME, Krankina ON, Yatskov M, Matthews E. 2001. Predicting broad-scale carbon stores of woody detritus from plot-level data. In: Lai R, Kimble J, Stewart BA editors. Assessment methods for soil carbon. New York: CRC. p 533–52.

Harmon ME, Sexton J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. US LTER Network Office, College of Forest Resources, University of Washington: LTER Network publication 20. Seattle, 73 p.

Hart SC, Nason GE, Myrold DD, Perry DA. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology 75:880–91.

Hassink J, Whitmore AP. 1997. A model of the physical protection of organic matter in soils. Soil Sci Soc Am J 61: 131–9.

Janisch JE. 2001. Carbon storage in a Pacific Northwest forest ecosystem: a chronosequence approach [Masters thesis]. Corvallis: Oregon State University.

Johnson DW, Curtis PS. 2001. Effects of forest management on soil C and N storage: meta analysis. For Ecol Manage 140:227–38.

Krumlik GJ, Kimmins JP. 1976. Studies of biomass distribution and tree form in old virgin forests of south coastal British Columbia. In: Young HE editor. Forest biomass studies. Orono: University of Maine. p 361–73.

Law BE, Waring RH, Anthoni PM, Aber D. 2000. Measurements of gross and net ecosystem productivity and water exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. Global Change Biol 6:155–68.

Lloyd J. 1999. The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interaction with soil nutrient status. II. Temperature and boreal forest productivity and the combined effects of increasing CO_2 concentrations and increased nitrogen deposition at a global scale. Funct Ecol 13:439–59.

McCune B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga–Tsuga* forests of different ages in western Oregon and Washington. Bryologist 96:405–11.

McCune B, Amsberry KA, Camacho FJ, Clery S, Cole C, Emerson C, Felder G, French P, Greene D, Harris R, others . 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. Northwest Sci 71:145–52.

Means JE, Acker SA, Harding DJ, Blair JB, Lefsky MA, Cohen WB, Harmon ME, McKee WA. 1999. Use of large-footprint scanning airborne lidar to estimate forest stand characteristics in the western Cascades of Oregon. Remote Sens Environ 67:298–308.

Means JE, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW. 1994. Software for computing plant biomass: BIOPAK users guide. General technical report PNW-GTR-340. Portland (OR): USDA Forest Service. 184 p.

Means JE, MacMillan PC, Cromack K Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, USA. Can J For Res 22:1536–46.

Parker GG, Harmon ME, Lefsky MA, Chen J, Van Pelt R, Weiss SB, Thomas SC, Winner WE, Shaw DC, Franklin JF. 2004. Three-dimensional structure of an old-growth *Pseudotsuga–Tsuga* forest and its implications for radiation balance, microclimate, and atmospheric gas exchange. Ecosystems 7:440–53.

Paw U KT, Falk M, Suchanek TH, Ustin SL, Chen J, Park Y-S, Winner WE, Thomas SC, Hsiao TC, Shaw RH, others. 2004. Carbon dioxide exchange between an old-growth forest and the atmosphere. Ecosystems 7:513–24.

Randerson JT, Chapin FS, Harden J, Neff JA, Harmon ME. 2002. Scaling terrestrial net carbon fluxes: a definition of net ecosystem production (NEP) that includes disturbance and non-CO_2 carbon fluxes. Ecol Appl 12:937–47.

Remillard SM. 1999. Soil carbon and nitrogen in old-growth forests in western Oregon and Washington [Masters thesis]. Corvallis: Oregon State University.

Richter DD, Markewitz D, Trumbore SE, Wells CG. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400:56–8.

Ryan MG. 1991a. The effect of climate change on plant respiration. Ecol Appl 1:157–67.

Ryan MG. 1991b. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiol 9:255–66.

Ryan MG, Binkley D, Fownes JH. 1997. Age-related decline in forest productivity: pattern and process. Adv Ecol Res 27:213–62.

Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP, Running SW. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia (Berl) 101:133–40.

Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie RE. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nutrient status. Tree Physiol 16:333–43.

Schlesinger WH. 1990. Evidence from chronosequence studies for a low carbon storage potential of soils. Nature 348:232–4.

Schowalter TD. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. Can J For Res 19:318–22.

Shaw DC, Franklin JF, Klopatek J, Freeman E, Bible K, Newton T, Greene S, Wade-Murphy J. 2004. Ecological setting of the Wind River old-growth forest. Ecosystems 7:427–39.

Smithwick EA, Harmon ME, Acker SA, Remillard SM. 2002. Potential upper bounds of carbon stores in the Pacific Northwest. Ecol Appl 12:1303–17.

Sollins P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can J For Res 12:18–28.

Sollins P, Cline SP, Verhoeven T, Sachs D, Spycher G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can J For Res 17:1585–95.

Sprugel DG. 1990. Components of woody-tissue respiration in young *Abies amabilis* trees. Trees 4:88–98.

Swanson FJ, Fredrickson RL, McCorison FM. 1982. Material transfer in a western Oregon forested watershed. In: Edmonds RL editor. Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross: Stroudsburg (PA). p 233–66[US/IBP Synthesis Series 14.].

Turner DP, Cohen WB, Kennedy RE. 1999. Alternative spatial resolution and estimation of carbon flux over a managed landscape in Western Oregon. Landscape Ecol 10:1–12.

Waring RH, Schroeder PE, Oren R. 1982. Application of the pipe model theory to predict canopy leaf area. Can J For Res 12:556–60.

Winner WE, Thomas SC, Berry JA, Bond BJ, Cooper CE, Hinckley TM, Ehleringer JR, Fessenden JE, Lamb B, McCarthy S. and others 2004. Canopy carbon gain and water use: analysis of old-growth conifers in the Pacific Northwest. Ecosystems 7:482–97.

Wofsey SC, Goulden ML, Munger JW, Fan S-M, Baldwin PS, Daube BC, Bassow SL, Bazzaz FA. 1993. Net exchange of CO_2 in a midlatitude forest. Science 260:1314–7.