SPATIAL PATTERNS OF FOREST CHARACTERISTICS IN THE WESTERN UNITED STATES DERIVED FROM INVENTORIES

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Abstract. In the western United States, forest ecosystems are subject to a variety of forcing mechanisms that drive dynamics, including climate change, land-use/land-cover change, atmospheric pollution, and disturbance. To understand the impacts of these stressors, it is crucial to develop assessments of forest properties to establish baselines, determine the extent of changes, and provide information to ecosystem modeling activities. Here we report on spatial patterns of characteristics of forest ecosystems in the western United States, including area, stand age, forest type, and carbon stocks, and comparisons of these patterns with those from satellite imagery and simulation models. The USDA Forest Service collected groundbased measurements of tree and plot information in recent decades as part of nationwide forest inventories. Using these measurements together with a methodology for estimating carbon stocks for each tree measured, we mapped county-level patterns across the western United States. Because forest ecosystem properties are often significantly different between hardwood and softwood species, we describe patterns of each. The stand age distribution peaked at 60-100 years across the region, with hardwoods typically younger than softwoods. Forest carbon density was highest along the coast region of northern California, Oregon, and Washington and lowest in the arid regions of the Southwest and along the edge of the Great Plains. These results quantify the spatial variability of forest characteristics important for understanding large-scale ecosystem processes and their controlling mechanisms. To illustrate other uses of the inventory-derived forest characteristics, we compared them against examples of independently derived estimates. Forest cover compared well with satellite-derived values when only productive stands were included in the inventory estimates. Forest types derived from satellite observations were similar to our inventory results, though the inventory database suggested more heterogeneity. Carbon stocks from the Century model were in good agreement with inventory results except in the Pacific Northwest and part of the Sierra Nevada, where it appears that harvesting and fire in the 20th century (processes not included in the model runs) reduced measured stand ages and carbon stocks compared to simulations.

Key words: Century model; FIA; forest carbon stocks; forest cover; forest inventories; forest type; MODIS; western United States.

INTRODUCTION

Forests are locally and globally important ecosystems, providing habitat, timber resources, carbon (C) storage, and recreational opportunities. In the western United States, forests are currently subjected to changing environmental conditions, and future projections continue or enhance these drivers of change. Recent climate variability in the West, in the form of increasing temperatures, enhanced precipitation, or drought, has resulted in forest responses such as massive dieback in the Southwest (Breshears et al. 2005) and changes in C fluxes (Hicke et al. 2002, Nemani et al. 2002).

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Atmospheric pollution affects western forests, causing, for example, reductions in growth due to ozone damage (e.g., Arbaugh et al. 1998) or modifications to biogeochemical cycling following nitrogen deposition (Rueth et al. 2003). Changes in forest cover resulting from human influence have significant impacts on forest biodiversity and function (Parmenter et al. 2003). Natural disturbances such as fire (Westerling et al. 2006) and insect outbreaks (Logan et al. 2003) have increased in recent years, and are predicted to continue increasing with future climate change (Bachelet et al. 2003, Hicke et al. 2006). Invasive species, such as white pine blister rust (Kinloch 2003) or sudden oak death (Barrett et al. 2006). are putting some western forests at risk. Changing natural disturbance and harvest regimes throughout the last century have influenced forest age, structure, and species composition (e.g., Covington and Moore 1994, Minnich et al. 1995, Westerling et al. 2006). These changes have significant impacts within forest ecosystems, for example, on biogeochemical cycling (Kashian et al. 2006).

Forests play a significant role in the global carbon cycle. In the Northern Hemisphere, forests and woodlands were a carbon sink of 0.6–0.7 Pg C/yr in the early 1990s (Goodale et al. 2002), as compared to an increase of atmospheric CO₂ of 3.2 Pg C/yr (Intergovernmental Panel on Climate Change 2001). Estimates of the net C flux in the United States from various methods, including atmospheric inverse modeling, forest inventories, bookkeeping models, and carbon cycle models, are between 0.1 and 1 Pg C/yr (Pacala et al. 2001), with western forests significant contributors to the sink. Denser forests and increased forest cover in this region in response to human suppression of fire and/or grazing are thought to be currently sequestering carbon (Houghton et al. 2000, Pacala et al. 2001). Modeled contemporary net C flux in the United States following recent climate change and CO₂ fertilization was largest in the higher elevation forested ecosystems of the West (Schimel et al. 2002). An analysis of satellite-derived gross primary production (GPP) indicated that areas in the western United States with significant GPP occur at higher elevations (typically associated with forest ecosystems; Schimel et al. 2002).

Characterizing the state of forest properties is crucial for gauging the response of forests to these driving processes. Multiple types of information are available for such analysis, including plot-level studies, remotely sensed imagery, and modeling (e.g., VEMAP Members 1995, Hicke et al. 2002, Monson et al. 2002, Schimel et al. 2002). Here we discuss forest characteristics estimated from inventories, which have unique features that provide significant advantages for studying forest properties. In the United States, inventories produced by the USDA Forest Service include field measurements of millions of trees on more than 125000 plots distributed across the lower 48 states (Smith 2002). These ground-based measurements were taken within a spatially extensive framework, about one plot every 2500 ha. Forest ecosystem properties can be estimated from these in situ measurements at plot to national scales. Inventory-based studies are valuable for establishing baselines for studies of future change, calculating carbon sequestration, and understanding spatial patterns and controls on forest processes. Forest characteristics from inventories are also valuable for comparison with estimates from the other sources listed above.

In this study, we focus on four key forest characteristics available from USDA Forest Service inventories: forest area, stand age, forest type, and carbon stocks. Each of these has been identified as a key indicator for tracking the condition of forests in the United States (H. John Heinz III Center for Science 2002). Forest area is used to identify land cover changes, estimate carbon sequestration, and quantify habitat. Although U.S. forests are not subjected to the extensive clearing in the tropics (Nepstad et al. 1999, DeFries et al. 2002, Asner et al. 2005), monitoring changes in forest area is still needed and required by federal law (Smith 2002). Stand age is a strong determinant of ecosystem structure and biogeochemical cycling. Stand development following disturbance governs net C fluxes through the release of carbon to the atmosphere from dead material as well as the regrowth of the stand (e.g., Hicke et al. 2003, Litvak et al. 2003, Kashian et al. 2006). Finally, stand age can provide clues about past disturbances. Forest types (dominant species) define phenological traits, leaf morphology, and habitat types. For example, aspen stands are broad-leaf, deciduous trees that are typically more productive and are associated with more biological diversity than nearby evergreen needleleaf pine stands (Gower et al. 1997, Simonson et al. 2001). Carbon sequestration has been proposed in forests as a means of partially offsetting anthropogenic emissions, and changes in C stocks indicate whether forests are carbon sources or sinks. Biomass measurements can also be used for estimating the potential for and consequences of wildfire (Rothermel 1972, Bessie and Johnson 1995, Kashian et al. 2006).

Multiple methods exist for estimating biomass from inventory measurements. Growing stock volume aggregated to the county or state level has been combined with expansion factors to estimate biomass at the same aggregated spatial resolution (Birdsey 1992, Brown et al. 1999). A second method, which we employ here, uses diameter measurements from individual trees together with allometric equations that convert diameters to biomass (Jenkins et al. 2001). The method using countylevel growing stock volume has the advantage of a simpler, less computationally intensive approach. The tree-level method using diameter measurements has the advantage that additional information is available at the plot (e.g., topography) or tree level (e.g., species), reducing uncertainties associated with growing stock volume methods and facilitating more detailed analysis that can be used to address complex questions about forest attributes, forest dynamics, and their relationship to large-scale environmental patterns.

Forest characteristics from inventories, particularly biomass, have typically been reported at regional or national scales (Birdsey 1992, Turner et al. 1995, Birdsey and Lewis 2003). Goodale et al. (2002) reported northern hemisphere forest net carbon budgets by nation using forest inventories. Finer resolution regional studies have focused on county-level (Brown et al. 1999) or 0.5° gridded results (Jenkins et al. 2001) for eastern forests. Comparable finer resolution studies for the western United States are lacking to date.

Our objectives were to map the spatial patterns in the western United States of each of the above four forest properties using the most recent, complete Resources Planning Act (RPA) inventory database and distinguish patterns in hardwood vs. softwood forests. Our results are complementary to previously published studies focused on forest biomass in the eastern United States, and are at finer spatial resolution than past national studies. Furthermore, we report on additional forest characteristics beyond biomass that are important to ecological studies. A secondary objective was to demonstrate the utility of the inventory-derived characteristics through comparisons with other sources of information. Thus, for forest attributes that have been estimated through other means (e.g., remotely sensed imagery), we provide comparisons. These comparisons are not meant to quantify differences in detail or evaluate potential shortcomings in a particular method, but are included as illustrative.

Methods

Forest inventory database

In the United States, the Resources Planning Act (RPA) of 1928 mandated that the USDA Forest Service monitor properties and report conditions of U.S. forests (Smith 2002). Regular reports track forest properties at the state to national scale (Smith et al. 2004). Prior to the late 1990s, the Forest Inventory and Analysis (FIA) surveyed private lands, whereas the National Forest System (NFS) was responsible for surveying national forest lands. The large amount of public ownership of forests in the West (compared to the East) implies that the inclusion of NFS inventories is critical for accurate assessments of forest properties. These "periodic" inventories occurred nominally every 10 years (Smith 2002). In the late 1990s, responsibility for the nationwide forest inventory of all lands was assumed by the FIA, and methods shifted to an "annual" inventory, in which a subset of plots is measured every year.

"Phase 1" inventory plots were established to measure forest cover area (see Smith [2002] and Alerich et al. [2004] for details). Remotely sensed information at each Phase 1 plot was interpreted to produce a land-use classification, which was further refined for forests by type, volume, and other stand characteristics. Measurements from ground plots were then used to correct the classification and provide additional information not available from the remote sensing. The classification was also used to develop expansion factors that allow plotlevel information to be scaled to populations. These population values are aggregated to produce countylevel information.

Every 2500-ha, "Phase 2" fixed-radius or variableradius ground plots were established. Multiple tree and stand characteristics were recorded by field crews. Diameter at breast height (dbh) was measured and species was noted, and stand age for each forested condition (an area within a plot with common land ownership, forest type, stand size and density, and other characteristics [Alerich et al. 2004]) was determined by coring two to three dominant or codominant trees identified in the field (USDA Forest Service 2005). If the condition had not experienced severe disturbance since the previous disturbance, the prior stand age may simply have been updated to the current year and recorded. Age was either identified to the nearest year or binned into 10-year classes for ages <100 years, 20-year classes for ages between 100 and 200 years, and 100-year classes for ages >200 years. To account for variability in the measurement years among the plots, we computed the year of stand origin by subtracting the stand age from the measurement year.

Analysis

We used inventory information from the RPA database, from the Forest Inventory and Analysis (FIA) web site and downloaded in 2005 (data available online).⁶ The RPA database includes plots on private lands measured by the FIA program as well as plots measured by the National Forest System that were not then the responsibility of FIA. Under the current annualized inventory system, FIA measures all plots, but few states have made substantial progress toward a complete inventory of all established plots. For example, as of 2004, Colorado had completed only three of 10 subcycles. Thus, we chose to analyze the older but more complete RPA database. In this analysis, we included twelve states west of the Great Plains with significant forest area. Except where noted otherwise, we considered all forest lands, including productive ("timberland") and stands not classified as timberland.

We calculated county area using the following equation (Alerich et al. 2004):

$$A = \sum_{i} (E_{\mathrm{A},i} \times c_i) \tag{1}$$

where A is area of a county, $E_{A,i}$ is the area expansion factor of each plot within a county (units of area), and c_i is the proportion of the plot with the desired condition (unitless). $E_{A,i}$ and c_i were obtained from the RPA database. The summation occurs over all plots of interest within a county. Typically, plots have one condition each but may have more. For computing total area, all land conditions were used (i.e., excluding water). For computing forest area, primary forest characteristics include $\geq 10\%$ stocking currently or in previous inventories. Stocking is determined from a look-up table using tree species and dbh (USDA Forest Service 2005). In western woodlands where stocking cannot be determined, a stand is considered forested if it has at least 5% canopy cover currently or in the past. "Timberland" conditions meet the forest condition requirements and in addition have a site productivity (in terms of wood volume) of $>0.24 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (20 $ft^3 \cdot acre^{-1} \cdot yr^{-1}$; Alerich et al. 2004).

We calculated the carbon stock of each tree (C_t , units of g C) in the RPA database from the tree species and

⁶ (http://fia.fs.fed.us)



FIG. 1. Methods of calculating carbon stocks from the tree level to the county level. Boxes with text in italics indicate variables from the RPA database.

dbh observations, including timber and non-timber species, together with allometric equations that convert diameters to biomass (Fig. 1 diagrams the process flow). We used the allometric equations of Jenkins et al. (2003) and Jenkins et al. (2004), who compiled >1800 equations and conducted a meta-analysis using >100 published studies to determine a consistent, nationalscale database of regression equations for computing aboveground biomass for tree species in the United States. This set of allometric equations is broken down into four hardwood species groups, five softwood species groups, and one woodland species group. Using the inventory species table provided by Jenkins et al. (2003), we assigned each species to the appropriate Jenkins species group to identify the proper allometric equations to be used. We also used the component equations developed by Jenkins et al. (2003) to estimate coarse root biomass and therefore calculated total tree biomass that included foliage, wood, and coarse roots. These component equations were broken down into two classes: hardwoods and softwoods. Both the allometric equations for aboveground biomass and the component equations were functions of dbh only.

We summed the carbon stocks of live trees in each plot using

$$C_{\rm p} = \sum_{j} [C_{\rm t}(j) \times \text{TPA}(j)]$$
(2)

where C_p is the plot-level C stock (units of Mg C/ha), $C_t(j)$ is the amount of carbon in the *j*th tree in the plot, and TPA(*j*) is the trees per acre expansion factor (after conversion from per acre to per ha) from the RPA database for the *j*th tree in the plot. We then aggregated the plot-level C stocks to the county level:

$$C_{\rm c} = \sum_{i} [E_{\rm V}(i) \times C_{\rm p}(i)] \tag{3}$$

where C_c is the county-level C stock (units of Mg C), $E_V(i)$ is the volume expansion factor (units of ha) of the *i*th plot in the county of interest, and $C_p(i)$ is the carbon associated with the ith plot. $E_V(i)$ was taken from the RPA database. We then computed carbon density (Mg C/ha) at the county level as

$$C = C_{\rm c}/A \tag{4}$$

where A is the forest area with live trees within each county.

We used the condition-level forest type variable from the RPA database to divide area, stand age, and carbon stocks between hardwoods and softwoods. The forest type indicates the dominant species within a condition, and so we may be assigning some subdominant softwood trees to hardwood forest types (e.g., blue spruce within the aspen forest type) and vice versa. Forest type is an attribute of stands, not individual trees; many stands contain individual trees that are not of the species used to name the type. However, it is the dominant species that have the greatest influence on most ecological characteristics (e.g., phenology, canopy characteristics, and wildlife habitat).

Inventory sampling errors for area are mandated not to exceed 3% per 1 million acres of timber (2% per one million ha; Alerich et al. 2004) at the 67% confidence level. Guidelines for volume sampling errors in the West are 10% per 1 billion cubic feet of growing stock on timberland (0.5% per 1×10^9 m³; Alerich et al. 2004). Smaller areas, such as counties, have larger sampling errors. We calculated sampling errors in timberland area and volume by county.

For spatially explicit mapping of inventory attributes, the finest spatial resolution available is the county. Maps showing, for example, forest carbon density by county illustrate spatial patterns of forest C stocks, and are useful to those interested in a particular county. However, these maps do not reveal the amount of total forest area within a county unless compared to a map of forest area. In some areas of the western United States where forest cover is low (e.g., in Arizona or Nevada), mapping county-level values may enhance their importance compared to the county forest area. Thus, we also plotted the county carbon density values for only those pixels identified as forest from the moderate-resolution imaging spectroradiometer (MODIS) land cover classification (discussed in Other data sources). Lacking additional information about plot locations, we assigned each forested MODIS pixel the same county carbon density. This map reduces the visual impact of a county with high C density but little forest area compared with counties with large forest area.



FIG. 2. (a) Mean plot measurement year within each county as reported in the Resources Planning Act (RPA) database. White counties are associated with states not considered (e.g., Texas), or with counties that did not have or did not report forest inventory information in this RPA database. (b) Distribution of measurement years for all plots. Most plots were inventoried in the late 1990s, though in a few states, the most recent (state-level) inventories in the RPA database were conducted as early as 1983 (Colorado).

Other data sources

To compare inventory estimates of forest area with other sources, we downloaded a 1-km global land cover classification product derived from MODIS satellite reflectances (MOD12Q1). The product was developed using a supervised classification methodology that combined training sites interpreted from high-resolution imagery with ancillary data (Friedl et al. 2002). The algorithm takes advantage of the multispectral, multitemporal nature of MODIS imagery. We used the International Geosphere–Biosphere Programme classification map, and identified the following types as forest: evergreen needleleaf forest, evergreen broadleaf forest, deciduous needleleaf forest, deciduous broadleaf forest, and mixed forests. These forest types have canopy cover >60% and height >2 m. We excluded shrubland and



FIG. 3. Forest area by county in the western United States. (a) Forest area from Resources Planning Act (RPA) database, defined as any land that is at least 10% stocked by trees or 5% crown cover, as a percentage of total land area. (b) Percent forest area that is a softwood forest type. (c) Forest cover from moderate-resolution imaging spectroradiometer (MODIS) 1-km satellite land cover classification product as a percentage of total county land area. (d) Difference in percent forest area (RPA – MODIS). Good overall agreement exists between MODIS forest types and RPA timberland, though regional biases occurred.

savanna cover classes, instead comparing MODIS forest classes with RPA timberland. Percent forest area within each county was computed by summing the forested 1km MODIS grid cells within a county and dividing by the total area of all land grid cells within a county.

We compared the inventory-based forest types to a satellite-derived FIA product. This product was generated from a classification of satellite reflectances at the 1km spatial resolution (Zhu and Evans 1994). The same eastern and western forest types as in the RPA database were used in the classification with the exception that California mixed conifer and western oak types were specified in the RPA database but not in the satellite map. A separate map of percent forest cover for each pixel was also produced by Zhu and Evans. We estimated the dominant forest type at the county level by combining the percent forest cover map with the forest type map.

We compared forest carbon stocks with results from the Century biogeochemistry model (Parton et al. 1994). Century models carbon stocks and fluxes in multiple vegetation classes (e.g., forests) through the simulation of multiple carbon pools. Carbon fixed by plants (net primary production) is allocated among living plant parts; as plants die or leaves drop, carbon is transferred to dead pools, then soil pools. As part of the Vegetation



FIG. 4. RPA percent timberland area vs. MODIS percent forest area by county. Thick symbols and error bars indicate averages and standard deviations, respectively, for 10% RPA timberland area bins. The solid line is the 1:1 line; the dashed line is from linear least-squares regression (using all counties). Regression equation, mean bias error (MBE), root-mean-square error (RMSE), R^2 , and standard error of estimate (SEE) are shown.

Mapping and Analysis Project (VEMAP [VEMAP Members 1995]), monthly carbon stocks and fluxes in the coterminous United States were simulated in the 20th century at 0.5° spatial resolution by Century. After initializing carbon pools with a 3000-year spin up, actual climate, observed atmospheric CO₂ concentrations, and a map of vegetation classes were used to estimate carbon cycling from 1895 to 1993. In the Pacific Northwest and northwestern California, fires were simulated every 300 years, with the last burn specified in 1800. In contrast, fire return intervals for interior forests were specified as every 100 years, with the last simulated fire occurring in 1900. These results have been described in previous studies (VEMAP Members 1995, Schimel et al. 2000). To compare with RPA estimates, Century forest carbon stocks were summed in foliage, wood, and root pools and averaged for the 1984-1993 period. Because of the inconsistent "cell" boundaries but similar spatial resolution between the Century grid and the county boundaries, we were unable to directly compare the two carbon density estimates.

RESULTS

We analyzed over 1.7×10^6 tree measurements on about 47 000 plots in 428 counties and 12 western states. The majority of these states had inventories in the late 1990s (Fig. 2a, b). Some states had earlier inventories, for example, Colorado (1983), Wyoming (1984), and Nevada (1989).

Sampling errors in timberland area were typically <5% at the county level for those regions with significant forest area (Appendix: Fig. A1a). Sampling errors in timberland volume were <8% in the Pacific

Northwest, California, and the Northern Rockies (Appendix: Fig. A1b). Higher values, on the order of 10–20%, occurred in the Southern Rockies or in counties with minimal forest area (e.g., in Nevada) where volumes were lower by county.

Forest area

Forest area in the 12 western states was 94 Mha, or 29% of the total land area (Fig. 3a). Timberland area, or forest area with a minimum productivity, was 62 Mha, or 19% of the total land area and 66% of the forest area. Spatial patterns of timberland were similar to those of forest area (Appendix: Fig. A2a). Softwoods comprised 81% of the forest area (Fig. 3b) and 87% of the timberland area in the West (Appendix: Fig. A2b). Hardwoods dominated in coastal and southern California, in Arizona, and in the Great Plains. Lower softwood percentages in timberland compared to forest land occurred in Nevada, Utah, and western Colorado, where hardwood forests (e.g., aspen) were more productive than softwood forests dominated by pinyon-juniper. In other locations with extensive lower productivity mesquite or oak woodland (e.g., southwest Arizona, California), more productive softwood forests contributed to a higher percentage of timberland area.

The majority of MODIS forest cover in the West was evergreen needleleaf, with 85% of the forest area containing this forest class (Appendix: Fig. A2c). The mixed forests class contributed 12% of the forest area. MODIS-derived forest area had similar spatial patterns as RPA timberland (Fig. 3c), and similar total area (56 Mha vs. 62 Mha of RPA timberland). Mapping differences revealed some spatial patterns (Fig. 3d).



FIG. 5. (a) Regional (western United States) distribution of stand age (by area) for all trees (crosses), softwoods (diamonds), and hardwoods (triangles). (b) Regional distribution of year of stand origin.

MODIS percent forest cover in counties along the coast from California to Washington was typically higher than the RPA percent timberland area by 5–20%. In contrast, on the east side of the Cascades, in the Sierra Nevada, and throughout most of the Rockies, RPA estimates were higher than MODIS estimates by 5–20%. The comparison between the two estimates of percent forest area within a county suggested agreement between MODIS and RPA estimates, with the least-squares regression line very close to the 1:1 line, $R^2 = 0.91$, and a root-mean-square error of 9% (Fig. 4).

Stand age

Mean stand age (weighted by area within a given county) for all forests across the region was 101 years (Fig. 5a). Softwoods had a mean stand age of 105 years, and the mean age of hardwoods was 76 years. The softwoods distribution (and thus the total distribution) was sharply peaked, with most areas having stand ages of 60–100 years. The hardwoods were more evenly distributed among the young age classes, but like the softwoods, exhibited a rapid decrease in area of older stands. The majority of stands (by area) originated in the few decades around 1900, with some stands originating much earlier, before 1800 (Fig. 5b).

Counties with significant forest area throughout the West had mean stand ages >80 years (Fig. 6a), mostly driven by softwood stand age (Fig. 6d). An exception occurred in the coastal region of Washington and Oregon, where stand ages were <50 years. Hardwood stand ages were younger than those of softwoods (Fig. 6c). Hardwoods in the southern states were typically older than those in the northern states (>80 years vs. <60 years). Spatial patterns of the year of stand origin were variable across the region (Fig. 6b). For locations with significant forest area, coastal Oregon and Wash-



FIG. 6. (a) Mean stand age for all forest types. (b) Mean year of stand origin. (c) Mean stand age for hardwoods. (d) Mean stand age for softwoods. Typical stand ages throughout the region were 80–100 years. The youngest stands were in the Coast Ranges and on the west side of the Cascades in Washington and Oregon. Hardwoods tended to occur in younger stands than softwoods by several decades.

ington stands were most recently disturbed, typically after the 1920s, with some counties as late as the 1940s and 1950s. Stands in eastern Washington, northern Idaho, and northwestern Montana also originated in the early to mid-1900s. In contrast, stands in California and Colorado were established earlier, in the mid-1800s.

Forest types

In the western United States, softwood forest types dominated, with pinyon-juniper forest types covering the most forest area (21 Mha), followed by Douglas-fir and ponderosa pine types (Figs. 7 and 8a). Very little pinyon-juniper forest was productive enough to be considered timberland, whereas most of the area associated with other softwoods was considered timberland. Western oak and aspen/birch and forest types had the largest area among hardwood forest types, with 4–5 Mha each. The satellite-derived FIA map of forest types (Fig. 8b) generally agreed with the RPA inventory estimates. In the satellite-derived map, ponderosa pine occurred on the eastern side of the northern Cascades and lodgepole pine occurred in much of the northern Rockies; Douglas-fir was specified in these areas in the inventory map. The confusion matrix (Table 1) revealed better agreement in the pinyon-juniper, Douglas-fir, and ponderosa pine type than other forest types. For aspen/birch, the satellite-derived classification did not have enough area in any county to qualify as dominant, whereas the RPA database had 13 aspen/birch-dominated counties.



FIG. 7. Area of forest and timberland (forests that meet a minimum level of productivity) by forest type group in the western United States.

Outside the Great Basin and eastern slope of the Rockies, the RPA forest types plotted were not the majority, but instead constituted a smaller fraction of the total forest area (i.e., <50%; Fig. 8c). For example, in the northern Rockies, in counties where it is most common, Douglas-fir made up only 20-30% of the total area. Although the satellite-derived FIA map showed similar patterns, the percentage of area occupied by the dominant forest type was higher than estimated from the RPA inventory, particularly in the Northwest (Fig. 8d). For example, on the east side of the Cascades, the FIA map reported that ponderosa pine occurred in 40-70% of the forest area, whereas the RPA inventory values were 20-40%. This difference suggests that the forests in the RPA inventory database were more heterogeneous than those in the satellite-derived FIA map.

Carbon stocks

Regionally, total carbon stored in live biomass pools (wood, foliage, coarse roots) was 6012 Tg C; 87% was in softwood forest types. Carbon density (carbon per area) was 74 Mg C/ha. Softwoods had higher carbon density (76 Mg C/ha) compared with hardwoods (63 Mg C/ha). Spatial patterns of carbon density revealed that most C occurred in the coastal regions (including the Cascade Mountains) from northern California northward (>120 Mg C/ha; Fig. 9a). The forests of the Sierra Nevada also had high carbon density, with values exceeding 100 Mg C/ha. Interior forests stored less C. In the northern Rockies, values were around 80 Mg C/ha, whereas in Colorado, stocks were typically <80 Mg C/ha. Softwoods stored most of the carbon except in some regions of coastal California and southern Arizona. Distributing county-level carbon density values to only forested locations (determined from the MODIS land cover classification) highlighted the regions with significant forest area, and deemphasized the low forest cover in the Great Basin region (Nevada and surrounding areas) as well as in the Southwest (Fig. 9b).

Carbon stocks in interior forests (i.e., in the Rocky Mountains and Southwest where forest cover is significant) from the Century VEMAP simulations generally were similar to those from the RPA database (Fig. 9c). Carbon densities from both estimates in these forests were around 50 Mg C/ha or below. Notable disagreements occurred in the Pacific Northwest and in the Sierra Nevada. The RPA database reported values of ~100 Mg/ha in these regions, occasionally reaching 150 Mg/ha. In contrast, Century reported values of 200–450 Mg/ha.

DISCUSSION

The stand age distribution of forests across the West peaked at 60-100 years; once differences in measurement year are accounted for, this pattern is similar to that reported in a national assessment of forest characteristics based on similar data as ours (Smith et al. 2004). This pattern contrasts with theoretical age distributions based on a random fire return interval (Van Wagner 1978, Taylor and Carroll 2004), and indicates that western forests are not in a steady state condition. These theoretical distributions follow a negative exponential function, with the largest fraction in the youngest age classes, in contrast to the inventory results. (The inventory results presented here are based on area, not number of stands; although we found that averaging the inventory plots produced roughly similar attribute patterns as the more proper area weighting, the area weighting may mask some variability at the plot level.) Climate may act to impose spatial synchrony on wildfires (Swetnam and Betancourt 1990, 1998, Westerling et al. 2003, Schoennagel et al. 2005). A random fire return interval, and thus a negative exponential age distribution, may therefore not represent historical conditions (i.e., pre-European settlement). Large areas burned in the late 1800s and early 1900s in some regions are attributed to favorable climate conditions as well as to Euro-American settlement (Shinneman and Baker 1997, Swetnam and Betancourt 1998, Veblen et al. 2000). In some areas, human influences (e.g., grazing, fire suppression) during this time and later reduced fire return intervals dramatically. The reduction in prevalence of both stand-replacing and understory fire as disturbances has led to the expansion of forests along forest-grassland ecotones (Mast et al. 1998) as well as the additional recruitment of trees within stand types that have been historically characterized by a low stem density, such as ponderosa pine in the Southwest (Covington and Moore 1994). The strong influence of stand age on such ecosystem processes as net C fluxes



FIG. 8. Dominant forest types (by area) from (a) the RPA inventory measurements and (b) the Forest Inventory and Analysis (FIA) satellite-derived classification. Also shown is the percent area of the dominant forest type within each county from the (c) RPA inventory and (d) FIA satellite data sets. Douglas-fir, ponderosa pine, and lodgepole pine forest types dominate in the mountainous areas, with pinyon–juniper covering the largest area in the drier regions. The RPA inventory had more Douglas-fir and lodgepole pine forest in the northern regions compared with the FIA satellite data set, though these forest types were less dominant (i.e., covered a smaller percentage of each county) than represented in the FIA satellite classes.

(Hicke et al. 2003, Pregitzer and Euskirchen 2004, Kashian et al. 2006) illustrates the importance of understanding the causes and consequences of the disturbance-induced patterns in regional stand age distribution.

Stand ages, forest cover and type, and climate combined to determine patterns of carbon stocks. Despite younger stand ages, the higher forest cover and favorable growing conditions of the Pacific Northwest resulted in the highest forest C stocks. Slightly lower stocks occurred in the Sierra Nevada in forests with older stands and reduced area of productive forest (timberland). The continental climate of the Rocky Mountains, including lower temperatures and precipitation, caused reduced C stocks despite high forest cover. In the Southwest, arid and semi-arid conditions produced sparser forest cover and lower forest biomass.

In the West, softwoods dominated hardwoods in terms of cover and C stocks. Yet the importance of hardwoods in some regions (e.g., California), their different age structure, and their different dynamics (e.g., phenology) suggest that these forest types should be considered separately in regional ecosystem studies in the West. In some locations such as the Pacific Northwest, softwood forest types associated with early successional species such as *Alnus* had younger stand

Forest type	Nonforest	Pinyon– juniper	Douglas- fir	Ponderosa pine	Fir–spruce– mountain hemlock	Lodgepole pine	Hemlock– Sitka spruce
Nonforest	0	0	0	0	0	0	0
Pinvon-juniper	6	84	ĩ	8	1	3	Õ
Douglas-fir	Õ	3	44	19	3	14	ĩ
Ponderosa pine	6	5	1	52	1	1	0
Fir-spruce-mountain hemlock	0	3	1	3	5	3	0
Lodgepole pine	1	1	0	0	4	23	0
Hemlock-Sitka spruce	0	0	2	0	0	0	4
CA mixed conifer	0	0	0	7	1	0	0
Aspen-birch	1	5	1	1	3	1	0
Western oak	4	1	0	4	0	1	0
Other softwoods	4	1	0	0	1	0	0
Other hardwoods	50	3	4	2	0	0	0
Total	72	106	54	96	19	46	5

TABLE 1. Confusion matrix between county-level RPA forest types and FIA satellite-derived forest types.

Notes: The confusion matrix lists the number of trees within each combination of forest types from the two classification methods as identified by the row and column headings. Diagonal elements indicate classification agreement between both data sets; off-diagonal elements indicate disagreement. Columns are from satellite-derived classification; rows are inventory-derived classification. Overall agreement (sum of diagonal elements divided by total number of counties) is 52%.

ages, influencing carbon stocks. However, these stands constituted typically less than 20% of a county's forest area, and therefore the impact of these species was minimal at these spatial scales.

Western forests contain less total carbon than eastern forests (which store 10 250 Tg C) (Brown et al. 1999). Hardwoods constituted the majority of carbon in eastern forests (80%), whereas softwoods dominated in western forests (87%). Carbon density in western hardwoods was lower than in eastern hardwoods (63 vs. 80 Mg C/ha), yet carbon density in softwoods was substantially higher in the West (76 vs. 55 Mg C/ha; Brown et al. 1999).

Our C stock results are comparable to those of other inventory-based methods. Turner et al. (1995) reported regional average C densities in the Pacific Northwest of 120 Mg C/ha on the west side of the Cascades and 50 Mg C/ha on the east side. Birdsey and Lewis (2003) calculated that the C density in Washington was 91 Mg C/ha. We find similar values in these regions (Fig. 9). Westwide, our estimates of 6012 Tg C were higher than that reported by Birdsey and Lewis (2003) by about 10%.

Forest cover definitions vary widely, as do means of estimating cover (Hansen and DeFries 2004). The MODIS data set slightly underestimated forest area compared to the RPA estimates as indicated by the mean bias error, particularly at the lower percent forest area values. This may be attributable to the International Geosphere–Biosphere Programme definition of forest cover classes used in the MODIS algorithm, which specifies canopy cover >60%. Our calculation of percent MODIS forest cover at the county level assumed that each MODIS pixel was 100% covered by forest. The inventory estimates reported here used ground-based measurements, subsampling, and different cover definitions (forest vs. timberland) than the spatially explicit satellite-derived land cover classification product. However, after choosing the cover characteristics in each data set that produced the most consistent comparison, i.e., timberland compared to forest types only (no shrublands or savannas), we found good agreement between the MODIS and RPA cover estimates.

The large differences between the inventory and Century carbon stocks in the coastal states were most likely a result of disturbances since 1900, mainly harvesting and fire, that reduced stand ages and therefore biomass. These disturbances were not included in the Century model runs, which simulated forest disturbances in 1800, earlier than realistic (see stand age map, Fig. 6). Thus, modeled stands were older and resulting carbon stocks were higher in these regions in the 1980s and 1990s than estimates from inventories.

This database of forest characteristics is useful for studies that model biogeochemical cycling over larger scales (e.g., VEMAP Members 1995, McGuire et al. 2001). The variables reported here are important in driving biogeochemical cycle dynamics. In addition, this information can assist in estimating carbon dynamics as forested areas undergo changes following fire, insect outbreaks, or harvest. Recent changes in disturbance and harvest regimes are not reflected in the many current model simulations. Inventory-based estimates of these state variables are valuable for validating simulation runs as well as understanding the importance of missing processes in models, as we demonstrate. They also may be useful in newer data assimilation techniques that constrain model results in optimal ways using rigorous mathematical methods (Braswell et al. 2005, White and Luo 2005, Williams et al. 2005, Sacks et al. 2006).

Are the inventory-derived forest characteristics more accurate than other sources? At the plot level, observations of tree diameters, species, and stand age suggest that inventories produce highly accurate results of stand age, biomass/carbon stocks, and forest type. Scaling to coarser resolution products relies on the inventory

TABLE 1. Extended.

CA mixed conifer	Aspen- birch	Western oak	Other softwoods	Other hardwoods	Total
0	0	0	0	0	0
0	0	0	0	0	103
0	0	0	1	1	86
0	0	0	0	2	68
0	0	0	1	0	16
0	0	0	0	0	29
0	0	0	0	0	6
0	0	0	0	0	8
0	0	0	0	1	13
0	0	0	0	12	22
0	0	0	0	1	7
0	0	0	1	14	74
0	0	0	3	31	432

program's sampling methods, whose uncertainties are mapped in Appendix: Fig. A1. Therefore, we suggest that inventory methods may be more accurate than other spatially explicit sources since ecosystem models may not include all relevant processes (as illustrated here), and remotely sensed imagery that relies on optical imagery that may have errors associated with sparse forests and/or lack of sensitivity to biomass at high leaf area (Zhang and Kondragunta 2006) or may have difficulty in discriminating forest types (Zhu and Evans 1994). Forest cover, on the other hand, may not be as accurately represented in the inventory as in the satellite imagery, in part because the remotely sensed product is spatially complete and the inventory method relies on spatial sampling. Improvements in estimates of some forest properties such as biomass will occur through advances in remote sensing (e.g., lidar), whereas improvements in estimates of other attributes, such as stand age, may remain elusive, suggesting a continued reliance on inventory estimates.

Several sources of uncertainty exist that may influence our results. Stand ages are subject to some uncertainty since field crews subjectively select representative trees on the plots and since ages were often estimated in the field from cores. Grouping by 20-year age bins minimizes these issues, however, and we feel that the gross patterns described in this paper are realistic. A second source of uncertainty is that the measured plots and surrounding area used to develop area and volume population expansion factors represent only a fraction of the landscape, and so may smooth out some variability. This sampling error is accounted for in the calculated standard errors.

Another uncertainty is the wide range of measurement years across the West. Although we quantified this 20year range (Fig. 2), we urge caution when interpreting the results. With respect to stand age, the indication of non-steady state conditions from the sharply peaked age distribution implies that the range of measurement years could result in under- or overestimates of important regional variability in stand age. Ideally, spatial comparisons of stand ages (as we show here) would be derived from concurrent inventories. Instead, the range of measurement years could flatten or sharpen age distributions depending on the year of local disturbance. Analyses using future inventories will alleviate these concerns.

Finally, the application of national-scale allometric equations for computing biomass from dbh produces uncertainty associated with stand-level and regional variability. The stand-level source of variability cannot be captured with the existing inventory sampling design, but instead would require additional sampling. Although their generality may produce regional biases, national-scale allometric equations have the advantage of minimizing expense and maximizing simplicity, transparency, and consistency.

CONCLUSIONS

Inventories provide an excellent means of evaluating forest ecosystem properties. The Resources Planning Act database provided by the USDA Forest Service contains information about a variety of properties based on millions of tree measurements on public and private lands. The most recent RPA database consists of inventories typically from the late 1990s, but also includes earlier and later inventories. The design of the Forest Service inventory permits spatial analysis at the county scale and coarser, although the use of a finer resolution forest cover map (e.g., from MODIS) allows county-level values to be distributed to forested areas only.

Measurements in the western United States were analyzed to assess forest area, stand age, dominant forest type, and carbon stocks. We employed a method that includes every tree measured within a plot to calculate carbon stocks, thus avoiding uncertainties associated with expanding county-level growing stock volume to include non-timber species and tree sizes. Inventory- and satellite-derived area and forest type were generally comparable across a range of forest area. Overall, stand ages of western forests peaked in the 60– 100 year classes, likely the result of fires and human activities beginning in the 1800s.

In contrast to eastern forests, western forest carbon stocks are dominated by softwoods; hardwoods are significant in limited regions, such as the coastal regions of central California. Carbon stocks were concentrated in the coastal and Cascade areas of Washington, Oregon, and northern California. Forests in the Sierra Nevada and Rocky Mountains had lower amounts. Good agreement occurred between inventory-based carbon stocks and those estimated using a historical model run of a biogeochemical model. Exceptions occurred in regions where harvesting and natural disturbances within the last 100 years reduced stand ages (and therefore biomass) compared to model results, which simulated up to 200 years of post-disturbance growth.



FIG. 9. (a) Carbon density in forests calculated from the RPA database. (b) Carbon density plotted only for forested locations within a county as determined from the MODIS land cover classification. (c) Carbon density for forests from the Century biogeochemical model using the 1984–1993 average from VEMAP simulation (VEMAP Members 1995). The color key in panel (a) applies to panels (b) and (c) as well. The most forest carbon occurred in the coastal forests from northern California north. Most of the carbon in the West was in softwoods except along the coast of southern California and in southern Arizona. Good agreement occurred between the inventory carbon stocks and the Century simulations except in the Pacific Northwest and Sierra Nevada. In these regions, disturbances that were not accounted for in the Century modeling reduced stand ages and therefore carbon stocks compared to model estimates.

Inventories will continue to provide important information about forest ecosystems. With recent interest in understanding forest dynamics at landscape to regional scales, spatially explicit analyses of inventory measurements will remain valuable for describing patterns and understanding driving processes. Furthermore, with the advance of satellite imagery and biogeochemical modeling, inventories provide valuable information for syntheses and comparisons among different methodologies (Baccini et al. 2004, Van Tuyl et al. 2005, Masek and Collatz 2006, Zhang and Kondragunta 2006).

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LITERATURE CITED

- Alerich, C. L., L. Klevgard, C. Liff, and P. D. Miles. 2004. The forest inventory and analysis database: database description and users guide version 1.7. (http://www.ncrs2.fs.fed.us/ 4801/fiadb/fiadb_documentation/FIADB_v17_122104.pdf)
- Arbaugh, M. J., P. R. Miller, J. J. Carroll, B. Takemoto, and T. Procter. 1998. Relationships of ozone exposure to pine injury in the Sierra Nevada and San Bernardino Mountains of California, USA. Environmental Pollution 101:291–301.
- Asner, G. P., D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller, and J. N. Silva. 2005. Selective logging in the Brazilian Amazon. Science 310:480–482.
- Baccini, A., M. A. Friedl, C. E. Woodcock, and R. Warbington. 2004. Forest biomass estimation over regional scales using multisource data. Geophysical Research Letters 31:L10501 [doi: 10510.11029/12004GL019782].
- Bachelet, D., R. P. Neilson, T. Hickler, R. J. Drapek, J. M. Lenihan, M. T. Sykes, B. Smith, S. Sitch, and K. Thonicke. 2003. Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles 17:1045 [doi: 1010.1029/2001GB001508].
- Barrett, T. M., D. Gatziolis, J. S. Fried, and K. L. Waddell. 2006. Sudden oak death in California: What is the potential? Journal of Forestry 104:61–64.
- Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76:747–762.
- Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. General Technical Report GTR-WO-59. USDA Forest Service, Washington, D.C., USA.
- Birdsey, R. A., and G. M. Lewis. 2003. Carbon in United States forests and wood products, 1987–1997: state-by-state estimates. General Technical Report NE-310. USDA Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, USA.
- Braswell, B. H., W. J. Sacks, E. Linder, and D. S. Schimel. 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. Global Change Biology 11:335–355.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences (USA) 102:15144–15148.
- Brown, S. L., P. Schroeder, and J. S. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. Forest Ecology and Management 123:81–90.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92:39–47.
- DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, and J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proceedings of the National Academy of Sciences (USA) 99:14256–14261.
- Friedl, M. A., et al. 2002. Global land cover mapping from MODIS: algorithms and early results. Remote Sensing of Environment 83:287–302.
- Goodale, C. L., et al. 2002. Forest carbon sinks in the Northern Hemisphere. Ecological Applications 12:891–899.
- Gower, S. T., J. G. Vogel, J. M. Norman, C. J. Kucharik, S. J. Steele, and T. K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Research–Atmospheres 102:29029– 29041.
- Hansen, M. C., and R. S. DeFries. 2004. Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km advanced very high resolution radiometer (AVHRR) data for the years 1982–99. Ecosystems 7:695–716.

- H. John Heinz III Center for Science, Economics, and the Environment. 2002. The state of the nation's ecosystems: measuring the lands, waters, and living resources of the United States. Cambridge University Press, Cambridge, UK.
- Hicke, J. A., G. P. Asner, E. S. Kasiske, N. H. F. French, J. T. Randerson, G. J. Collatz, B. J. Stocks, C. J. Tucker, S. O. Los, and C. B. Field. 2003. Postfire response of North American boreal forest net primary productivity analyzed with satellite observations. Global Change Biology 9:1145– 1157.
- Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, and C. Field. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. Global Biogeochemical Cycles 16: 10.1029/2001GB001550.
- Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research–Biogeosciences 111:G02019 [doi: 02010.01029/ 02005JG000101].
- Houghton, R. A., J. L. Hackler, and K. T. Lawrence. 2000. Changes in terrestrial carbon storage in the United States. 2: the role of fire and fire management. Global Ecology and Biogeography 9:145–170.
- Intergovernmental Panel on Climate Change. 2001. Climate change 2001: the scientific basis. Contribution of the Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jenkins, J. C., R. A. Birdsey, and Y. Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level inventory data. Ecological Applications 11:1174– 1193.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. Forest Science 49:12–35.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive database of biomass equations for North American tree species. General Technical Report NE-319. USDA Forest Service, Newtown Square, Pennsylvania, USA.
- Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. BioScience 56:598–606.
- Kinloch, B. B. 2003. White pine blister rust in North America: past and prognosis. Phytopathology 93:1044–1047.
- Litvak, M., S. Miller, S. C. Wofsy, and M. Goulden. 2003. Effect of stand age on whole ecosystem CO2 exchange in the Canadian boreal forest. Journal of Geophysical Research 108 [doi: 10.1029/2001JD000854].
- Logan, J., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.
- Masek, J. G., and G. J. Collatz. 2006. Estimating forest carbon fluxes in a disturbed southeastern landscape: Integration of remote sensing, forest inventory, and biogeochemical modeling. Journal of Geophysical Research 111:G01006 [doi: 01010.01029/02005JG000062].
- Mast, J. N., T. T. Veblen, and Y. B. Linhart. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. Journal of Biogeography 25:743–755.
- McGuire, A. D., et al. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO2, climate and land use effects with four process-based ecosystem models. Global Biogeochemical Cycles 15:183–206.
- Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. Conservation Biology 9:902– 914.

- Monson, R. K., A. A. Turnipseed, J. P. Sparks, P. C. Harley, L. E. Scott-Denton, K. Sparks, and T. E. Huxman. 2002. Carbon sequestration in a high-elevation, subalpine forest. Global Change Biology 8:459–478.
- Nemani, R., M. White, P. Thornton, K. Nishida, S. Reddy, J. Jenkins, and S. Running. 2002. Recent trends in hydrologic balance have enhanced the terrestrial carbon sink in the United States. Geophysical Research Letters 29: 10.1029/ 2002GL024867.
- Nepstad, D. C., A. Verissimo, A. Alencar, C. Nobre, E. Lima, P. Lefebvre, P. Schlesinger, C. Potter, P. Moutinho, E. Mendoza, M. Cochrane, and V. Brooks. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398:505–508.
- Pacala, S. W., et al. 2001. Consistent land- and atmospherebased U.S. carbon sink estimates. Science 292:2316–2320.
- Parmenter, A. W., A. Hansen, R. E. Kennedy, W. Cohen, U. Langner, R. Lawrence, B. Maxwell, A. Gallant, and R. Aspinall. 2003. Land use and land cover change in the Greater Yellowstone ecosystem: 1975–1995. Ecological Applications 13:687–703.
- Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel. 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture, and management. Pages 147–167 *in* Quantitative modeling of soil forming processes. Soil Science Society of America, Madison, Wisconsin, USA.
- Pregitzer, K. S., and E. S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10:2052–2077.
- Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. Research Paper INT-115. USDA Forest Service, Ogden, Utah, USA.
- Rueth, H. M., J. S. Baron, and E. J. Allstott. 2003. Responses of Engelmann spruce forests to nitrogen fertilization in the Colorado Rocky Mountains. Ecological Applications 13: 664–673.
- Sacks, W. J., D. S. Schimel, R. K. Monson, and B. H. Braswell. 2006. Model-data synthesis of diurnal and seasonal CO2 fluxes at Niwot Ridge, Colorado. Global Change Biology 12: 240–259.
- Schimel, D., T. G. F. Kittel, S. Running, R. Monson, A. Turnipseed, and D. Anderson. 2002. Carbon sequestration studied in western U.S. mountains. EOS, Transactions, American Geophysical Society 83:445,–449.
- Schimel, D. J., et al. 2000. Contribution of increasing CO2 and climate to carbon storage by ecosystems in the United States. Science 287:2004–2006.
- Schoennagel, T., T. T. Veblen, W. H. Romme, J. S. Sibold, and E. R. Cook. 2005. ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. Ecological Applications 15:2000–2014.
- Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in Ponderosa pine landscapes of the Black Hills. Conservation Biology 11:1276–1288.
- Simonson, S. E., P. A. Opler, T. J. Stohlgren, and G. W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation 10:1369– 1386.
- Smith, W. B. 2002. Forest inventory and analysis: a national inventory and monitoring program. Environmental Pollution 116:S233–S242.
- Smith, W. B., P. D. Miles, J. S. Vissage, and S. A. Pugh. 2004. Forest resources of the United States, 2002. General

Technical Report NC-241. USDA Forest Service North Central Research Station, St. Paul, Minnesota, USA.

- Swetnam, T. W., and J. L. Betancourt. 1990. Fire–Southern Oscillation relations in the southwestern United States. Science 249:1017–1020.
- Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11:3128–3147.
- Taylor, S. W., and A. L. Carroll. 2004. Disturbance, forest age dynamics and mountain pine beetle outbreaks in BC: a historical perspective. Pages 41–51 *in* T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.
- 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.
- USDA Forest Service. 2005. Forest inventory and analysis national core field guide. Volume 1: field data collection procedures for Phase 2 Plots, Version 3.0. U.S. Department of Agriculture, Forest Service, Washington Office. Internal report. On file with: U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis, Arlington, Virginia, USA.
- Van Tuyl, S., B. E. Law, D. P. Turner, and A. I. Gitelman. 2005. Variability in net primary production and carbon storage in biomass across Oregon forests: an assessment integrating data from forest inventories, intensive sites, and remote sensing. Forest Ecology and Management 209:273– 291.
- Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research 8:220–227.
- Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10:1178–1195.
- VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. Global Biogeochemical Cycles 9:407–438.
- Westerling, A. L., T. J. Brown, A. Gershunov, D. R. Cayan, and M. D. Dettinger. 2003. Climate and Wildfire in the Western United States. Bulletin of the American Meteorological Society 84:595–604.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.
- White, L. W., and Y. Q. Luo. 2005. Model-based data assessment for terrestrial carbon processes: implications for sampling strategy in FACE experiments. Applied Mathematics and Computation 167:419–434.
- Williams, M., P. A. Schwarz, B. E. Law, J. Irvine, and M. R. Kurpius. 2005. An improved analysis of forest carbon dynamics using data assimilation. Global Change Biology 11:89–105.
- Zhang, X. Y., and S. Kondragunta. 2006. Estimating forest biomass in the USA using generalized allometric models and MODIS land products. Geophysical Research Letters 33: L09402 [doi: 09410.01029/02006GL025879].
- Zhu, Z., and D. L. Evans. 1994. U.S. forest types and predicted percent forest cover from AVHRR data. Photogrammetric Engineering and Remote Sensing 60:525–531.

APPENDIX

A figure showing sampling errors at the 67% confidence limit reported for timberland area and timberland volume, and a figure showing forest area by county in the western United States (*Ecological Archives* A017-096-A1).