POTENTIAL UPPER BOUNDS OF CARBON STORES IN FORESTS OF THE PACIFIC NORTHWEST

Erica A. H. Smithwick,[1,3] Mark E. Harmon,[1] Suzanne M. Remillard,[1]
Steven A. Acker,[1,4] and Jerry F. Franklin[2]

[1]*Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA*
[2]*College of Forest Resources, University of Washington, Seattle, Washington 98195 USA*

Abstract. Placing an upper bound to carbon (C) storage in forest ecosystems helps to constrain predictions on the amount of C that forest management strategies could sequester and the degree to which natural and anthropogenic disturbances change C storage. The potential, upper bound to C storage is difficult to approximate in the field because it requires studying old-growth forests, of which few remain. In this paper, we put an upper bound (or limit) on C storage in the Pacific Northwest (PNW) of the United States using field data from old-growth forests, which are near steady-state conditions. Specifically, the goals of this study were: (1) to approximate the upper bounds of C storage in the PNW by estimating total ecosystem carbon (TEC) stores of 43 old-growth forest stands in five distinct biogeoclimatic provinces and (2) to compare these TEC storage estimates with those from other biomes, globally. Finally, we suggest that the upper bounds of C storage in forests of the PNW are higher than current estimates of C stores, presumably due to a combination of natural and anthropogenic disturbances, which indicates a potentially substantial and economically significant role of C sequestration in the region. Results showed that coastal Oregon stands stored, on average, 1127 Mg C/ha, which was the highest for the study area, while stands in eastern Oregon stored the least, 195 Mg C/ha. In general, coastal Oregon stands stored 307 Mg C/ha more than coastal Washington stands. Similarly, the Oregon Cascades stands stored 75 Mg C/ha more, on average, than the Washington Cascades stands. A simple, area-weighted average TEC storage to 1 m soil depth (TEC_{100}) for the PNW was 671 Mg C/ha. When soil was included only to 50 cm (TEC_{50}), the area-weighted average was 640 Mg C/ha. Subtracting estimates of current forest C storage from the potential, upper bound of C storage in this study, a maximum of 338 Mg C/ha (TEC_{100}) could be stored in PNW forests in addition to current stores.

Key words: biomass; carbon offsets; carbon storage; disturbance; old-growth forests; Pacific Northwest, USA; sequestration.

INTRODUCTION

Managing forests to enhance carbon sequestration is one means of reducing CO_2 concentrations in the atmosphere to mitigate potential threats from global climate change (Vitousek 1991, Brown 1996). The magnitude and duration of carbon (C) sequestration over the long term can be constrained by knowing the upper bounds (or limit) of C storage, relative to current C storage. The use of "baseline" studies in science has been long heralded as a way to bound scientific understanding. For example, Bender et al. (2000:6) conclude that scientists "... need to have baseline studies from relatively un-impacted regions of the earth to discern mechanisms and magnitudes of modern human impacts, and, importantly, examine factors that influ-

enced carbon and nutrient dynamics in pre-industrial environments." We suggest that setting an upper bound to carbon sequestration potential is equally necessary to constrain estimates of uncertain C sequestration predictions and ideally to inform scientists and managers of the limits of the system. Once the upper bounds of C storage are identified over broad biogeoclimatic gradients, C sequestration, and its economic implications, can be assessed most effectively.

One way to measure past changes in carbon storage from the terrestrial biosphere to the atmosphere is to measure the change in C stores in terrestrial ecosystems between two points in time. This has been called the "difference" approach (Turner et al. 2000b). It has been used to measure changes in forest inventory data over time (Kauppi et al. 1992, Krankina and Dixon 1994) and to estimate the change in landscape C stores over time using multi-date remote sensing imagery (Cohen et al. 1996). Similarly, the difference approach can be used to constrain potential carbon sequestration by substracting current C storage from the upper bounds.

However, while there is significant information on

current C stores, it is difficult to constrain the magnitude and duration of C sequestration potential because few stands exist in which the upper bounds of carbon storage can be measured directly. Most forests never reach their upper bound of C storage due to the combined effects of anthropogenic and/or natural disturbances that cause a reduction in C storage from their potential. While old-growth forests maintain higher levels of C storage than are found earlier in succession (Odum 1969, Janisch and Harmon 2002, Franklin et al., *in press*), managed forests in temperate regions may contain as little as 30% of the living tree biomass and 70% of the soil C found in old-growth forests (Cooper 1983). Disturbances of old-growth temperate forests may reduce C storage for at least 250 yr, and with continual harvesting, C storage may be reduced indefinitely (Harmon et al. 1990).

Due to the lack of field data to estimate the upper bounds of C sequestration potential, models are used to predict future C sequestration. However, many ecosystem models rely on current, rather than potential, estimates of C densities (C storage on an area basis) to initiate and validate model simulations, such as from remote sensing. Current C density estimates may reflect integrated ecosystem responses to past degradation and/or disturbance processes. For example, Brown et al. (1991) suggest that current C densities in the tropics reflect historical degradation by selective logging and other forms of human disturbance. Regrowth in these and other secondary forests may have a larger role in explaining the "missing" C sink than previously thought (Houghton et al. 1998).

It is also difficult to estimate C sequestration potential since most field studies do not account for all manageable pools of C. By including total ecosystem carbon (TEC), we provide sufficient data from which managers will be able to make accurate predictions about how much carbon can be sequestered in the future. We additionally calculate TEC to a depth of 100 cm (TEC_{100}) and to a depth of 50 cm (TEC_{50}), since the latter may be more amenable for C sequestration activities in the short term. We present TEC values to 100 cm unless otherwise specified to fully account for the upper bounds of these ecosystems.

In this paper we: (1) approximate the upper bounds of C storage in the Pacific Northwest (PNW) region of the United States by estimating TEC of 43 old-growth forest stands in five biogeoclimatic zones and (2) compare these TEC storage estimates to those from other regions, globally. These old-growth forests are at or near steady state (inputs ≈ outputs) based on recent studies (Long and Turner 1975, Turner and Long 1975, DeBell and Franklin 1987; Acker et al., *in press*; Franklin et al., *in press*). The stands have not experienced catastrophic disturbances for 150–1200 yr and are therefore appropriate locations to determine the upper bounds of C storage in the absence of human or natural disturbances. Certainly, the stands have had minor gap-

phase disturbances such as single-tree mortality events from wind or disease. However, these are endogenous disturbances (Bormann and Likens 1979), resulting in an oscillation of steady-state conditions around a mean. In this paper, we are concerned with an estimate of the long-term, upper bound of C storage. We recognize, however, that at shorter temporal scales and smaller spatial scales, steady-state conditions may not occur.

Previously, Grier and Logan (1977) showed that late-successional *Pseudotsuga menziesii* forests of the western Cascades of Oregon had greater stores of biomass than had been measured by other studies in the region (Turner and Long 1975, Fujimori et al. 1976). This study extends the work of Grier and Logan (1977) by examining trends in a complete inventory of all the significant C pools along a wide biogeoclimatic gradient, not just the Oregon Cascades, providing estimates of the upper bounds of C storage as well as its variability between biogeoclimatic regions.

METHODS

Site description

Sampling was conducted in 43 stands at seven sites in western Oregon and Washington. The sites are located within five of the general physiographic provinces described by Franklin and Dyrness (1988). Assuming the sites are representative (Table 1; Franklin and Dyrness 1988), we designated each site to a respective province: Oregon Coast (ORCOAST), Washington Coast (WACOAST), Oregon Cascades (ORCASC), Washington Cascades (WACASC), or Eastern Oregon (OREAST). ORCOAST was represented by 8 stands at Cascade Head Experimental Forest; WACOAST was represented by 7 stands on the Olympic Peninsula; ORCASC was represented by 14 stands at the H. J. Andrews Experimental Forest; WACASC was represented by 10 stands at Mt. Rainer National Park and Wind River Experimental Forest (T. T. Munger Research Natural Area); and OREAST was represented by 4 stands at Metolius Research Natural Area and Pringle Falls Research Natural Area (Fig. 1, Table 1).

All sites were part of a permanent plot network designed to observe and monitor changes in composition, structure, and functions of forest ecosystems over long time periods (see Acker et al. [1998] for a complete description of the history and characteristics of the network). The 43 old-growth sites used in this study are located on lands managed by either the United States Forest Service (USFS) or the National Park Service and are maintained by the H. J. Andrews Experimental Forest Long-Term Ecological Research program (LTER) and The Cascade Center for Ecosystem Management (a cooperative effort between Oregon State University, the Pacific Northwest Research Station of the USFS, and the Willamette National Forest). Data from the network is stored in the Forest Science Data

Bank of the Department of Forest Science at Oregon State University.

The youngest stands in our study were at Cascade Head, in the ORCOAST. Their average age is 150 yr, having developed after a catastrophic crown fire, the Nestucca Burn, in the late 1840s (Harcombe 1986; Acker et al., *in press*). Stands at the Olympic Peninsula have not had a stand-replacing disturbance for 230–280 yr, while the remaining stands have not had a catastrophic disturbance for 450–1200 yr (Table 1).

In the PNW, there is a strong east-west gradient in precipitation and temperature. Climate is generally mild and moist in the coastal sites, with cooler temperatures at high elevations and lower precipitation east of the mountains. For example, mean annual temperature ranges from 11.4°C at a low elevation stand in H. J. Andrews to 3.8°C at Pringle Falls. Mean annual precipitation ranges from 3669 mm at the South Fork of the Hoh River, Olympic Peninsula, to 355 mm at Metolius RNA. Sites within the Oregon and Washington coastal provinces are represented by *Tsuga heterophylla–Picea sitchensis* habitats, while higher elevation sites are represented by *P. menzsiesii–Thuja heterophylla* habitats. East of the Cascades, *Pinus ponderosa* habitats predominate.

At each site, between 3 and 14 stands were sampled. Each stand was composed of 1–72 (median = 16) plots (Table 1). In addition to aboveground measurements within the stand, soil C was estimated from soil pits located just outside the measured area of the stand. The C pools (in megagrams of carbon per hectare) that were measured are described below. A biomass : C ratio of 2 : 1 was used for all calculations except for soil organic carbon estimates, where C density values were calculated directly. Unless otherwise described, TEC for each stand was calculated as an average of the plots on a per-hectare basis. TEC for each province (e.g., ORCASC, ORCOAST, etc.) was calculated as the average of the stands in that province.

Above- and belowground tree C

Estimation of above- and belowground tree C included the following pools: stem wood, stem bark, live and dead branches, foliage, live and dead coarse roots, and fine roots. In each stand, the diameters of all trees (>5 cm diameter at breast height [DBH, measured at 1.3 m above the ground surface]) were measured. The biomass of stem wood, stem bark, and live and dead attached branches were calculated by applying species-specific allometric equations from BIOPAK (Means et al. 1994). In some cases, species-specific equations were not available so we made substitutions with equations for similar species. We tested the effect of these substitutions by switching equations within and between families of tree species (while maintaining the observed distribution of DBH). In general, within-family conifer substitutions accounted for very small variations in biomass (e.g., 2.7%, *Abies amabilis* for *Abies*

procera). Between-family conifer substitutions were more significant (e.g., 19%, *Tsuga heterophylla* for *A. amabilis*) but were rare. Hardwoods only occupied 1.3% of the stems in the region so we assumed that uncertainty in these equations was not significant.

Foliage carbon stores were calculated from leaf area index (LAI, in square meters per square meter) using species-specific leaf area (SLA, in grams per square centimeter) estimates found in the literature (Appendix B). We obtained LAI estimates from calculating sapwood area (SA, in square centimeters) or sapwood thickness from DBH using species-specific biomass equations (Appendix B). Predicting LAI from SA is preferable to prediction of LAI directly from DBH, as the latter overestimates LAI and leaf mass for mature and old-growth forests (Marshall and Waring 1986, Turner et al. 2000*a*). We derived species-specific allometric equations to predict SA from DBH for *Picea sitchensis*, *Pinus contorta*, and *Pinus ponderosa* using data from the permanent plots and published data from western softwoods (Lassen and Okkonen 1969). We applied appropriate substitution equations when species-specific allometric equations were lacking (Appendix B).

Fine-root biomass was not directly measured due to time constraints and due to its spatial and temporal variability. Instead, we assumed that fine-root biomass is ~2% of total aboveground biomass (Grier and Logan 1977: Table 7). Since ~1.6 times more fine-root biomass is present in dry sites than wet sites (Santantonio and Hermann 1985: Table 3), we assumed that ~3% of aboveground biomass (2% × 1.6) is allocated belowground in OREAST, where precipitation is limited (Gholz 1980). This is in general agreement with current understanding about tree physiology that, in water- or nutrient-limited sites, more NPP is allocated to fine roots (Waring and Running 1998).

We estimated live, coarse-root biomass (>10 mm diameter) for each tree from equations for *Pseudotsuga menziesii* in Santantonio et al. (1977) and corrected the values for different tree species using species-specific green densities (U.S. Forest Products Laboratory 1974). Dead, coarse-root biomass was estimated by assuming that it is the same proportion of coarse woody debris (logs and snags) as the proportion of live coarse-root biomass is to aboveground tree biomass. For example, at stand RS01 (H. J. Andrews), live coarse-root biomass is 29% of aboveground tree biomass (live and dead branches, foliage, stem bole, stem bark). Therefore, we assumed that dead, coarse-root biomass was 29% of coarse woody debris (29% of 44.9) or 13.1 Mg C/ha. In this calculation, we assumed that the ratio of above- and belowground decomposition rates does not diverge through time. We tested this assumption by calculating dead, coarse-root biomass with differing decay rates and comparing the ratio of roots to boles through time. We would need to double the decay rates of dead, coarse roots to see a 10% decrease in the ratio

ERICA A. H. SMITHWICK ET AL.

TABLE 1. Stand characteristics of the five study provinces in the Pacific Northwest, USA.

Site	Stand name (if applicable)	Stand	Size (ha)	Latitude N (°)	Longitude W (°)	Elevation (m)	Age (yr)†
ORCASC							
H. J. Andrews		RS01	1.0	44.202	122.257	510	460
		RS02	1.0	44.217	122.243	520	460
		RS03	1.0	44.260	122.159	950	460
		RS07	0.3	44.213	122.148	490	460
		RS10	0.3	44.213	122.217	610	450
		RS12	0.3	44.227	122.122	1020	460
		RS15	0.3	44.212	122.236	720	460
		RS16	0.3	44.214	122.241	670	460
		RS20	1.0	44.222	122.249	700	450
		RS22	1.0	44.274	122.140	1290	450
		RS23	1.0	44.227	122.123	1020	450
		RS27	1.0	44.254	122.175	790	450
		RS29	1.0	44.231	122.146	800	450
		RS31	1.0	44.262	122.181	900	450
ORCOAST							
Cascade Head		CH01	0.4	45.046	123.897	305	150
		CH03	0.4	45.044	123.901	280	150
		CH04	0.4	45.065	123.941	259	150
		CH05	0.4	45.065	123.942	259	150
		CH07	0.4	45.063	123.939	244	150
		CH08	0.4	45.065	123.944	271	150
		CH10	0.4	45.062	123.990	396	150
		CH12	0.4	45.049	123.898	280	150
OREAST							
Metolius RNA		MRNA	4.5	44.488	121.631	933	300
Pringle Falls RNA		PF27	1.0	43.707	121.609	1353	400
		PF28	1.0	43.709	121.603	1372	400
		PF29	1.0	43.706	121.613	1353	500
WACASC							
Mt. Rainier NP	White River (R.)	AB08	1.0	46.919	121.538	1050	500
	Nisqually R.	AE10	1.0	46.768	121.742	1430	300
	Nisqually R.	AG05	1.0	46.748	121.803	950	700
	Nisqually R.	AV06	1.0	46.777	121.783	1060	750
	Nisqually R.	TO04	1.0	46.741	121.887	640	750
	Ohanapecosh R.	AO03	1.0	46.827	121.546	853	1000
	Ohanapecosh R.	AV02	1.0	46.823	121.551	841	1000
	Carbon R.	AV14	1.0	46.960	121.843	1080	1200
	Carbon R.	TO11	1.0	46.995	121.880	610	550
Wind River	T. T. Munger RNA	MUNA	4.5	45.828	121.969	411	470
WACOAST							
Olympic Peninsula	S. Fork Hoh R.	HR01	1.0	47.779	123.908	244	280
	S. Fork Hoh R.	HR02	1.0	47.779	123.908	244	280
	S. Fork Hoh R.	HR02	1.0	47.779	123.908	250	280
	S. Fork Hoh R.	HR04	1.0	47.779	123.908	250	280
	Quinault RNA	HS02	1.0	47.429	123.873	122	230
	Quinault RNA	HS03	1.0	47.430	123.873	122	230
	Twin Creeks RNA	HS04	1.0	47.834	123.990	152	230

Note: Site abbreviations are: ORCASC, Oregon Cascades; ORCOAST, Oregon coast; OREAST, eastern Oregon; WACASC, Washington Cascades; WACOAST, Washington coast.

† Ages were determined from tree core data (S. A. Acker and M. E. Harmon, *unpublished data*); Mt. Rainier ages were determined from age class maps (Franklin et al. 1988).

‡ Precipitation data were from PRISM (precipitation–elevation regressions on independent slopes model; Daly et al. 1994), and temperature data were from the POTT (potential temperature) model (Dodson and Marks 1997). Methods used to calculate the values for each stand are described by Remillard (1999).

§ Soil pit data used for stands RS01–RS16 are from Brown and Parsons (1972).

‖ Abbreviations are from Garrison et al. (1976). See Appendix A for tree species names.

of roots to boles. Given the range of decay rates for this region reported by Chen et al. (2001), we would not expect this to be the case. Thus, we have confidence that this assumption is appropriate.

Alternatively, to improve confidence in our esti-mates, we calculated coarse- and fine-root biomass with a regression equation developed by Cairns et al. (1997), which predicts total root biomass from aboveground biomass. We then calculated fine-root biomass as a ratio of fine roots to total roots (Cairns et al. 1997: Fig. 4).

Table 1. Extended.

Temperature (°C)‡	Precipitation (mm)‡	No. soil pits§	No. plots	Habitat type‖	Dominant species‖
11.4	1719	2	16	PSME/HODI	PSME, ACMA
10.9	1868	2	16	TSHE/BENE	PSME, TSHE
7.8	2202	2	16	TSHE-ABAM/RHMA-LIBO	PSME, THPL
5.8	2260	2	1	TSHE/OXOR	PSME, TSHE
10.1	2003	2	1	TSHE/RHMA/GASH	PSME, TSHE
7.0	2332	2	1	ABAM/VAAL/COCA	PSME, TSHE
8.9	1906	2	1	TSHE/POMU	PSME, TSHE
10.3	1869	2	1	TSHE/CACH	PSME, PILA
10.4	1859	1	16	PSME/HODI	PSME, PILA
3.8	2282	2	16	ABAM/VAME/XETE	ABPR, PSME
7.1	1240	2	16	ABAM/VAAL/COCA	TSHE, PSME
8.5	2118	2	24	TSHE-ABAM/RHMA-LIBO	PSME, TSHE
8.0	2264	2	16	TSHE-ACCI/POMU	PSME, THPL
8.1	2101	2	16	TSHE-ABAM/RHMA-LIBO	PSME, THPL
8.3	2658	2	4	TSHE/OXOR	TSHE, PISI
8.6	2660	2	4	TSHE/OXOR	TSHE, PISI
9.0	2554	2	4	TSHE/OXOR	TSHE, PISI
9.0	2552	2	4	TSHE/OXOR	TSHE, PISI
8.7	2559	2	4	TSHE/OXOR	TSHE, PISI
9.0	2549	2	4	TSHE/OXOR	TSHE, PISI
7.9	2417	2	4	TSHE/OXOR	TSHE, PISI
8.5	2651	3	4	TSHE/OXOR	TSHE, PISI
8.1	355	4	72	PIPO/PUTR	PIPO
5.7	545	2	16	PIPO	PIPO, PICO
5.0	539	2	16	PIPO	PIPO, PICO
5.8	549	2	16	PIPO	PIPO, PICO
7.3	2076	2	16	ABAM/BENE	TSHE, THPL
4.1	2812	1	16	ABAM/ERMO	ABAM, CHNO
6.1	2421	2	16	ABAM/GASH	ABAM, THPL
6.0	2658	2	16	ABAM/VAAL	ABAM, TSHE
8.8	2166	2	16	TSHE/OPHO	TSHE, PSME
6.6	2257	1	16	ABAM/OPHO	ABAM, TSHE
5.4	2249	1	16	ABAM/VAAL	ABAM, TSHE
3.9	2500	2	16	ABAM/VAAL	ABAM, TSHE
8.1	2112	2	16	TSHE/OPHO	PSME, TSHE
7.8	2496	8	21	TSHE/BENE	PSME, TSHE
8.2	3669	2	16	TSHE/OXOR	TSHE, PISI
8.2	3669	2	16	TSHE/OXOR	TSHE, PISI
8.2	3669	2	16	TSHE/OXOR	TSHE, PISI
8.2	3669	2	16	TSHE/OXOR	TSHE, PISI
8.9	2899	2	16	TSHE/OXOR	TSHE
8.9	2893	2	16	TSHE/OXOR	TSHE, PISI
8.9	3026	2	16	TSHE/OXOR	TSHE, PISI

We compared the fine, and live, coarse-root biomass estimates from these two methods. Since the methods used in Santantonio et al. (1977) allow for the separation of live and dead coarse roots, we present these root estimates in the final TEC calculations.

Understory C

To determine understory C, dimensional measurements including cover and/or basal diameters were taken within each stand. Small tree (<5 cm) and shrub diameters, as well as shrub and herb cover, were measured along four transects within the stand. Transects were either 25 m or 50 m in length, depending on stand size.

The percentage of shrub and herb cover was measured using line transects. Herb cover classes were noted for each species in 0.2 × 0.5 m micro-plots placed at systematic intervals of ~1 m. Diameters of shrub and small tree stems were tallied in a 1 m wide belt transect by species and basal diameter classes (i.e., diameter at ground). Allometric biomass equations for total aboveground biomass (BAT) were selected using BIOPAK (Means et al. 1994) by assembling the appropriate combination of equations describing com-
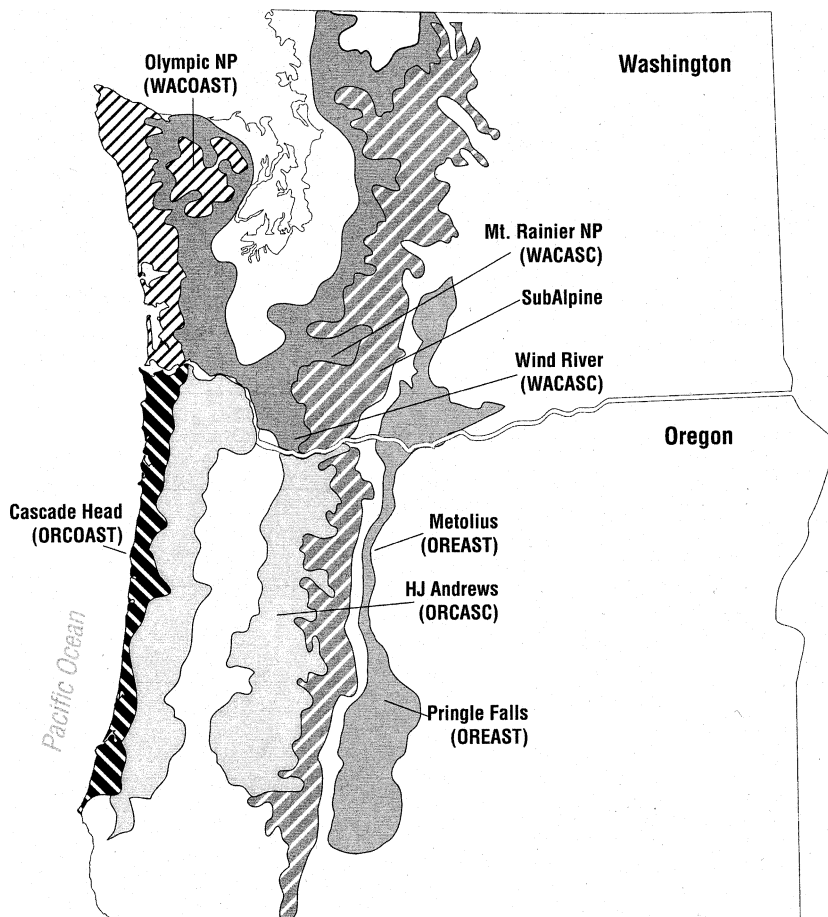
FIG. 1. Locations of sites used to measure old-growth biomass in the Pacific Northwest, USA, within each of the physiographic provinces (ORCASC, Oregon Cascades; ORCOAST, Oregon coast; OREAST, eastern Oregon; WACASC, Washington Cascades; WACOAST, Washington coast). Boundaries of provinces were adapted from Franklin and Dyrness (1998: Fig. 27).

ponents of biomass. For shrubs, if we could not predict BAT by one equation, we used a combination of equations (e.g., entire aboveground = live branch + total stem + total foliage). We assigned a substitute equation for shrub and herb species whose biomass equations could not be found or whose basal areas or cover values were outside of the range for which the species-specific equations were developed. Total biomass per stand was calculated by summing biomass per species on each transect and then averaging the biomass per transect for each stand.

Coarse-woody-debris C

Coarse woody debris (CWD) included standing and fallen detrital biomass (≥ 10 cm diameter; ≥ 1 m in length). For each fallen tree, we measured the length, end diameter, and middle diameter. For each snag, we measured the height and end diameters. In addition to these dimensions, we recorded the species and decay class of each piece. The decay class is an index of the stage of decay of the log or snag, indicating its physical

and biological characteristics, density, and nutrient content (Harmon and Sexton 1996). We converted the data to volumes and then to biomass using wood densities specific to its decay class and species (Harmon and Sexton 1996).

Fine-woody-debris C

Downed, fine-woody-debris biomass (≥ 1 cm, <10 cm diameter) was estimated by harvesting downed branches and twigs in five 1-m^2 micro-plots placed evenly along the transects used to sample herbs, shrubs, and small trees. The fresh mass of dead branches was determined on a portable electronic scale (Harmon and Sexton 1996) and subsamples were weighed in the field and later oven dried to determine a dry mass : wet mass correction factor.

Organic horizon C

This pool included the forest floor and buried rotten wood. A 5 cm diameter corer was used to collect samples of the O horizon at five locations along each tran-

sect that was used to sample fine woody debris. We separated the samples into fine, litter-derived material and coarse, wood-derived material based on color and texture. Each core sample was oven dried (55°C), weighed and analyzed for loss on ignition (LOI) to determine ash-free mass, which was used to calculate the proportion of organic matter in the sample. Organic matter was converted to C using a 2:1 ratio of ash-free biomass to C.

Mineral soil C

Mineral soil organic C (SOC, in megagrams of carbon per hectare) estimates for these stands were reported by Remillard (1999), and detailed methods are described therein; we will describe the methods briefly here. On the perimeter of each stand, one to three 1-m³ soil pits were used for a total of 79 soil pits. Pits were located to best represent the stand in terms of slope, aspect, vegetation density, and cover. The number of soil pits per stand ranged from one to eight, depending on soil heterogeneity. At each pit, soil samples were collected from three mineral soil layers (0–20 cm, >20–50 cm, and >50–100 cm).

SOC was calculated on a layer basis using the following formula:

$$SOC = C \times D \times S \times L \times 100$$

where C is the organic C concentration (in carbon grams per kilogram) of the C-bearing fraction; D is the bulk density (in grams per cubic centimeter) of this fraction; S is the C-bearing fraction as a proportion of total sample volume; L is the layer depth (in centimeters); and 100 is the conversion factor (10^8 cm²/ha $\times 10^{-6}$ Mg/g) to yield the desired units (megagrams of carbon per hectare).

To obtain the organic C concentration, samples were sieved and hand-sorted into the following components: <2 mm C-bearing soil fraction, 2–4 mm C-bearing soil fraction, >4 mm C-bearing soil fraction, >2 mm rock (non-C-bearing), and >2 mm buried wood, roots, and charcoal. The C-bearing fraction >2 mm was either hardened soil aggregates or soft, weathered rocks, which have been shown to be nutrient-rich and an important component of C stores (Ugolini et al. 1996, Corti et al. 1998, Cromack et al. 1999). Buried wood, roots, and charcoal accounted for <3% of the sample mass and were disregarded in mineral SOC estimates. Subsamples (50–100 g) of the <2 mm, 2–4 mm, and >4 mm C-bearing fractions were analyzed for total C and N concentration using a LECO CSN 2000 analyzer (St. Joseph, Michigan, USA) by the Central Analytical Laboratory, Oregon State University, Corvallis, Oregon, USA. A mass-weighted C concentration was computed for each size class by knowing the total C concentration (in carbon grams per kilogram) and the oven-dry mass of the material. Bulk density was determined for each soil layer with a core sampler for non-rocky soils or by excavating a known volume of
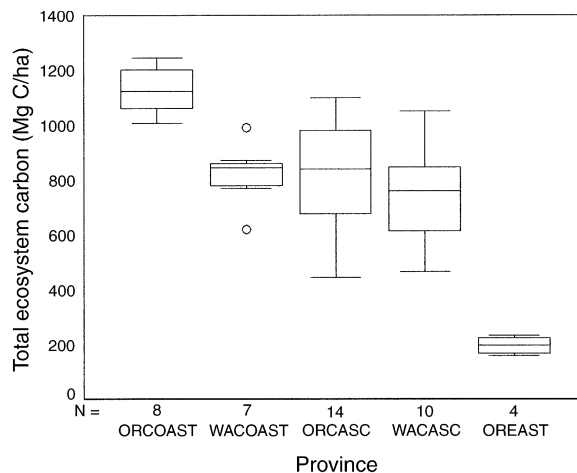

FIG. 2. Boxplot of stand total ecosystem carbon by province. Box length is the interquartile range, which is the distance needed to span the middle 50% of the cases. The "whiskers" are the adjacent values, which are the most extreme cases that are within 1.5 box lengths of the upper and lower edge of the box. See legend to Fig. 1 for explanations of province abbreviations.

soil for rocky soils. In addition to these 79 soil pits, data from Brown and Parsons (1972) for eight soil pits (0–100 cm depth) in the H. J. Andrews, ORCASC, were also used (Table 1).

Epiphytes

We did not include epiphytes in our estimate of TEC. Epiphytes may account for only 0.06% of aboveground tree biomass (e.g., 17.8 kg of 29 174 kg in Pike et al. 1977) or perhaps even less (0.003%; M. E. Harmon, K. Bible, M. J. Ryan, H. Chen, and J. Klopatek, *unpublished manuscript*), indicating that the exclusion of this pool does not lead to significant underestimates of total C stores.

RESULTS

There was significant variation of TEC$_{100}$ averages between provinces (Fig. 2) and among the stands (Table 2). ORCOAST stands stored, on average, 1127 Mg C/ha (1006–1245 Mg C/ha, $n = 8$), which was the highest for the study area, while stands in OREAST stored the least, 195 Mg C/ha (158–252 Mg C/ha, $n = 4$). In general, ORCOAST stands (mean = 1127 Mg C/ha, range = 1006–1245 Mg C/ha, $n = 8$) stored slightly more than WACOAST stands (mean = 820 Mg C/ha, range = 767–993 Mg C/ha, $n = 7$). Similarly, ORCASC stands (mean = 829 Mg C/ha, range = 445–1097 Mg C/ha, $n = 14$) stored more, on average, than the WACASC (mean = 754 Mg C/ha, range = 463–1050 Mg C/ha, $n = 10$). The lowest C density among the 43 stands was at Pringle Falls, OREAST (PF27), where only 158 Mg C/ha was stored, while the highest C density was at stand CH04 at Cascade Head, ORCOAST, with 1245 Mg C/ha.

ERICA A. H. SMITHWICK ET AL.

TABLE 2. Average C pools (in megagrams of carbon per hectare) for 43 old-growth stands in the Pacific Northwest, USA.

Stand	Live branch	Dead branch	Foliage	Stem bark	Stem wood	Fine roots	Live coarse roots	Dead coarse roots
ORCASC								
RS01	18.0	4.0	4.2	57.4	208.5	5.8	85.0	13.1
RS02	28.6	4.9	4.7	55.5	230.8	6.5	93.6	19.7
RS03	42.1	7.1	5.4	60.1	309.3	8.5	136.0	34.2
RS07	37.1	6.3	4.2	71.0	299.8	8.4	106.9	15.3
RS10	22.4	5.3	5.1	57.8	227.1	6.4	69.1	9.3
RS12	66.2	11.0	4.9	98.0	441.7	12.4	152.8	24.2
RS15	42.3	6.9	4.4	98.9	380.0	10.6	141.4	32.2
RS16	28.9	5.1	4.0	86.9	306.3	8.6	115.9	14.6
RS20	16.9	4.0	4.4	50.3	186.5	5.2	71.4	5.9
RS22	31.0	5.2	8.9	53.0	244.2	6.8	93.9	46.0
RS23	52.5	8.6	4.3	43.9	262.6	7.4	99.0	25.5
RS27	54.8	9.4	5.9	108.1	452.4	12.6	189.8	17.9
RS29	45.2	7.2	4.4	91.4	413.9	11.2	198.3	20.5
RS31	45.4	7.5	5.9	88.3	364.7	10.2	157.0	27.4
ORCOAST								
CH01	77.5	12.5	6.3	22.0	291.9	8.2	102.8	22.2
CH03	60.6	9.6	5.8	22.3	389.1	9.7	148.7	21.8
CH04	55.9	9.4	6.9	26.4	416.3	10.3	153.0	21.4
CH05	56.1	8.8	6.7	26.5	448.5	10.9	170.0	18.3
CH07	69.1	11.3	6.8	24.1	338.9	9.0	119.1	16.1
CH08	73.1	11.8	6.9	21.7	285.5	8.0	94.4	18.6
CH10	51.8	7.7	5.6	21.1	400.0	9.7	155.5	16.3
CH12	67.7	10.9	5.8	20.7	317.1	8.4	115.7	26.3
OREAST								
MRNA	13.9	1.6	0.5	15.6	53.0	2.5	24.9	8.6
PF27	11.2	1.0	0.4	11.7	44.0	2.1	20.1	5.3
PF28	13.0	1.3	0.4	14.4	49.6	2.4	22.7	4.3
PF29	17.6	1.6	0.8	17.7	71.7	3.3	36.1	5.5
WACASC								
AB08	42.5	7.1	12.5	25.4	197.2	5.7	94.1	21.0
AE10	37.1	11.2	9.2	34.1	271.2	7.3	99.1	11.8
AG05	33.0	7.5	9.1	47.1	266.8	7.3	99.2	20.2
AO03	60.0	12.6	11.4	47.7	380.2	10.2	147.0	28.6
AV02	58.4	11.8	9.1	35.4	284.9	8.0	96.2	27.8
AV06	24.1	5.1	8.6	24.0	147.9	4.2	48.2	12.9
AV14	53.7	11.9	8.7	30.8	295.1	8.0	121.7	9.8
MUNA	41.1	7.2	4.8	49.3	248.5	7.0	31.8	3.8
TO04	43.4	7.1	4.4	39.7	266.1	7.2	100.1	9.2
TO11	55.0	8.7	5.1	68.1	419.8	11.1	159.6	36.1
WACOAST								
HR01	39.7	5.6	6.1	13.5	240.2	6.1	95.3	26.3
HR02	51.0	5.8	8.6	17.6	389.5	9.4	161.5	26.5
HR03	31.2	3.4	5.4	9.9	236.9	5.7	99.5	22.6
HR04	59.5	7.8	6.9	14.5	332.7	8.4	137.1	18.6
HS02	61.7	9.5	5.9	14.5	237.3	6.6	89.3	23.8
HS03	50.8	7.5	7.4	14.5	266.6	6.9	100.6	18.7
HS04	53.9	8.2	6.6	24.7	289.6	7.7	116.3	35.0

Notes: See Table 1 for study province abbreviations. The abbreviation nm means "not measured."
† Values are means from other reported values in the field.

Almost all C pools were consistent between provinces in their percentage of TEC (calculated from Table 2). The live branch pool averaged 5.9 ± 0.4% (means ± 1 SE) of TEC_{100} for all provinces ($n = 5$). The dead branch and foliage pool averaged 0.9 ± 0.1% and 0.7 ± 0.1%, respectively. Stem wood averaged 33.8 ± 1.7% while stem bark averaged 5.1 ± 1.4% of TEC_{100}. The fine-root pool averaged 1.0 ± 0.1% of TEC_{100} for all provinces while live and dead coarse roots averaged 13.4 ± 0.5% and 2.6 ± 0.2%, respectively. The standard deviation of fine-root biomass could be much larger or smaller since fine-root biomass was calculated simply as a ratio to aboveground biomass and therefore represents the variability of the latter numbers. Fine woody debris averaged 2.0 ± 0.6%, forest floor averaged 2.7 ± 0.6%, and rotten wood averaged 1.8 ± 0.7%. The log pool averaged 5.6 ± 0.6%, and the snag pool averaged 3.3 ± 0.6%. Of all ecosystem C pools, stem wood was the most significant component, ranging from 28.0% of TEC_{100} in OREAST stands to 37.0% in the Cascades.

Mean SOC values varied widely between provinces

TABLE 2. Extended.

Fine woody debris	Forest floor	Rotten wood	Logs	Snags	Soil	Shrubs	Herbs	Total
9.5	13.3	0.0	20.8	24.1	122.5†	1.0	nm	587.4
16.4	22.5	0.0	45.0	23.4	122.5†	0.6	nm	674.8
29.2	18.3	15.9	60.6	45.9	122.5†	2.2	nm	897.3
13.1	13.0	17.1	38.9	21.1	122.5†	0.2	nm	775.0
13.9	16.1	10.5	35.6	7.1	122.5†	1.6	nm	609.9
7.0	31.3	25.2	32.3	66.1	122.5†	1.5	nm	1097.3
11.0	7.5	0.0	33.9	87.3	122.5†	0.1	nm	978.9
8.3	22.9	0.0	18.5	35.8	122.5†	2.2	nm	780.5
13.8	21.3	0.0	12.4	9.4	41.9	0.1	0.4	443.8
33.3	28.5	22.2	69.0	98.5	179.2	0.5	0.3	920.4
5.1	18.5	26.0	36.6	59.1	102.8	1.7	0.3	753.9
12.6	23.3	11.2	54.3	5.1	121.8	0.5	0.3	1079.8
9.7	6.4	29.8	49.5	8.5	146.5	0.6	0.4	1043.4
8.6	19.5	0.0	75.9	13.4	143.2	1.7	0.2	969.0
18.1	16.9	54.9	53.5	35.0	472.3	2.3	0.1	1196.4
15.2	21.4	0.0	45.0	26.5	346.7	0.8	0.3	1123.5
11.2	27.7	24.5	40.0	32.0	407.4	2.6	0.2	1245.2
18.1	16.7	23.8	45.0	14.0	339.2	0.8	0.3	1203.8
17.4	30.5	25.7	40.0	21.0	275.4	1.0	0.1	1005.7
20.0	40.3	4.4	54.0	24.5	377.2	2.0	0.1	1042.4
16.8	13.8	3.4	34.5	16.5	326.3	0.8	0.4	1080.4
18.4	13.1	37.6	69.4	26.5	380.1	0.9	0.3	1118.9
6.9	14.9	0.0	14.3	14.8	58.7	1.0	0.3	231.6
8.5	6.1	0.0	8.9	9.0	29.2	0.0	0.0	157.5
10.1	8.6	0.0	9.3	5.6	32.1	0.1	0.0	173.7
8.2	10.1	0.0	8.8	7.9	27.0	0.2	0.0	216.5
11.2	11.3	61.1	57.4	6.3	59.9	0.5	0.2	613.3
24.1	11.2	21.2	25.6	17.8	262.6	1.2	0.0	844.9
10.0	9.0	41.8	53.1	20.8	54.7	0.6	0.1	680.2
10.5	17.5	27.5	55.3	44.3	95.9	0.3	0.2	949.6
10.4	26.9	45.9	84.9	30.4	109.3	1.8	0.1	841.1
6.0	28.3	18.1	32.1	24.0	78.1	1.5	0.3	463.1
15.0	6.5	37.3	20.2	12.2	204.8	1.4	0.2	837.2
9.4	33.3	17.1	16.6	24.9	116.6	1.4	0.8	613.5
5.8	30.8	25.1	4.6	28.5	75.6	0.5	0.3	648.5
20.9	16.3	13.9	85.6	40.3	109.0	0.2	0.4	1050.1
5.4	6.7	21.5	73.1	11.0	216.5	nm	nm	767.0
17.2	8.2	15.8	66.4	11.3	204.2	nm	nm	993.0
13.2	8.8	12.1	53.0	12.0	109.0	nm	nm	622.8
5.6	10.3	0.0	44.8	12.5	131.6	nm	nm	790.3
7.7	10.1	0.0	74.7	13.1	288.5	0.2	0.4	843.3
9.2	18.4	19.3	50.5	14.0	264.6	0.3	0.4	849.7
6.0	23.0	30.7	87.0	28.4	153.3	0.8	0.5	871.6

(Table 3), highlighting the large biogeoclimatic variability in the PNW. The percentage of SOC_{100} relative to TEC_{100} ranged between 15.0% for the Washington Cascades to 32.0% at the Oregon Coast with a mean of 21.1% (SE = 3.3%). ORCOAST stands stored 10 times the SOC that is stored in OREAST (365.5 vs. 36.7 Mg C/ha). ORCOAST stands stored, on average, 130 Mg C/ha more SOC than stands at WACOAST and about three times as much as was found in the stands in the Oregon and Washington Cascades. As a percentage of TEC_{50}, SOC_{50} was, in general, a smaller proportion of total C, ranging from 11.4% in the WA-

CASC to 24.5% in ORCOAST (16.5 ± 2.4%, mean ± 1 SE).

In each of the five provinces, total tree C, total detrital C, and total understory C were consistent percentages of TEC, respectively (Table 3). Understory biomass was very small in all provinces (0.1 ± 0.02%). Aboveground tree C (live and dead branches, foliage, stem wood, and bark) was the largest component of TEC_{100} and TEC_{50}. Aboveground tree C was between 41% and 52% of TEC_{100} (46 ± 2.1%) and 45–54% of TEC_{50} (49 ± 1.7%). Belowground tree C (fine roots, live and dead coarse roots) ranged between 14.4% (OR-

TABLE 3. The relative amounts of understory, above- and belowground tree, detrital, and soil organic carbon (SOC) in the five study provinces as a percentage of total ecosystem carbon (TEC; in megagrams of carbon per hectare).

Study province	TEC_{100}†	TEC_{50}‡	Understory§	Tree	
				Aboveground‖	Belowground¶
ORCASC	829.4	805.7	1.1 (0.13, 0.14)	431.7 (52.0, 53.6)	152.6 (18.4, 18.9)
ORCOAST	1127.0	1009.0	1.6 (0.14, 0.16)	464.7 (41.2, 46.1)	161.8 (14.4, 16.0)
OREAST	194.8	187.0	0.4 (0.21, 0.21)	85.3 (43.9, 45.6)	34.5 (17.7, 18.4)
WASCASC	754.2	719.3	1.2 (0.16, 0.17)	380.2 (50.4, 52.9)	125.4 (16.6, 17.4)
WACOAST	819.7	767.7	0.4 (0.05, 0.01)	363.5 (44.3, 47.4)	146.0 (17.8, 19.0)

Notes: See Table 1 for study province abbreviations. Values in parentheses represent the percentages of TEC_{100} and TEC_{50}, respectively.

† Understory, tree, detrital, and SOC (0–100 cm).

‡ Understory, tree, detrital, and SOC (0–50 cm).

§ Shrubs and herbs.

‖ Live and dead branch, foliage, stem bark, and stem wood.

¶ Fine roots and live and dead coarse roots.

Fine woody debris, forest floor, rotten wood, logs, and snags (excluding dead coarse roots, dead branches).

COAST) and 18.4% (ORCASC) of TEC_{100} (17.0 ± 0.71%) and between 16.0% (ORCOAST) and 19.0% (WACOAST) of TEC_{50} (17.9 ± 0.6%). ORCOAST had the lowest percentage of total tree C. This is because soil C represents a larger proportion of TEC at OR-COAST relative to the other provinces (Table 3). Detrital carbon (fine woody debris, dead coarse roots, dead branches, forest floor, rotten wood, logs, snags) ranged between 14.5% in the ORCOAST to 23.2% of TEC in the OREAST (19 ± 1.5%) for TEC_{100} and between 13.2% (ORCOAST) and 20.3% (OREAST) for TEC_{50} (16.3 ± 1.28%). Stands in eastern Oregon had much less detritus C (45.2 Mg C/ha) compared to coastal and Cascades stands (145.7–163.9 Mg C/ha), even though the percentage relative to TEC was the greatest. Among detrital pools, however, there was significant variation between provinces (see Table 2). ORCOAST had 46% more fine, woody debris and forest floor than WA-COAST and 39% more snag C. However, WACOAST had 35% more C in the form of logs than ORCOAST. ORCASC and WACASC stands had a similar distribution of C in their detrital pools although the WA-CASC stands had >60% more rotten wood than OR-CASC.

The percentage of root C relative to TEC differs depending on the method used to estimate root C. When using the regression equation developed by Cairns et al. (1997), TRCD averaged 13.4% of TEC. When using the Santantonio et al. (1977) equations, and adjusting for species density, roots averaged 17.0% of TEC. Root to shoot ratios (R:S) were the same for the ORCOAST and ORCASC regardless of which method was used. Both methods showed higher R:S for stands in OR-EAST, where more resources are stored belowground.

DISCUSSION

Confidence in site estimates

As a proportion of TEC, estimation errors of the foliage pool are not significant. Foliage biomass is only 0.7%, on average, of TEC in these old-growth forests,

and therefore even gross estimation errors would not significantly affect TEC. Indeed, we would have to increase the foliage pool 18 times to increase TEC by 10%. Similarly, we would have to increase shrub biomass 100 times to increase TEC by 10%. Nonetheless, prediction of foliage and understory biomass is critical for estimation of productivity and further species-specific equations need to be developed for this purpose.

Because of the effort required to directly measure coarse- and fine-root biomass, we used published allometric relationships instead. Review of the available root biomass literature is complicated because measurements often reflect limited spatial and temporal domains, making comparisons difficult, and because different authors use dissimilar definitions of fine and coarse roots. Dead coarse-root biomass averaged 2.6% of TEC. We would need to increase dead, coarse-root C by five times to change TEC by 10%. We would have to increase fine-root C 11 times to increase TEC by 10%. Therefore, although our estimates of these pools are rough, we have confidence that small changes in these pools will not affect TEC significantly. In contrast, live, coarse-root C is ~13.4% of TEC. Therefore, we would need to increase this pool only 1.5 times to observe a 10% increase in TEC.

Estimation errors in the stem wood pool have the potential to provide the greatest uncertainty in TEC since this pool represents the largest proportion of TEC (34%, on average). Yet, these are the pools about which we have the most confidence since >14 000 trees were measured for stem wood volume and since the allometric equations used to calculate biomass are well documented and validated (see BIOPAK, Means et al. 1994).

In addition, by including coarse soil aggregates and estimating SOC to a depth of 1 m, the soil C estimates used in this study represent an improvement on previous regional estimates of C storage in the PNW. Remillard (1999) found that 39–66% of SOC in soil pits was below 20 cm and up to 44% of SOC was found

TABLE 3. Extended.

Detrital#	SOC 0–100 cm, 0–50 cm	
121.4 (14.6, 15.1)	122.5, 98.8	(14.8, 12.3)
133.5 (11.8, 13.2)	365.5, 247.5	(32.4, 24.5)
37.9 (19.5, 20.3)	36.7, 28.9	(18.8, 15.5)
130.7 (17.3, 18.2)	116.6, 81.7	(15.5, 11.4)
114.4 (14.0, 14.9)	195.4, 143.0	(23.8, 18.6)

in C-bearing material >2 mm. Therefore, by reducing the degree that these C pools are underestimated results in more reliable estimates of the upper bounds of C storage in this region.

Role of disturbance

Our estimates of the upper bounds of C storage simply place a limit on C storage for the region, based on the unrealistic assumption that all forests eventually reach old-growth conditions. Instead, natural disturbances such as fire, wind storms, and landslides, as well as land conversion and management, create a mosaic of age classes on a landscape (Bormann and Likens 1979). In theory, some old-growth stands persist due to the stochastic nature of disturbance processes (Johnson and Van Wagner 1985), but natural and managed landscapes will store less C than landscapes covered completely by old-growth forests because of the high proportion of younger forests, which store less C than old-growth forests (Harmon et al. 1990). Despite these caveats, the theoretical construct of a completely old-growth landscape is useful as a neutral model (Gardner et al. 1987) in which one predicts the pattern (of C storage) in the absence of a process (e.g., human or natural disturbances; Turner 1989). Such models could be used to distinguish systematically the effects of different management strategies on C storage. By bounding estimates of C sequestration potential, managers can determine the efficacy of different sequestration strategies relative to their potential. Further, they would be able to determine the potential economic and environmental costs and benefits of various management strategies. By providing an upper bound on C storage in the region (based on sites where those processes have been absent), we place an upper limit on the results of such analyses.

Regional implications

To estimate the upper bounds of C storage for the PNW region, we multiplied the proportional area of each province (based on the area of the corresponding vegetation provinces in Franklin and Dyrness [1988]) by the average C storage in each province. These area-weighted estimates for each province were then summed. We used the following approximations of the area of each province to calculate the weighted estimates: *Picea sitchensis* zone in Oregon (i.e., OR-

COAST) was 8% of the study area; *P. sitchensis* in Washington (i.e., WACOAST) was 9%; *Tsuga heterophylla* in Oregon (i.e., ORCASC) and Washington (i.e., WACASC) was 32% and 17%, respectively; *Pinus ponderosa* (i.e., OREAST) was 13%; and *Abies amabilis* (subalpine zone) was 21% (adapted from Franklin and Dyrness [1988]: Fig. 27). Since subalpine stands were not represented by our study sites, we used a value of 401 Mg C/ha in the *A. amabilis* zone, taken as the average from studies by Boone et al. (1988: Fig. 1), Kimmins and Krumlik (1973: Tables 6 and 7, assuming soil and roots are each 20% of live biomass), and Grier et al. (1981: Table 2). Without a more formal geospatial analysis, this weighting procedure is a good first attempt at a regional estimate, allowing us to further constrain our estimate of the upper bounds of C storage. Before weighting, the average, upper bound of C storage was 745 Mg C/ha ($n = 43$ stands) to a depth of 100 cm. After weighting, the average upper bound of C storage was 671 Mg C/ha. Recalculating to SOC to 50 cm, a depth more amenable to forest sequestration practices in the short term, the average, upper bound of C storage was 640 Mg C/ha. For the latter calculation, SOC in the subalpine zone was assumed to be half of that in the former calculation to 100 cm.

At the regional level, exogenous disturbances such as increasing CO_2, natural disturbances, and climate change will further change this regional capacity to store additional carbon. The eventual regional capacity to sequester C in the PNW may be, therefore, much different than the potential capacity we outline here. Regional predictions of actual carbon sequestration will require a more detailed accounting of all significant endogenous and exogenous factors that control it. However, by constraining these estimates with the potential values we describe, it may be possible to place limits on the system.

Comparison with global studies

The C densities we measured in old-growth forests of the PNW are higher than C density values reported for any other type of vegetation, anywhere in the world (Fig. 3; Appendix C). Unfortunately, comparisons of our study to other carbon-density estimates is hampered since estimates often reflect sites whose disturbance histories are poorly documented. The biomass or C estimates of other studies often include effects of non-catastrophic, disturbance legacies (e.g., selective logging, light fires) or may represent stands that are in early to middle stages of succession after a stand-clearing disturbance such as a harvest, blow down, or heavy fire. Moreover, definitions of major ecosystem pools (live, detrital, soil) differ among studies. For example, Schlesinger (1977:51) defined detrital C as ''the total carbon in dead organic matter in the forest floor and in the underlying mineral soil layers,'' while Grier and Logan (1977) excluded soil C in their definition of detritus. In general, the distinction between litter, de-
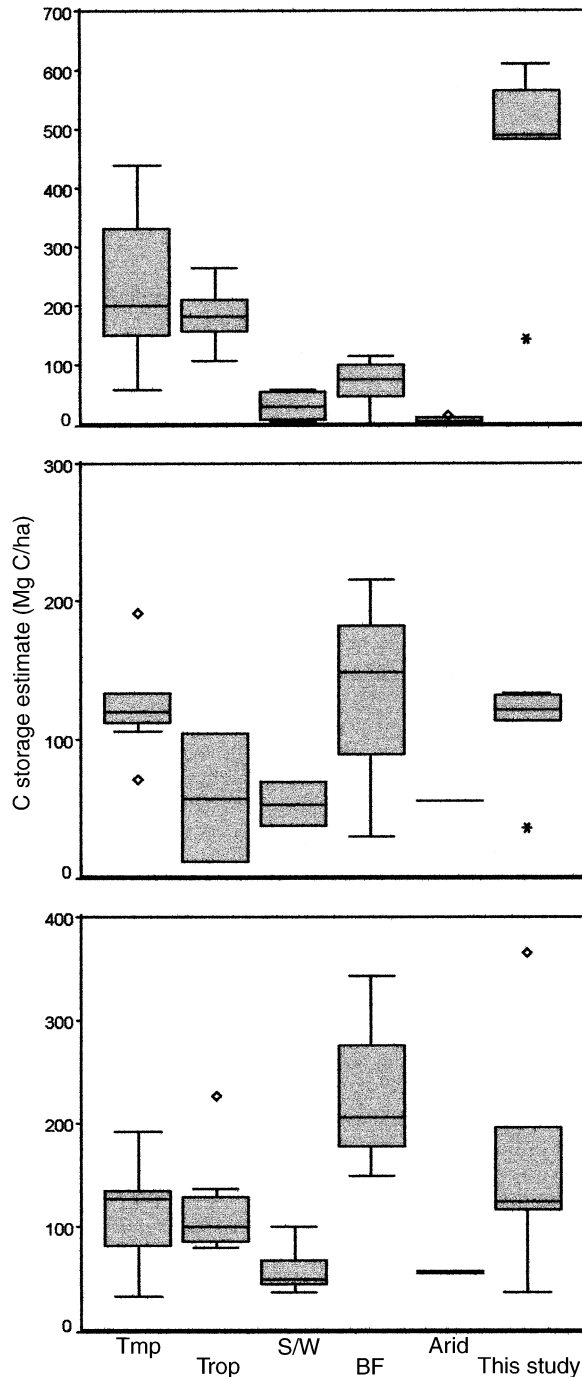
FIG. 3. Boxplots describing C storage estimates from the literature for (a) live, (b) detrital, and (c) soil organic carbon pools, compared to the mean C storage among provinces in the Pacific Northwest, USA. Box length is the interquartile range, which is the distance needed to span the middle 50% of the cases. The ''whiskers'' are the adjacent values, which are the most extreme cases that are within 1.5 box lengths of the upper and lower edge of the box. A mild outlier (diamond) is between 1.5 and 3 box lengths from the upper or lower edge of the box. An extreme outlier (asterisk) is more than 3 box lengths from the upper or lower edge of the box. Note different y-axis values. Tmp, temperate forest; Trop, tropical forest; S/W/G, savanna, woodland, grassland; BF, boreal forest. Sources may be found in Appendix C.

tritus, and soil C is not consistent between studies, making comparisons difficult (Matthews 1997).

Other limited studies in the region have demonstrated the potential of PNW old-growth forests to support large amounts of biomass. Fujimori et al. (1976), measuring only stem, branch, and leaf dry masses, reported biomass values of 669–882 Mg/ha (335–441 Mg C/ha) in *Picea sitchensis*, *T. heterophylla*, and *A. amabilis* zones in Oregon and Washington. Means et al. (1999) estimated aboveground biomass (trees, foliage, shrubs, herbs) at the H. J. Andrews forest as 965 ± 174 Mg/ha (or 483 ± 87 Mg C/ha). Grier and Logan (1977), who studied a 450-yr old-growth stand in Watershed 10 of the H. J. Andrews, found total organic matter accumulations, including SOC to 1 m, ranging from 1008 to 1514 Mg/ha (or 504–757 Mg C/ha). These studies at the H. J. Andrews were within the range of TEC that we measured at the H. J. Andrews (445–1097 Mg C/ha).

Why does old-growth in the PNW store so much C?

Trees in the PNW can reach massive sizes. Mild fall and winter conditions in much of the PNW facilitate continued productivity by coniferous evergreens at a time when deciduous trees are not able to photosynthesize. In addition, long, dry summers further hinder deciduous tree growth (Waring and Franklin 1979). Large conifer trees are able to maintain their growth by continued water conductivity through long, dry summers, which is facilitated with a tracheid xylem structure (Mencuccini and Grace 1996). The absence of frequent fires or storms in the productive regions of the PNW further supports massive trees with long lifetimes (Waring and Franklin 1979). In high-elevation sites, winter dormancy by coniferous tree species facilitates survival in cold conditions (Havrenek and Tranquillini 1995).

The large size of PNW trees means that they occupy a large proportion of ecosystem C storage relative to the national average. For example, Turner et al. (1995) estimated that half of actual total forest C in the conterminous U.S. was in the soil and that only 33% was in trees. Woody debris represented 10% of total C; the forest floor was 6% and the understory was 1% of total forest C. Birdsey et al. (1993) similarly estimated that only 31% of total C in the U.S. is currently in tree C (51% merchantable: 17% roots, 3% foliage, 6% snags, 24% other) and 59% was soil C. Litter, humus, and downed, coarse woody debris comprised 9% while understory was 1% of total C. These national averages are different than the 15–32% SOC and 53–67% tree C in the old-growth stands reported in this study. It should be noted that the absolute amount of SOC in the PNW is higher than the global average, although the relative proportion of ecosystem C that they represent is less due to the large amount of tree C in old-growth PNW forests. The detailed methods used to measure SOC probably allowed us to find higher ab-

solute C stores for this pool. However, the large proportion of tree C in this system, relative to the other studies mentioned above, indicates that the PNW may be more amenable to storing C through management and conservation efforts than other systems that store more C in soil.

C sequestration and economic implications

Future C management (e.g., Parson and Keith 1998) will require information on the upper bounds of C storage and the extent to which current forest C storage differs from it. In the U.S., Birdsey (1992) used national forest inventory data and other selected studies to estimate current (1987) organic C storage for trees, soil, forest floor, and understory vegetation. In this assessment, PNW forests accounted for 39% of TEC in the United States. Total C averaged 193.6 Mg C/ha for Oregon forests and 227.1 Mg C/ha for Washington forests (mean = 208.3 Mg C/ha, weighted by forest area [Birdsey 1992]). Turner et al. (1995) report an average C storage in PNW forests of 330 Mg C/ha. These studies present estimates that are significantly lower than our regional approximation of the upper bounds of C storage (671 Mg C/ha for TEC_{100} and 640 Mg C/ha for TEC_{50}) . In fact, our estimate is twice that of Turner et al. (1995) and more than three times that of Birdsey (1992).

Subtracting the estimate of Turner et al. (1995) of average current C storage in western Oregon and Washington from the upper bound of C storage in the region, forests could, theoretically, store an additional 310–341 Mg C/ha. To increase the C store to this level would require forest management aimed toward C sequestration, which may include protection from catastrophic, natural disturbances, lengthening of harvest rotations, and improvement in soil C storage.

Given recent estimates of the value of C in economic analyses (e.g., Romm et al. 1998) the average worth of each hectare of forest land could be thousands of dollars for additional C sequestration. Multiplied by the area of forest land in Oregon and Washington, this additional C storage would be worth billions of dollars (given the current value of the dollar). While we realize it is unlikely that large areas may be converted to old-growth forests given the other demands on timber resources, this rough calculation indicates a significant economic value that carbon storage could represent in this region.

CONCLUSIONS

Old-growth forest ecosystems can be used as an upper bound (or upper limit) on additional C sequestration potential. Currently, forest C storage in the PNW is less than this upper bound due to management practices and natural disturbances that lower the average age of the forests, reducing the time for large tree boles, detrital biomass, and soil C to accrue. The relative effect of natural disturbances and human management on future C sequestration can be best gauged by comparisons to the upper bounds of C storage as presented in this study. The upper bound (or limit) of the global, terrestrial biosphere to sequester additional carbon could be improved with similar studies in other regions. If management strategies were such to allow forests to return closer to the C stores found in old-growth forests, the PNW would have considerable ability to sequester additional C. This could have significant economic implications.

LITERATURE CITED

Acker, S. A., P. A. Harcombe, M. E. Harmon, and S. E. Greene. *In press.* Biomass accumulation over the first 150 years in a coastal Oregon spruce-hemlock forest. Vegetation Science.

Acker, S. A., W. A. McKee, M. E. Harmon, and J. F. Franklin. 1998. Long-term research on forest dynamics in the Pacific Northwest: a network of permanent forest plots. Pages 93–106 in F. Dallmeier and J. A. Comiskey, editors. Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring. Parthenon, New York, New York, USA.

Bender, M., et al. 2000. The changing C cycle: a terrestrial focus. Report of the Workshop on the Terrestrial C Cycle. National Science Foundation, Division of Earth Sciences, Arlington, Virginia, USA.

Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. USDA Forest Service General Technical Report WO-59.

Birdsey, R. A., A. J. Plantinga, and L. S. Heath. 1993. Past and prospective carbon storage in United States forests. Forest Ecology and Management **58**:33–40.

Boone, R. D., P. Sollins, and K. Cromack, Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. Ecology **69**:714–722.

Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forest. American Scientist **67**:660–669.

Brown, R. B., and R. B. Parsons. 1972. Soils of the reference stands—Oregon IBP. Internal Report 128. College of Forest Resources, University of Washington, Seattle, Washington, USA.

Brown, S. 1996. Mitigation potential of carbon dioxide emissions by management of forests in Asia. Ambio **25**:273–278.

Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1991. Biomass of tropical forests of south and southeast Asia. Canadian Journal of Forest Research **21**:111–117.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia **111**:1–11.

Chen, H., M. E. Harmon, and R. P. Griffiths. 2001. Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. Canadian Journal of Forest Research **31**:246–260.

Cohen, W. B., M. E. Harmon, D. O. Wallin, and M. Fiorella. 1996. Two decades of carbon flux from forests of the Pacific Northwest. BioScience **46**:836–844.

Cooper, C. F. 1983. Carbon storage in managed forests. Canadian Journal of Forest Research **13**:155–166.

Corti, G., F. C. Ugolini, and A. Agnelli. 1998. Classing the soil skeleton (greater than two millimeters): proposed approach and procedure. Soil Science Society of America Journal **62**:1620–1629.

Cromack, K., Jr., R. E. Miller, O. T. Helgerson, R. G. Smith, and H. W. Anderson. 1999. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. Soil Science Society of America Journal **63**:232–239.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology **33**:140–158.

DeBell, D. S., and J. F. Franklin. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. Western Journal of Applied Forestry **2**:111–114.

Dodson, R., and D. Marks. 1997. Daily air temperature interpolation at high spatial resolution over a large mountainous region. Climate Research **8**:2–20.

Franklin, J. F., and D. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Franklin, J. F., W. H. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The forest communities of Mount Rainier National Park. Scientific Monograph Series Number 19. U.S. Department of the Interior, National Park Service, Washington, D.C., USA.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. Carey, D. Thornburgh, D. R. Berg, D. Lindenmayer, M. E. Harmon, W. Keeton, and D. C. Shaw. *In press.* Disturbances and the structural develoment of natural forest ecosystems with some implications for silviculture. Forest Ecology and Management.

Fujimori, T., S. Kawanabe, H. Saito, C. C. Grier, and T. Shidei. 1976. Biomass and net primary production in forests of three major vegetation zones of the northwestern United States. Journal of the Japanese Forestry Society **58**:360–373.

Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology **1**:19–28.

Garrison, G. A., J. M. Skovlin, C. E. Poulton, and A. H. Winward. 1976. Northwest plant names and symbols for ecosystem inventory and analysis. General Technical Report PNW-GTR-46.

Gholz, H. L. 1980. Structure and productivity of *Juniperus occidentalis* in central Oregon. American Midland Naturalist **103**:251–261.

Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs **47**:373–400.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Canadian Journal of Forest Research **11**:155–167.

Harcombe, P. A. 1986. Stand development in a 130-year-old spruce–hemlock forest based on age structure and 50 years of mortality data. Forest Ecology and Management **14**:41–58.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science **247**:699–702.

Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. LTER Network Office, University of Washington, Seattle, Washington, USA.

Havrenek, W. M., and W. Tranquillini. 1995. Physiological processes during winter dormancy and their ecological significance. Pages 95–124 *in* W. K. Smith and T. M. Hinckley, editors. Ecophysiology of coniferous forests. Academic Press, San Diego, California, USA.

Houghton, R. A., E. A. Davidson, and G. M. Woodwell. 1998. Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. Global Biogeochemical Cycles **12**:25–34.

Janisch, J. E., and M. E. Harmon. 2002. Successional changes in live and dead wood stores: implications for net ecosystem productivity. Tree Physiology **22**:77–89.

Johnson, E. A., and C. E. Van Wagner. 1985. The theory and use of two fire history models. Canadian Journal of Forest Research **15**:214–220.

Kauppi, P. E., K. Mielikainen, and K. Kuusela. 1992. Biomass and carbon budget of European forests from 1971–1990. Science **256**:70–74.

Kimmins, J. P., and G. J. Krumlik. 1973. Comparison of the biomass distribution and tree form of old virgin forests at medium and high elevations in the mountains of South Coastal British Columbia, Canada. International Union of Forest Research Organizations (IUFRO) Biomass Studies. University of Maine Press, Orono, Maine, USA.

Krankina, O. N., and R. K. Dixon. 1994. Forest management options to conserve and sequester terrestrial carbon in the Russian Federation. World Resources Review **6**:88–101.

Lassen, L. E., and E. A. Okkonen. 1969. Sapwood thickness of Douglas-fir and five other western softwoods. USDA Forest Service Research Paper FPL-124.

Long, J. N., and J. Turner. 1975. Aboveground biomass of understorey and overstorey in an age sequence of four Douglas-fir stands. Journal of Applied Ecology **12**:179–188.

Marshall, J. D., and R. H. Waring. 1986. Comparison of methods of estimated leaf-area index in old-growth Douglas-fir. Ecology **67**:975–979.

Matthews, E. 1997. Global litter production, pools, and turnover times: estimates from measurement data and regression models. Journal of Geophysical Research **102**:18771–18800.

Means, J. E., S. A. Acker, D. J. Harding, J. B. Blair, M. A. Lefsky, W. B. Cohen, M. E. Harmon, and W. A. McKee. 1999. Use of large-footprint scanning airborne lidar to estimate forest stand characteristics in the western Cascades of Oregon. Remote Sensing of Environment **67**:298–308.

Means, J. E., H. A. Hansen, G. J. Koerper, P. B. Alaback, and M. W. Klopsch. 1994. Software for computing plant biomass—BIOPAK users guide. General Technical Report PNW-GTR-340.

Mencuccini, M., and J. Grace. 1996. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. Tree Physiology **16**:459–468.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–269.

Parson, E. A., and D. W. Keith. 1998. Fossil fuels without CO_2 emissions. Science **282**:1053–1054.

Pike, L. H., R. A. Rydell, and W. C. Denison. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. Canadian Journal of Forest Research **7**:680–699.

Remillard, S. M. 1999. Soil carbon and nitrogen in old-growth forests in western Oregon and Washington. Thesis. Oregon State University, Corvallis, Oregon, USA.

Romm, J., M. Levine, M. Brown, and E. Petersen. 1998. A road map for U.S. carbon reductions. Science **279**:669–670.

Santantonio, D., and R. K. Hermann. 1985. Standing crop, production, and turnover of fine roots on dry, moderate,

and wet sites of mature Douglas-fir in western Oregon. Annals of Science Forestry **42**:113–142.

Santantonio, D., R. K. Hermann, and W. S. Overton. 1977. Root biomass studies in forest ecosystems. Pedobiologia **17**:1–31.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. Annual Review of Ecology and Systematics **8**:51–81.

Turner, D. P., S. A. Acker, J. E. Means, and S. L. Garman. 2000*a*. Assessing alternative allometric algorithms for estimating leaf area of Douglas-fir trees and stands. Forest Ecology and Management **126**:61–76.

Turner, D. P., W. B. Cohen, and R. E. Kennedy. 2000*b*. Alternative spatial resolution and estimation of carbon flux over a managed forest landscape in western Oregon. Landscape Ecology **45**:441–452.

Turner, D. P., G. J. Koerper, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. Ecological Applications **5**:421–436.

Turner, J., and J. N. Long. 1975. Accumulation of organic matter in a series of Douglas-fir stands. Canadian Journal of Forest Research **5**:681–690.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**:171–197.

Ugolini, F. C., G. Corti, A. Agnelli, and F. Piccardi. 1996. Mineralogical, physical, and chemical properties of rock fragments in soil. Soil Science **161**:521–542.

U.S. Forest Products Laboratory. 1974. Wood handbook: wood as an engineering material. USDA Agricultural Handbook 72.

Vitousek, P. M. 1991. Can planted forests counteract increasing atmospheric carbon dioxide? Journal of Environmental Quality **20**:348–354.

Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science **204**:1380–1386.

Waring, R. H., and S. W. Running. 1998. Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, California, USA.

APPENDIX A

A table presenting scientific and common names of observed tree species and their abbreviations is available in ESA's Electronic Data Archive: *Ecological Archives* A012-012-A1.

APPENDIX B

A table presenting the source of equations used to calculate foliage biomass is available in ESA's Electronic Data Archive: *Ecological Archives* A012-012-A2.

APPENDIX C

A table presenting a comparison with estimates from the literature for vegetation, detritus, and soil carbon stores in ecosystems around the globe is available in ESA's Electronic Data Archive: *Ecological Archives* A012-012-A3.