

Chapter 14

Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management

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14.1 Forest Management and Carbon Sequestration

Forests account for a large fraction of the carbon stored in global soils and vegetation (Dixon et al. 1994). Accordingly, considerable effort has been devoted to understanding the impact of land use and forest management on carbon sequestration, and thus on climate change (Harmon et al. 1990; Lugo and Brown 1992; Heath and Birdsey 1993; Dixon et al. 1994; Houghton et al. 1999; Caspersen et al. 2000; Fang et al. 2001; Pacala et al. 2001; Birdsey et al. 2006). The optimal strategy for forest management aimed at carbon sequestration is controversial. On the one hand, logging diminishes the pool of standing carbon and can result in a large net transfer of carbon to the atmosphere (Harmon et al. 1990; Vitousek 1991; Schulze et al. 2000; Harmon 2001; Harmon and Marks 2002). On the other hand, if the harvested wood has a sufficiently long residence time or is used to offset fossil fuel emissions, repeated harvest and regrowth can effectively sequester carbon (Vitousek 1991; Marland and Marland 1992; Marland and Schlamadinger 1997).

For a given parcel of land, the relative merits of plantation forestry vs old-growth protection or restoration depends, in part, on the late-successional carbon storage trajectory. Classical models of ecosystem development propose that live biomass density (biomass per unit area) increases over time to an asymptote (Kira and Shidei 1967; Odum 1969). In contrast, reviews of biomass dynamics in the forest ecology literature tend to emphasize the variety of patterns that can ensue over the course of succession (Peet 1981, 1992; Shugart 1984). In the context of forest management aimed at carbon sequestration, of particular interest is the possibility that live biomass density may decline late in succession in some ecosystems (Loucks 1970; Bormann and Likens 1979). For example, data in Canada's National Forest Biomass Inventory indicate that biomass declines are common in some types of 'overmature' stands, and these declines are accounted for in the Carbon Budget Model of the Canadian Forest Sector (Kurz and Apps 1999).

The expected trajectory of live biomass density over time does not in itself determine the optimal strategy for carbon sequestration. Additional factors that must be considered include (1) the impacts of management on other forest carbon

pools, particularly soils (Johnson and Curtis 2001) and coarse woody detritus (Harmon 2001; Janisch and Harmon 2002); and (2) the amount of carbon stored under different management scenarios in forests, wood products, landfills, and displaced fossil fuel emissions (e.g., due to biofuel production; Marland and Marland 1992; Marland and Schlamadinger 1997; Liski et al. 2001; Harmon and Marks 2002; Kaipainen et al. 2004). Furthermore, carbon sequestration must be balanced with other management objectives, such as maintaining biodiversity and protecting and restoring old-growth forests (Thomas et al. 1988; Messier and Kneeshaw 1999; Schulze et al. 2002). Nevertheless, were substantial declines in live biomass density expected as forests aged, this would clearly be one factor to consider in devising forest management policies.

Little old-growth forest remains on productive land in the United States (US). In western Washington and Oregon, for example, roughly 20% of the original old-growth remained in the 1980s (Greene 1988; Spies and Franklin 1988), and this fraction has undoubtedly decreased. In the eastern US, less than 1% of the presettlement forest is thought to remain (Davis 1996). Considerable controversy has arisen over the fate of the remaining old-growth in the Pacific Northwest (Thomas et al. 1988), while in the eastern US, there are urgent pleas from conservationists to set aside large tracts of second growth as future old-growth reserves (Zahner 1996). From a carbon sequestration perspective, the attractiveness of protecting or expanding old-growth habitat depends, in part, on the expected late-successional biomass trajectory. The primary goal of this chapter is to quantify these trajectories for different US forest types. We assembled biomass chronosequences for US forest types using data from the US Forest Service's Forest Inventory and Analysis (FIA) program. Where possible, we compared late-successional FIA biomass estimates to old-growth biomass estimates in the literature.

14.2 Mechanisms of Biomass Decline

First, we review mechanisms that could result in late-successional declines in forest biomass, focusing on aboveground live tree biomass (AGB, in per area units). Understanding the effects of these mechanisms on total forest carbon storage would need to consider additional pools (e.g., soils, coarse woody detritus), particularly in cases where declines in live biomass are concurrent with the accumulation of undecomposed dead biomass [see Sect. 14.2.3 and cf. Chaps. 5 (Wirth and Lichstein), 8 (Knohl et al.), 11 (Gleixner et al.) and 21 (Wirth), this volume].

14.2.1 *Transition from Even- to Uneven-Aged Stand Structure*

Peet (1981) suggested that, depending on the degree of population synchrony in mortality and the time lag between mortality and regeneration, a range of succes-

sional patterns in AGB could occur, including an increase to an asymptote, an increase to a peak followed by a decline to a lower asymptote, or oscillations. A well-known example of how the timing of growth and mortality could cause a late-successional biomass decline involves the 'stand-breakup' hypothesis of Bormann and Likens (1979). Following major disturbance, such as stand-replacing fire, hurricane, or logging, AGB increases as the initially even-aged cohort of trees matures, but may decline as the canopy breaks up (Bormann and Likens 1979). Canopy breakup (i.e., synchronous mortality of a substantial fraction of canopy trees) may occur if the initial cohort is dominated by individuals with similar natural lifespans. In addition, death of large canopy trees may induce a mortality wave if other trees are damaged directly by the falling dead trees, or indirectly by increased wind exposure or insect/disease pressure (Oliver and Larson 1996). Eventually, the landscape may reach a dynamic equilibrium, termed the 'shifting mosaic,' with patches in various stages of development (Bormann and Likens 1979). In the context of AGB declines, the key point is that an even-aged cohort of large trees, characteristic of mature second-growth and plantation forests, can have higher AGB than an uneven-aged old-growth forest. While this scenario is plausible, the transition from an even- to an uneven-aged forest will not necessarily result in an AGB decline. Depending on the growth and mortality rates of surviving trees (which may be released from competition as the even-aged cohort breaks up), as well as the rate of biomass accumulation by younger cohorts, AGB (averaged across the landscape) may increase, decrease, or remain essentially constant during the transition to an old-growth state. At question here is not the validity of the landscape-scale steady-state concept (the 'shifting mosaic'), but whether or not attainment of this steady state typically involves a decline in AGB. In lieu of sufficient data to test their hypothesis directly, Bormann and Likens (1979) presented simulation results from the JABOWA model (Botkin et al. 1972) as evidence in support of their hypothesized AGB decline.

14.2.2 Large Mortality Events

The demographic transitions discussed by Bormann and Likens (1979) and Peet (1981) are generic; i.e., they do not require particular mortality events to trigger AGB declines, but rather view declines as a likely consequence of normal demographic processes. Large mortality events due to wind, fire, or insect outbreaks may also cause late-successional AGB declines. Depending on the severity of disturbance, these events may be viewed as stand-initiating disturbances that reset succession, or as perturbations to the successional trajectory of AGB. Although these disturbances may occur at any time during succession, to the extent that their severity or likelihood of occurrence increases with stand age, it is appropriate to view them as potential mechanisms of late-successional AGB decline. Susceptibility of forest stands to wind damage increases with stand age in some systems (Sprugel and Bormann 1981; Canham and Loucks 1984; Foster 1988), and numerous studies have reported a positive correlation between tree size and vulnerability

to wind (e.g., Greenberg and McNab 1998; Dunham and Cameron 2000; Peterson 2000; Veblen et al. 2001). Susceptibility of some forests to insect attack is also thought to increase with stand age. For example, mature stands of *Abies balsamea* in eastern Canada tend to suffer higher mortality to spruce budworm (*Choristoneura fumiferana*) than younger stands (Maclean 1980). Taylor and MacLean (2005) attributed late-successional wood-volume declines in *Abies balsamea* stands to the combined effects of spruce budworm and wind.

Although wind and insect outbreaks seem reasonable candidates for causes of late-successional AGB decline, the notion that fire could cause such a decline is in many cases problematic. Firstly, stand age may be relatively unimportant compared to weather in determining fire behavior of closed-canopy boreal forests (Bessie and Johnson 1995; Johnson et al. 1998). Secondly, in forests composed of fire-resistant species, susceptibility to fire decreases with tree size and age, and biomass may continue to accumulate for centuries in the presence of recurring surface fires (Wirth et al. 2002). Finally, in some systems (e.g., *Pinus ponderosa* in the southwestern US), dense, crowded stand conditions that encourage crown fire are often attributed to fire suppression, grazing, or logging, rather than natural stand-development (Cooper 1960; Allen et al. 2002; Brown et al. 2004).

14.2.3 Successional Changes in Growth Conditions

Numerous factors may lead to late-successional declines in annual net primary production (NPP) at the stand level (Gower et al. 1996; Ryan et al. 1997). If we express the annual biomass dynamics of a stand as:

$$\Delta \text{biomass} = \text{NPP} - \text{annual losses}$$

where annual losses include litter fall, root turnover, whole-tree mortality, etc., then it is clear that a NPP decline will not necessarily cause a biomass decline. Rather, a biomass decline occurs only if net primary production becomes smaller than the annual losses. Kutsch et al. (Chap. 7, this volume) review the extensive literature on mechanisms of NPP decline and also discuss the relevance of the phenomenon for natural forests. Here, we highlight two scenarios in which successional changes in conditions for growth or regeneration are likely to cause AGB declines.

In boreal forests, the accumulation on the forest floor of insulating moss, lichens, and dead organic matter over the course of succession leads to the development of cool, wet soil conditions ('paludification') with low mineralization rates (Van Cleve and Viereck 1981; Harper et al. 2005). As nutrients accumulate in dead organic matter, there may be insufficient nutrients available to replace AGB losses. In addition to nutrient limitation, development of thick beds of moss or lichen may directly inhibit seedling establishment, thus preventing tree regeneration (Strang 1973; Van Cleve and Viereck 1981). In the absence of fire, which leads

to increased nutrient availabilities and improved regeneration conditions (Van Cleve and Viereck 1981), the endpoint of succession in some boreal forests is a treeless bog (Strang 1973). Although AGB is likely to decline with paludification, total carbon storage may increase as moss, lichens, and dead organic matter accumulate.

Another scenario in which declining growth conditions could result in AGB declines involves species effects on litter quality and nutrient availability. Pastor et al. (1987) suggested that successional replacement of *Betula papyrifera* by *Picea* spp. in boreal North America could result in decreased nitrogen availability (due to poor quality of *Picea* litter) and reduced AGB. Increased understorey light levels and decomposition rates following breakup of the *Picea* canopy could again favor *Betula* regeneration and lead to cyclic succession (Pastor et al. 1987).

14.2.4 Species Effects on Forest Stature

In some systems, early-successional species are replaced later in succession by species of smaller stature. In the US Pacific Northwest, long-lived, early-successional *Pseudotsuga menziesii* (70–80 m height) is eventually replaced (in the absence of major disturbance) by *Tsuga heterophylla* (50–65 m) in coastal forests and *Abies amabilis* (45–55 m) in subalpine forests (Franklin and Hemstrom 1981). In boreal Quebec, late-successional AGB decline was attributed to replacement of *Populus tremuloides* by more shade-tolerant conifers, which are both shorter and more susceptible to insect attack (Pare and Bergeron 1995). Shugart (1984) gives several additional examples of declining forest stature with succession: replacement of *Pinus taeda* by *Quercus falcata* in Arkansas (southeastern US), and replacement of *Eucalyptus regnans* and *Eucalyptus obliqua* (both with a mean height over 90 m) by *Nothofagus-Atherosperma* forest (less than 40 m height) in Tasmania. Species effects on forest stature and AGB trajectories are explored in detail in Wirth and Lichstein (Chap. 5, this volume).

14.3 Aboveground Biomass Chronosequences for US Forests

Clearly, there are a variety of mechanisms that could cause late-successional declines in AGB. However, we are aware of few well-documented examples of this phenomenon in temperate forests. To assess the relevance of late-successional AGB declines for US forest management, we assembled chronosequences of mean AGB for different forest types across the coterminous US (excluding Alaska and Hawaii) using the US Forest Service's Forest Inventory and Analysis (FIA) database. Our main objective was to determine the relative frequency of expected late-successional AGB declines vs increases among US forest types. We adopted

the ‘space-for-time’ substitution approach (Pickett 1989), i.e., we assembled chronosequences from different-aged stands in different locations. A more direct approach to studying biomass dynamics would be to quantify biomass across time in remeasured plots (e.g., Peet 1981; Debell and Franklin 1987; Taylor and MacLean 2005). However, FIA remeasurement data are not currently available for the entire US. Therefore, we adopted the space-for-time approach, as it enabled us to examine chronosequences for all forested regions of the coterminous US. Because old-growth forests are rare in much of the US, and are therefore unlikely to be well-characterized by the FIA’s systematic sampling scheme (one plot per $\sim 2,400$ ha), we also searched the literature for AGB estimates from US old-growth forests.

14.3.1 Methods

14.3.1.1 FIA Data

In December 2006, we downloaded all available FIA data for the coterminous US from <http://fia.fs.fed.us/>; FIA documentation referred to below is available from this site. Roughly half of the data are plot remeasurements, the remainder being initial plot installations. We included both types of plots in our analysis and treated them equally because (1) remeasurement data exist only for some regions; and (2) even for the existing remeasurement data, assembling time series for individual plots is precluded by the plot-labeling system in the data currently available to the public. Accounting for temporal autocorrelation in AGB within remeasured plots would increase our statistical power to detect AGB declines or increases, but the fact that we could not do so (point 2 above) should not bias our results.

14.3.1.2 FIA Sampling and Plot Designs

Beginning in 1999, FIA sampling (i.e., the spatial arrangement of plots and their remeasurement intervals; Bechtold and Scott 2005; Reams et al. 2005) and plot designs have been standardized across the US (USDA 2006). The FIA divides the US into hexagons of $\sim 2,400$ -ha, with one plot randomly located within each hexagon. Field data are collected on plots located on both public and private lands classified as accessible forest. To be considered ‘forest,’ an area must be at least 10% stocked with trees, at least 0.4 ha in size, and at least 36.6 m wide. Inaccessible land includes hazardous conditions and private property where access is denied.

Each plot includes four 7.3 m radius subplots: a central subplot and three peripheral subplots whose centers are 18.3 m from the plot center at azimuths 0° , 120° , and 240° . The diameter and status (live, dead, or cut) is recorded for all trees (>12.7 cm diameter) within subplots and for all saplings (2.54–12.7 cm diameter)

within 2.07 m radius microplots (one per subplot). In some parts of the western US, subplot radii are extended to 18 m for large trees (diameter > 53.3, 61, or 76.2 cm, depending on region). Diameter is measured at breast height (1.37 m) or, in the case of multi-trunked western woodland species, at the root collar. Prior to 1999, sampling and plot designs varied by FIA unit (group of counties within a state), with most units adopting a plot design with five or ten variable-radius subplots (i.e., wedge-prism samples) for trees and fixed-radius microplots for saplings.

14.3.1.3 Data Stratification

Each tree or sapling is assigned to a ‘condition’ whose attributes include stand age, land ownership, soil class (xeric, mesic, or hydric), etc. (USDA 2006). Prior to 1999, each FIA plot was assigned a single condition. Beginning in 1999, a single plot could include multiple conditions, but multiple-condition plots (~20% of the post-1999 plots; ~10% of all plots) were excluded from our analysis. Thus, hereafter, we refer to condition attributes as plot attributes. We now describe the plot attributes used to stratify the data.

Forest Type

The FIA uses an algorithm to assign each plot to one of around 150 forest types based on current species composition¹. In most cases, forest type reflects species composition of the largest trees on a plot, but may reflect species composition of smaller trees if they are very dense, or if there is low stocking density of large trees. We adopt scientific names for each forest type, rather than the English names used by the FIA. Each of the names we present can unambiguously be matched to a forest type in the FIA documentation (Appendix D in USDA 2006).

We split several widespread FIA forest types dominated by species with morphologically distinct varieties (Flora of North America Editorial Committee 1993+): We split the *Pseudotsuga menziesii* type into coastal (var. *menziesii*) and Rocky Mountain (var. *glauca*) varieties. We split the *Pinus contorta* type into coastal (var. *contorta*), Cascades-Sierra Nevada (var. *murrayana*), and Rocky Mountain (var. *latifolia*) varieties. We split the *Pinus ponderosa* type into Cascades-Sierra Nevada (var. *ponderosa*) and Rocky Mountain (var. *scopulorum*) varieties. Because the FIA does not distinguish among the preceding varieties, we reclassified these forest types by comparing plot latitude–longitude to range maps (Flora of North America Editorial Committee 1993+). We also split the *Populus tremuloides* type into eastern and western types based on plot location.

We present AGB chronosequences (mean AGB of FIA plots vs age class) for each forest type separately. Stratifying the data by forest type has the advantage of

¹http://srsfia2.fs.fed.us/publicweb/statistics_band/stat_documents.htm

minimizing edaphic or other differences across stand ages; i.e., to the extent that species composition reflects the edaphic conditions of a site, we would expect different aged stands of the same forest type to have similar edaphic conditions. Although stratifying by forest type should limit the influence of confounding factors, we note that this strategy is not foolproof. For example, some shade-intolerant species that are replaced during succession by more tolerant species on mesic sites may persist as climax species on drier sites (Horn 1971; Franklin and Hemstrom 1981; Oliver and Larson 1996). To address this concern, we further stratified the data by soil class (see below) within each forest type.

Within each forest type, we pooled FIA data across all US states. Although many forest types are geographically restricted, some occur across large, heterogeneous areas. To determine if aggregation (pooling FIA plots from heterogeneous areas) strongly affected our results, we compared chronosequences derived from pooled data to chronosequences derived from smaller regions (New England, Southeast, upper Midwest, lower Midwest, mid-Atlantic, interior West). These comparisons (not shown) indicated that pooling did not qualitatively change our results.

Stratifying by forest type minimizes successional changes in AGB associated with species turnover (e.g., Sect. 14.2.4). To assess the importance of AGB changes associated with species turnover, we compared chronosequences of typical early-, mid-, and late-successional forest types in several US regions (see Sect. 14.3.2.3, Results, for details).

Soil Class

FIA field crews assign each plot to one of three soil physiographic classes (hereafter, 'soil classes'): xeric (dry), mesic (moderate but adequate moisture), and hydric (excessive moisture). Each of these classes is subdivided into about five subclasses, but this finer classification is available only for post-1999 inventories. Therefore, we used the coarse three-class scheme to stratify data within forest types.

Stand Age

We define stand age as time since the last stand-replacing disturbance (Table 14.1). Because stand age (according to our definition) is not available from the FIA, we used two different proxies for stand age that are available for each FIA plot: mean age of canopy trees (A_{μ}), and mean diameter at breast height (dbh) of the k largest trees (D_k). (Diameters measured at the root collar were converted to dbh; see Sect. 14.3.1.5.) We restrict our analysis to D_1 (the largest dbh in each plot) and D_2 . For each forest-type/soil-class combination with ≥ 250 FIA plots, we assembled three chronosequences, using A_{μ} , D_1 , or D_2 as the time axis defining the age classes. Although A_{μ} and D_k may depend on species composition, as well as stand age, this should not qualitatively affect our results because chronosequences within forest types, by definition, control for species composition.

Table 14.1 Glossary of abbreviations and terms used in text

Term	Definition
AGB	Aboveground live tree biomass density (Mg ha^{-1}), roughly half of which is carbon
FIA	United States Forest Service's Forest Inventory and Analysis program
Forest type	FIA assigns each plot to a forest type based on current species composition
Stand age	Time since last stand-replacing disturbance
A_μ	Mean age of canopy trees in a stand
D_k	Mean dbh of k largest trees in a stand or FIA plot; D_1 = dbh of largest tree

Below, we discuss the limitations associated with using A_μ and D_k as proxies for stand age. First, we describe the procedure for estimating A_μ (this variable is referred to as 'stand age' in the FIA documentation), which the FIA defines as "the average age of the live trees not overtopped in the predominant stand size-class" (USDA 2005). The FIA estimates A_μ by coring two or three dominant or codominant trees at the point of diameter measurement (breast height for most species) (USDA 2005). Depending on species and region, additional years (typically five or ten) are added to the age of the core to account for early growth (USDA 2005). Field crews have substantial latitude in selecting which trees to core, which – particularly when the predominant size-class is uneven-aged – can result in estimates of A_μ that do not accurately reflect a stand's history (R. Birdsey, personal communication). This should introduce noise into our analysis but should not bias our results.

If AGB peaks and then declines with stand age, then the shape of the relationship between AGB and A_μ or D_1 (or, more generally, D_k) depends on the details of how the decline occurs. First, consider the case where A_μ declines late in succession, as implied by the 'stand-breakup' hypothesis (Sect. 14.2.1), but D_1 continues to increase (Fig. 14.1a). This would occur if at least one canopy tree survived the transition from an even- to an uneven-aged stand structure. In this case, AGB would increase monotonically with A_μ , but would peak and decline with D_1 (Fig. 14.1d). Next, consider the case where A_μ increases with stand age, but D_1 peaks and then declines (Fig. 14.1b). This might occur if tree stature decreased with succession (e.g., due to decreased nutrient availability; Sect. 14.2.3). In this case, AGB would increase monotonically with D_1 , but would peak and decline with increasing A_μ (Fig. 14.1e). Finally, consider the case where both A_μ and D_1 peak and then decline with stand age (Fig. 14.1c). This would occur if a synchronized mortality event (e.g., insect outbreak; Sect. 14.2.2) killed all of the large trees in a stand, and would result in an increasing relationship between AGB and both A_μ and D_1 (Fig. 14.1f). Although it would appear, on the surface, that our methods would fail to detect an AGB decline under this scenario, synchronized mortality events often play out over a number of years. For example, although severe spruce budworm attacks may result in whole-canopy mortality, a decade or more may pass before the last individuals succumb (Maclean 1980). Thus, in many stands undergoing a severe mortality event, one or more large trees would still be sampled in inventory plots,

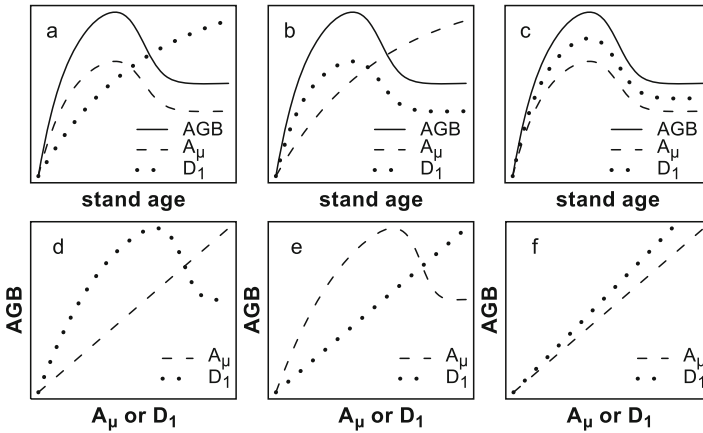


Fig. 14.1 Hypothetical relationships between aboveground live tree biomass (AGB), stand age, mean age of canopy trees in a stand (A_{μ}), and diameter at breast height (dbh) of largest tree (D_1) (Table 14.1) for three cases (a–c) in which AGB peaks and then declines to an asymptote with increasing stand age: **a** at least one canopy tree survives the transition from an even- to an uneven-aged old-growth stand, so that D_1 increases even as A_{μ} declines; **b** forest stature declines in old stands (e.g., due to paludification), but A_{μ} continues to increase; **c** both A_{μ} and D_1 peak and then decline with stand age, as would occur if a synchronous mortality event killed all large trees in a stand. Panels **d–f** show the relationships resulting from (a–c) if AGB is plotted against A_{μ} or D_1 [the stand age proxies available for United States (US) Forest Service’s Forest Inventory and Analysis program (FIA) plots]. See Sect. 14.3.1.3 for details. Note that the variables in the figure have different units, so their relative positions on the y -axis are arbitrary

and D_1 would remain a useful proxy for stand age. In many situations, then, the scenario depicted in Fig. 14.1c would reduce our statistical power to detect mean AGB declines, but would not prevent us from detecting declines if sample sizes were large enough.

In summary, if mean AGB declines with stand age, then mean AGB should also decline with A_{μ} or D_1 in most cases. The primary scenario in which our methods would fail to detect a mean AGB decline is where the decline results from mortality events that kill all large trees in a stand within a short enough time interval so that few stands are undergoing mortality at any given time.

14.3.1.4 Data Filtering

We excluded plots containing multiple FIA conditions (defined above), plots where there was clear evidence of artificial regeneration (e.g., plantations), and plots where any cut trees or saplings were recorded. Cut trees are not recorded on initial plot installations (USDA 2005), and it is likely that data from some of these plots were affected by past selective harvest. For remeasured plots, cut trees are only recorded if harvest occurred between the current and previous plot measurement (USDA 2005); thus, data from remeasured plots may be affected by selective harvest that predated the previous measurement.

14.3.1.5 Biomass Estimation

We estimated total aboveground live biomass (dry weight) for live trees and saplings in the FIA data using diameter-based allometries in Jenkins et al. (2003). To estimate these allometries, Jenkins et al. (2003) compiled biomass allometries from the literature for US tree species, generated pseudo-data from each published equation, and then fit an allometry to pseudo-data pooled within each of ten species groups. Following Jenkins et al. (2003), we used the hardwood biomass allometry of Freedman (1984) for hardwood trees with diameter >70 cm, and – for woodland species whose diameter is measured by the FIA at the root collar – we estimated dbh according to Chojnacky and Rogers (1999). This latter conversion was necessary because the Jenkins et al. (2003) allometries predict biomass from dbh.

AGB of each FIA plot (in Mg ha^{-1}) was estimated as the sum of individual tree and sapling biomasses after appropriate scaling of the individual estimates. This scaling entails dividing each individual estimate by the area on which the tree or sapling is sampled. This area reflects both the FIA plot design (e.g., fixed- vs variable-radius subplots; number of subplots) as well as adjustments for inaccessible land (e.g., if only two of four subplots could be sampled, then the area represented by each tree is doubled). The area sampled by each tree or sapling was calculated from the TPACURR (current trees per acre) field in the FIA SNAPSHOT data (USDA 2006).

14.3.1.6 Old-Growth Literature Data

We searched the published literature for AGB estimates for old-growth forests in the coterminous US. Because old-growth is rare in the eastern US, we also included studies from southeastern Canada. If the same stand was described in more than one study, we cite the one study that provided the most information (species composition, site characteristics, etc.). To be considered old-growth, we did not require that a forest had reached a ‘climax’ state of relatively stable species composition. Rather, we adopted a broad definition of old growth (see also Chap. 2 by Wirth et al., this volume) including both ‘true old-growth’ (in which the initial wave of regeneration following major disturbance has entirely disappeared) and ‘transition old-growth’ (in which relics of the initial regeneration wave still persist) (Oliver and Larson 1996). This broad definition allows for old-growth stands dominated by short-lived, early-successional species (Oliver and Larson 1996).

Many of the studies of old growth in the eastern US are in remnant patches with some history of human disturbance (e.g., selective culling of valuable trees). We included these studies if the stands were described by the original authors as ‘old growth,’ but we note any known disturbances in our results. We also included stands that, based on the authors’ description, we judged to be old-growth, even if the authors did not label them as such. Such cases involved forests recovering from natural disturbance that had attained the typical lifespan of the dominant canopy

species. We excluded AGB estimates from Whittaker (1966) because Busing et al. (1993) concluded that Whittaker (1966) non-randomly selected plots with unusually large trees, and because some of Whittaker's sites were sampled in larger plots by Busing et al. (1993) and Busing (1998). We also excluded the *Pinus ponderosa* study of Hicke et al. (2004) because these authors found that AGB was still rapidly increasing 200 years after fire.

We assigned one or more FIA forest types to each literature study, with multiple types assigned if there was no clear best match. For consistency with the FIA algorithm, we assigned forest types to literature studies based on current species composition. Our assignments differed from those of the original authors if the latter were based on potential climax, rather than current, species composition.

All studies used either locally developed allometries or published allometries to estimate biomass from diameter data. Although these allometries yield different estimates than the Jenkins et al. (2003) allometries that we applied to the FIA data, there should be no systematic bias in comparing our FIA results to the literature data because the Jenkins et al. allometries 'average over' those reported in the literature. Another inconsistency concerning the literature studies involves the minimum size of measured stems. However, since canopy trees comprise the vast majority of AGB, this should have little impact on our results.

14.3.2 Results

14.3.2.1 FIA Chronosequences within Forest Types

Chronosequences of mean AGB vs A_μ for the 79 forest-type/soil-class combinations represented by ≥ 250 FIA plots are shown in Fig. 14.2. The figure and the analyses presented below are restricted to age classes represented by ≥ 10 plots. Standard errors, which indicate our confidence in mean AGB, are small for age classes with many plots, regardless of the variability among plots. We do not present estimates of plot-to-plot variation, because we do not know how much of this variation reflects true heterogeneity among the sampled stands vs sampling errors due to small plot size (i.e., the minimum area sampled for trees is only 0.067 ha per plot under the current FIA plot design).

We tested for late-successional AGB declines/increases as follows: For each of the 79 chronosequences in Fig. 14.2, we performed three two-tailed *t*-tests (one for each time axis: A_μ , D_1 , and D_2 ; see Table 14.1) to determine if mean AGB in the oldest age class was significantly different from the largest mean AGB among all other age classes. Using A_μ as the time axis, there were four late-successional AGB declines and 18 increases out of 79 chronosequences (Table 14.2 and * symbols in Fig. 14.2). Of 79 chronosequences, 6 exhibited a late-successional decline in at least one of the three tests (time axes), whereas 52 chronosequences exhibited an increase in at least one of the three tests (Table 14.2); assuming that in most cases at least one of our time axes is a meaningful proxy for stand age, we can

conclude that late-successional AGB declines are rare among US forest types and that late-successional AGB increases are relatively common across the range of age classes adequately sampled by the FIA. Exactly which chronosequences show significant declines/increases changes somewhat depending on the details of the analysis (e.g., number of age classes; minimum sample size to include an age class), but our main results are robust to such details.

We did not correct for multiple testing (e.g., Bonferroni correction), so the nominal type I error rate (0.05) in the above tests is probably an underestimate. This bias may have resulted in our over-reporting late-successional declines and increases, but should not bias the relative frequency of declines vs increases.

Our estimates of AGB are similar to those from other studies that estimate AGB from FIA data. For example, reported mean AGB estimates from FIA plots in mature eastern US forests range from about 125 to 250 Mg ha⁻¹, depending on forest type and region (Brown et al. 1997; Schroeder et al. 1997; Jenkins et al. 2001). This range includes most of our mean estimates in older age classes in the eastern US (Fig. 14.2).

14.3.2.2 Comparison of Old-Growth Literature and Old FIA Plots

We located old-growth literature AGB estimates for 27/79 cases in Fig. 14.2. Literature values were similar regardless of whether the stands had been subject to selective cutting ('S' symbols in Fig. 14.2) or had no known history of human disturbance ('U' symbols). Therefore, we calculated a single mean literature value

Fig. 14.2a–e AGB chronosequences for soil-class/forest-type combinations with $n \geq 250$ FIA plots. Means and standard errors are shown for age classes with $n \geq 10$ plots. An asterisk above the error bar in the oldest age class indicates that its mean is significantly different from the largest mean of any other age class (Table 14.2). All y-axes have a maximum of 500 Mg ha⁻¹ except for *Pseudotsuga* and *Tsuga heterophylla* types on mesic soils (panels 61–63). Within each region/soil class, forest types are ordered alphabetically within coniferous and broad-leaved (angiosperm) types. The histograms show the age distribution of FIA plots; the bar heights are scaled so that the modal height is equal to the height of the panel frame. The total number of plots is given above each panel. The curves show the mean proportion of AGB in each age class comprised by trees in different dbh classes (see legends at top left): 2.54–50 cm dbh area below solid curve; 50–70 cm dbh area between solid and dashed curves; 70–100 cm dbh area between dashed and dotted curves; >100 cm dbh area above dotted curve. Old-growth AGB estimates from the literature are plotted as S or U at the far right of each panel: S indicates stands that have been selectively logged or otherwise disturbed (see Table 14.3 notes), U indicates stands with no known history of human disturbance, triangles indicate means of literature values. The same literature values are plotted for all soil classes with $n \geq 250$ FIA plots for a given forest type. See footnote v in Table 14.3 for key to literature references. Abbreviations: Ac. rub. *Acer rubrum*; Bet. al. *Betula alleghaniensis*; C-SN Cascades-Sierra Nevada variety; Frax. am./penn. *Fraxinus americana/pennsylvanica*; Jun. *Juniperus*; Liq./Liquidambar *Liquidambar styraciflua*; Lirio./Liriodendron *Liriodendron tulipifera*; Mag. vir. *Magnolia virginiana*; Nys. *Nyssa*; Pin. *Pinus*; Prunus ser. *Prunus serotina*; *Pseudotsuga Pseudotsuga menziesii*; Q. *Quercus*; Ulm. am. *Ulmus americana*

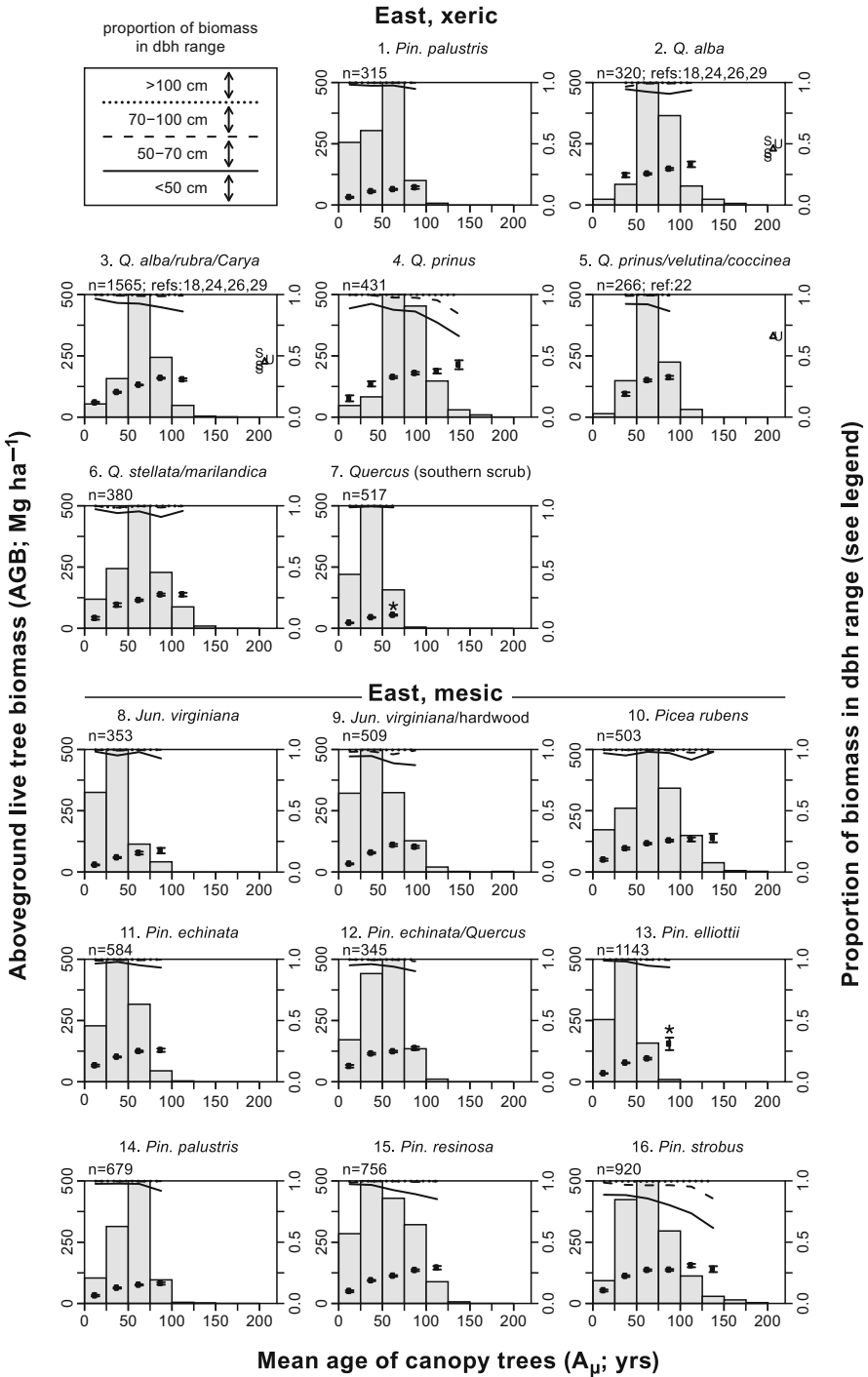


Fig. 14.2a (Continued)

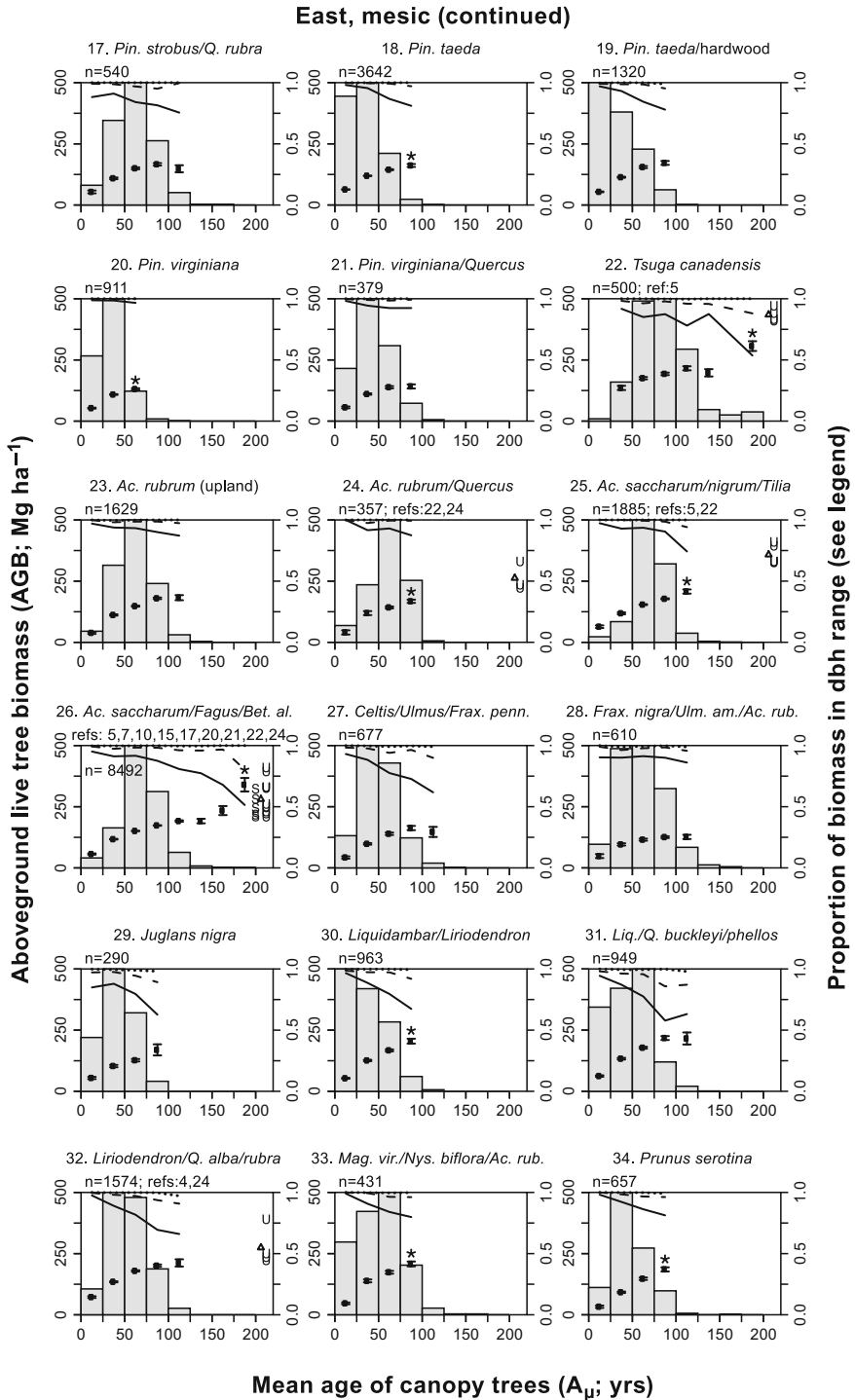


Fig. 14.2b (Continued)

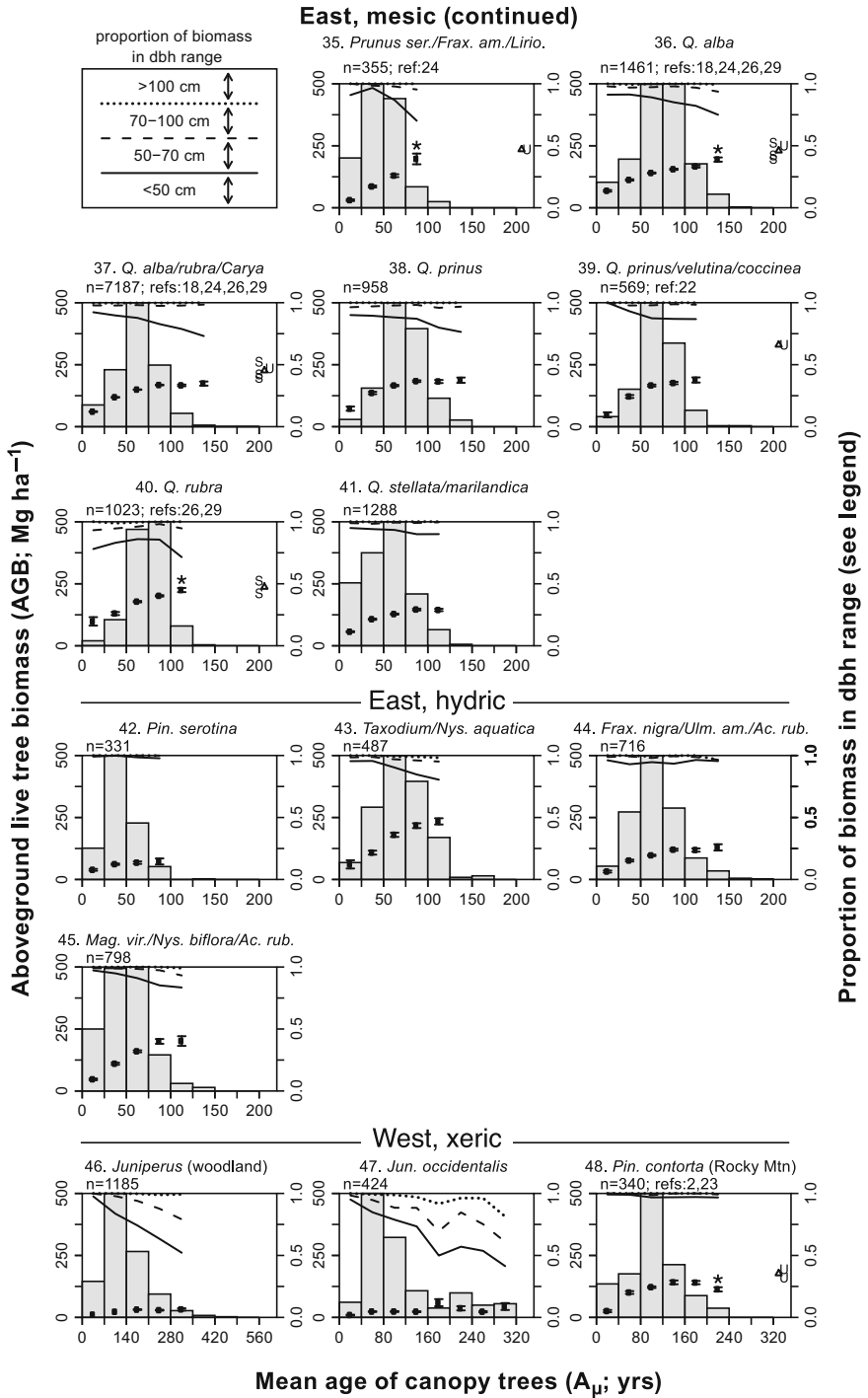


Fig. 14.2c (Continued)

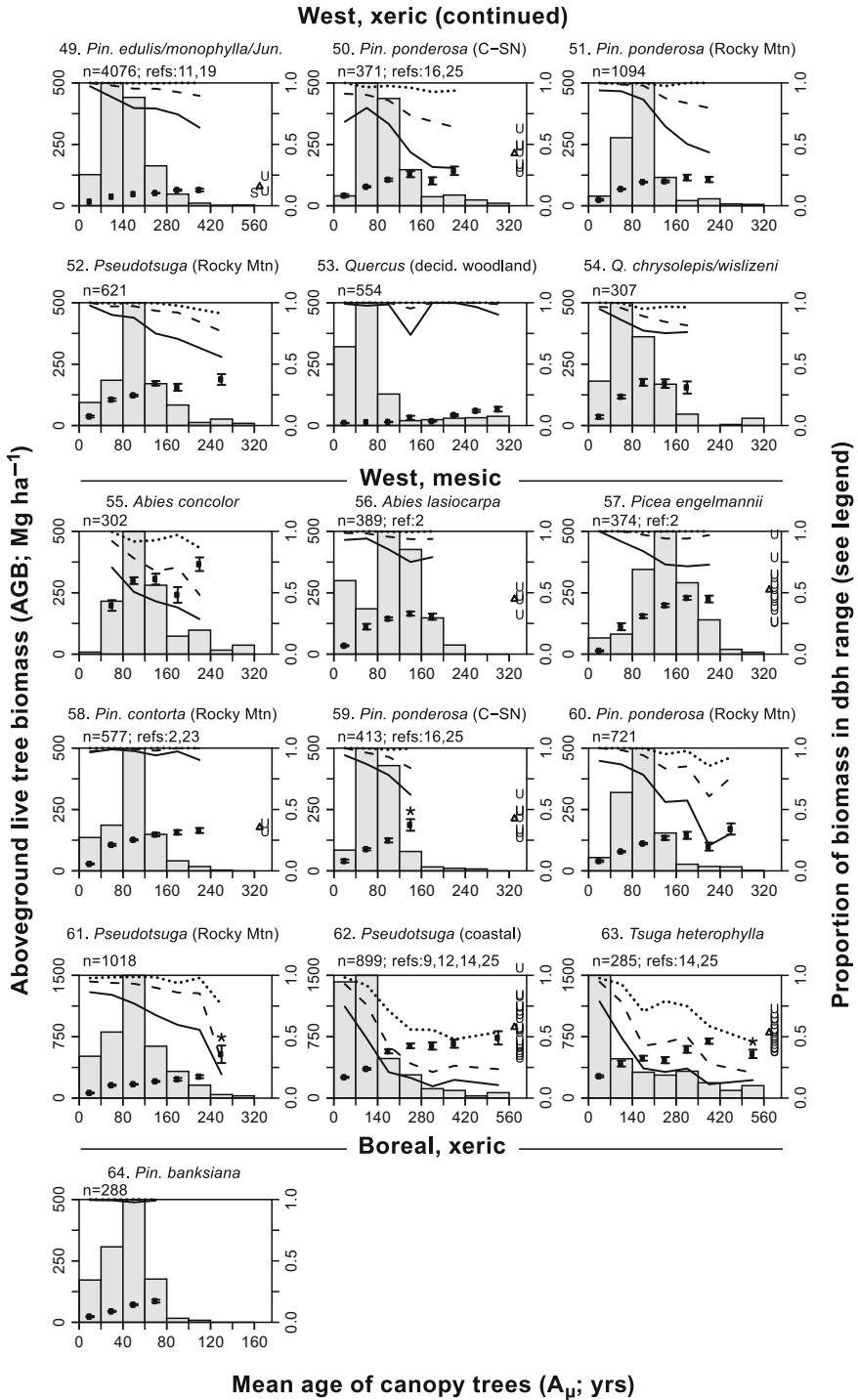


Fig. 14.2d (Continued)

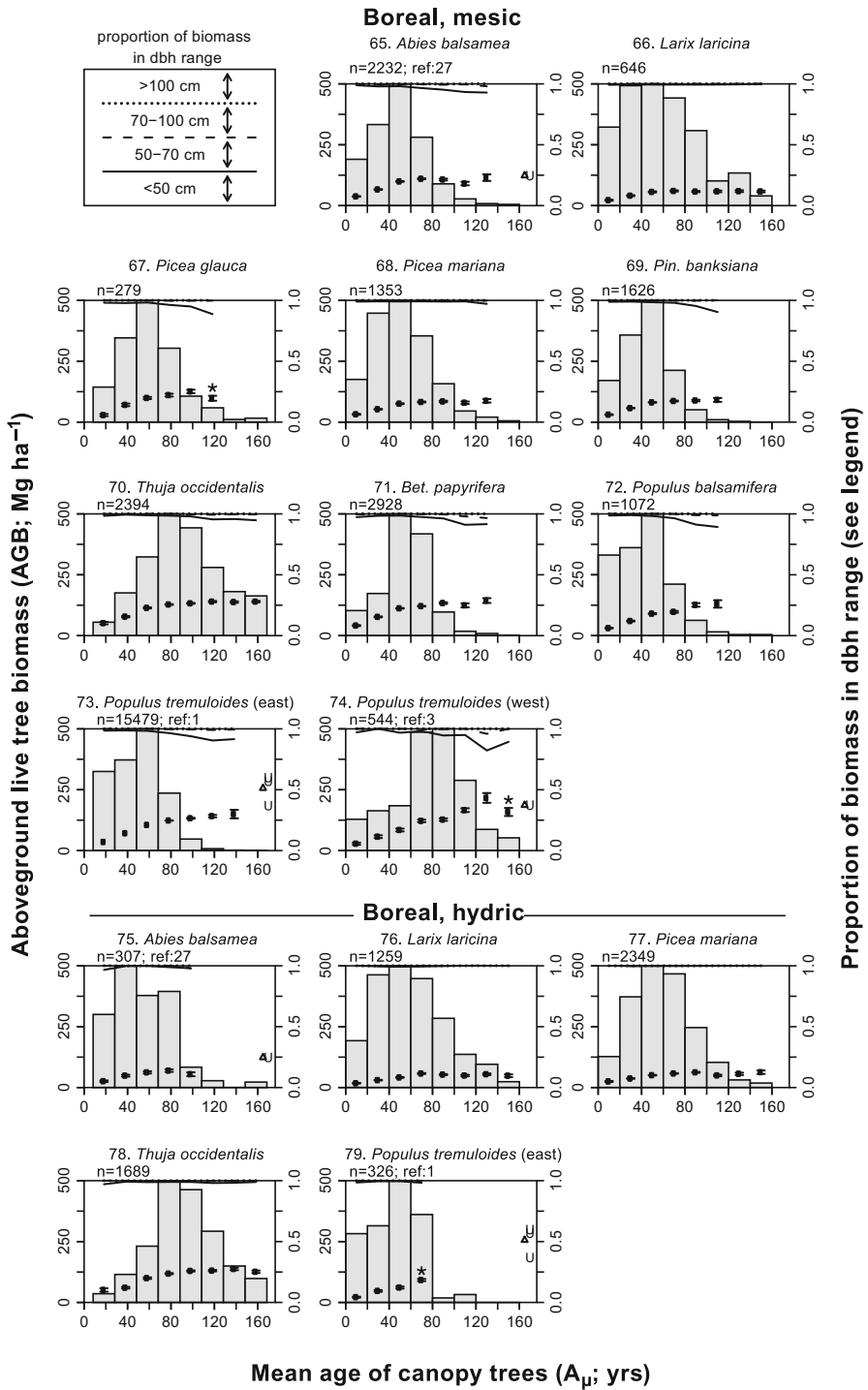


Fig. 14.2e (Continued)

(triangles in Fig. 14.2) for each of the 27 cases for which literature values were available. Mean literature values were higher than mean AGB in the oldest FIA age class in all but one case (Fig. 14.2, panel 26), and higher than the highest mean AGB of any FIA age class in all but two cases (Fig. 14.2, panels 26 and 74).

Some old-growth AGB estimates from the literature were considerably higher than FIA means, most notably the estimates from the eastern cove forests studied by Busing (1998; upper three literature values in Fig. 14.2, panels 22, 25, and 26) and the exceptional value for *Pseudotsuga* forest (1,591 Mg ha⁻¹; Fig. 14.2, panel 62) from Fujimori et al. (1976). The latter value is an estimate of stem biomass only; the AGB estimate for this stand would be even higher. (All other literature AGB values in Fig. 14.2 were calculated in a way comparable to our FIA estimates.)

For most of the eastern forest types, the contribution of large trees to AGB in the FIA data was small (typically < 5% of AGB due to trees with dbh >70 cm), even for the oldest age classes (see curves in Fig. 14.2 for AGB in different dbh classes). In contrast, Brown et al. (1997) found that trees with dbh >70 cm comprised 20–30% of total AGB in old-growth hardwood stands at different sites in the eastern US. Similarly, Mroz et al. (1985) recorded 12 trees ha⁻¹ with dbh >65 cm in two *Acer saccharum* stands in northern Michigan, which would account for roughly 20% AGB in their study. Spetich and Parker (1998) found that trees with dbh >100 cm accounted for 16% of total AGB in an old-growth mixed *Quercus* stand in Indiana. Based on geography, soil, and topography, the above studies are probably representative of old-growth hardwood forests in much of the eastern US. On unusually good sites in the eastern US, large trees may comprise an even greater proportion of AGB. For example, in the southern Appalachian mixed hardwood and *Tsuga canadensis* forests studied by Busing et al. (1993) and Busing (1998), trees with dbh >70 cm and >100 cm comprised about 70% and 25%, respectively, of total AGB. These stands are in moist, topographically sheltered ‘coves,’ and are of unusual stature among surviving eastern old-growth forests. In contrast, eastern old-growth on poor soils or near the northern or elevational limits of the temperate hardwood zone may have much lower AGB contributions of large trees. For example, Martin and Bailey (1999) found very few trees with dbh >50 cm in a transition northern-hardwood/subalpine-conifer old-growth stand in the White Mountains in New Hampshire. Similarly, Morrison (1990) found that trees with dbh > 50 cm comprised just 14.5% and 6.5% of total AGB in two old-growth *Acer saccharum* stands in northern Ontario.

In contrast to eastern forest types, large trees accounted for a substantial proportion of AGB in the FIA data for some western forest types, particularly those found at low to mid elevations on mesic soils. For example, trees with dbh > 100 cm accounted for roughly half of AGB in the oldest FIA age classes for the coastal *Pseudotsuga menziesii* and *Tsuga heterophylla* types (Fig. 14.2, panels 62 and 63). Trees with dbh > 100 cm are characteristic of old-growth *Pseudotsuga* forests in the Pacific Northwest (Franklin et al. 1981) and accounted for roughly 50–70% of total live stem biomass in five old-growth *Pseudotsuga* communities studied by Grier and Logan (1977).

Table 14.2 Number of FIA chronosequences in which the mean AGB of the oldest age class was significantly different than the largest mean AGB of any other age class (two-tailed *t*-test; $\alpha = 0.05$). Three tests were performed for each forest type, using A_{μ} , D_1 , or D_2 (Table 14.1) as the time axis defining the age classes. AGB increases with respect to D_1 and D_2 should be viewed with caution, due to the inherent circularity

	Coniferous forest types						Broad-leaved forest types														
	n total ^a			n declines ^b			n increases ^c			n total			n declines			n increases					
	A_{μ}	D_1	D_2	Any ^d	A_{μ}	D_1	D_2	Any	A_{μ}	D_1	D_2	Any	A_{μ}	D_1	D_2	Any	A_{μ}	D_1	D_2	Any	
East																					
Xeric	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	6
Mesic	15	0	0	0	4	1	3	6	19	0	0	0	0	0	0	0	0	9	9	8	14
Hydric	2	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
West																					
Xeric	7	1	0	0	1	0	6	4	6	2	0	0	0	0	0	0	0	0	1	2	2
Mesic	9	1	1	0	2	8	6	8	0	-	-	-	-	-	-	-	-	-	-	-	-
Hydric	0	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-
Boreal																					
Xeric	1	0	0	0	1	0	1	1	0	-	-	-	-	-	-	-	-	-	-	-	-
Mesic	6	1	0	0	1	0	2	2	4	1	0	0	1	0	0	1	0	4	3	4	4
Hydric	4	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1
Total	45	3	1	1	5	7	19	18	25	34	1	0	0	1	0	0	1	11	17	17	27

^aNumber of forest types that appear in Fig. 14.2, which includes forest-type/soil-class combinations with ≥ 250 FIA plots

^bNumber of forest types in which mean AGB of oldest age class was significantly less than the largest mean of any age class in a given chronosequence

^cNumber of forest types in which mean AGB of oldest age class was significantly greater than the largest mean of any other age class in a given chronosequence

^dNumber of forest types in which a significant difference was observed in at least one of the three tests (A_{μ} , D_1 , or D_2)

Table 14.3 Literature AGB estimates for old-growth forests in the coterminous US and southeastern Canada

Dominant species (in decreasing order of importance)	AGB (Mg ha ⁻¹) ^a	Age ^b	Panel numbers ^c	State/province	Reference key ^v
<i>Populus tremuloides</i>	284	55	73, 79	Minnesota	1 ^d
<i>Populus tremuloides</i>	299	74	73, 79	Minnesota	
<i>Populus tremuloides</i>	184	64	73, 79	Minnesota	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	130	400	57	Colorado	2
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	325	400	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	217	250	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	273	200	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	313	200	57	Colorado	
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	274	350	56	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	228	350	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	237	250	57	Colorado	
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	161	450	56	Colorado	
<i>Pinus contorta</i> , <i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	194	200	48, 57, 58	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	132	300	57	Colorado	
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	237	450	56	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	285	450	57	Colorado	
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	223	400	56	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	394	450	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	488	400	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	264	400	57	Colorado	
<i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	180	400	57	Colorado	
<i>Populus tremuloides</i>	186	123	74	Colorado	3 ^e
<i>Liriodendron tulipifera</i> , <i>Quercus alba</i> , <i>Quercus velutina</i>	390	340	32	New Mexico	4
<i>Liriodendron tulipifera</i> , <i>Quercus alba</i>	430	340	-	Maryland	
<i>Tsuga canadensis</i> , <i>Halesia carolina</i>	416	>400	22	Maryland	5 ^f
<i>Tsuga canadensis</i> , <i>Halesia carolina</i>	441	>400	22	Tennessee	
<i>Tsuga canadensis</i> , <i>Halesia carolina</i>	471	>400	22	Tennessee	

(continued)

Table 14.3 (Continued)

Dominant species (in decreasing order of importance)	AGB (Mg ha ⁻¹) ^a	Age ^b	Panel numbers ^c	State/province	Reference key ^v
<i>Acer saccharum</i>	394	>400	25, 26	Tennessee	
<i>Halesia carolina</i> , <i>Acer saccharum</i>	329	>400	25, 26	Tennessee	
<i>Halesia carolina</i> , <i>Aesculus octandra</i> , <i>Acer saccharum</i>	326	>400	25, 26	Tennessee	
<i>Tsuga canadensis</i> , <i>Acer rubrum</i> , <i>Halesia carolina</i>	410	>400	22, 25, 26	Tennessee	6 ^s
<i>Sequoia sempervirens</i>	3,350–4,642	>1,000	–	California	7
<i>Acer saccharum</i> , <i>Acer saccharinum</i> , <i>Fagus grandifolia</i>	218 ^{m,n}	–	26	Ohio	8 ^h
<i>Pinus albicaulis</i>	390	640	–	Montana	
<i>Pinus albicaulis</i>	240	360	–	Montana	
<i>Pinus albicaulis</i>	225	310	–	Montana	
<i>Pinus albicaulis</i>	206	330	–	Montana	
<i>Pseudotsuga menziesii</i>	1,591	>500	62	Oregon	9 ⁱ
<i>Abies procera</i> , <i>Pseudotsuga menziesii</i>	1,687	310	–	Washington	
<i>Acer saccharum</i> , <i>Betula alleghaniensis</i>	261	–	26	New Hampshire	10
<i>Juniperus monosperma</i> , <i>Pinus edulis</i>	53 ^o	350	49	Arizona	11
<i>Pseudotsuga menziesii</i>	665	450	62	Oregon	12
<i>Pseudotsuga menziesii</i>	976	450	62	Oregon	
<i>Pseudotsuga menziesii</i>	492	450	62	Oregon	
<i>Pseudotsuga menziesii</i>	808	450	62	Oregon	
<i>Pseudotsuga menziesii</i>	555	450	62	Oregon	
<i>Abies amabilis</i>	446	180	–	Washington	13
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	620	500	62, 63	Washington	14
<i>Acer saccharum</i> , <i>Quercus rubra</i> , <i>Fagus grandifolia</i>	230	400	26	Quebec	15
<i>Pinus ponderosa</i>	245	190	50, 59	Oregon	16
<i>Pinus ponderosa</i>	247	251	50, 59	Oregon	
<i>Pinus ponderosa</i> , <i>Calocedrus decurrens</i>	314	316	50, 59	Oregon	
<i>Betula alleghaniensis</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i>	209	–	26	New Hampshire	17
<i>Quercus alba</i> , <i>Acer saccharum</i> , <i>Carya glabra</i>	197 ^{m,p}	–	2, 3, 36, 37	Illinois	18
<i>Pinus monophylla</i> , <i>Juniperus osteosperma</i>	60–121	260–320	49	Nevada	19 ^j

<i>Acer saccharum</i> , <i>Betula alleghaniensis</i>	245 ^q	≥ 120	26	Ontario	20
<i>Acer saccharum</i>	210 ^q	≥ 120	26	Ontario	
<i>Acer saccharum</i>	324 ^r	—	26	Michigan	21
<i>Acer saccharum</i>	282 ^s	—	26	Michigan	
<i>Fagus grandifolia</i> , <i>Quercus prinus</i> , <i>Acer saccharum</i>	330 ^m	—	5, 24, 25, 26, 39	Kentucky	22 ^k
<i>Pinus contorta</i>	160	300	48, 58	Colorado	23
<i>Fagus grandifolia</i> , <i>Quercus alba</i> , <i>Acer saccharum</i>	250 ^m	—	2, 26, 32, 36	Indiana	24
<i>Fagus grandifolia</i> , <i>Acer spp.</i>	247 ^m	—	26	Indiana	
Mixed hardwoods	235 ^m	—	3, 24, 32, 35, 37	Indiana	
<i>Fagus grandifolia</i> , <i>Acer spp.</i> , <i>Liriodendron tulipifera</i>	222 ^m	—	24, 26, 32	Indiana	
<i>Pseudotsuga menziesii</i> , <i>Acer macrophyllum</i>	584	460	62	Oregon	25
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	649	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Thuja plicata</i>	848	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i> .	837	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	635	450	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	1,244	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	1,065	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Pinus lambertiana</i>	862	460	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Pinus lambertiana</i>	524	450	62	Oregon	
<i>Abies procera</i> , <i>Pseudotsuga menziesii</i>	685	450	—	Oregon	
<i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	744	450	63	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	1,261	450	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Thuja plicata</i>	1,124	450	62	Oregon	
<i>Pseudotsuga menziesii</i> , <i>Thuja plicata</i>	1,024	450	62	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	820	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	975	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	1,030	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	1,093	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	900	150	63	Oregon	

(continued)

Table 14.3 (Continued)

Dominant species (in decreasing order of importance)	AGB (Mg ha ⁻¹) ^a	Age ^b	Panel numbers ^c	State/province	Reference key ^v
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	798	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	972	150	63	Oregon	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	844	150	63	Oregon	
<i>Pinus ponderosa</i>	169	300	50, 59	Oregon	
<i>Pinus ponderosa</i> , <i>Pinus contorta</i>	137	400	50, 59	Oregon	
<i>Pinus ponderosa</i> , <i>Pinus contorta</i>	157	400	50, 59	Oregon	
<i>Pinus ponderosa</i> , <i>Pinus contorta</i>	219	500	50, 59	Oregon	
<i>Tsuga heterophylla</i> , <i>Thuja plicata</i>	569	500	50, 59	Oregon	
<i>Abies amabilis</i> , <i>Chamaecyparis nootkatensis</i>	726	300	63	Washington	
<i>Abies amabilis</i> , <i>Thuja plicata</i>	727	700	–	Washington	
<i>Abies amabilis</i> , <i>Tsuga heterophylla</i>	419	750	–	Washington	
<i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	721	750	63	Washington	
<i>Abies amabilis</i> , <i>Tsuga heterophylla</i>	1,024	1,000	–	Washington	
<i>Abies amabilis</i> , <i>Tsuga heterophylla</i>	799	1,000	–	Washington	
<i>Abies amabilis</i> , <i>Tsuga heterophylla</i>	800	1,200	–	Washington	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	1,113	550	62	Washington	
<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	702	470	62	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	610	280	63	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	945	280	63	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	574	280	63	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	843	280	63	Washington	
<i>Tsuga heterophylla</i>	658	230	63	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	694	230	63	Washington	
<i>Tsuga heterophylla</i> , <i>Picea sitchensis</i>	766	230	63	Washington	
<i>Quercus rubra</i> , <i>Quercus alba</i> , <i>Quercus macrocarpa</i>	211 ^t	–	2, 3, 36, 37, 40	Indiana	26
<i>Abies balsamea</i>	123	60	65, 75	New York	27 ^l
<i>Abies amabilis</i>	465	175	–	Washington	28
<i>Acer saccharum</i> , <i>Carya ovata</i> , <i>Quercus velutina</i>	262 ^{m, u}	–	2, 3, 36, 37, 40	Illinois	29

<i>Sequoia sempervirens</i>	732	-	California	30
<i>Sequoia sempervirens</i>	1,799	-	California	
<i>Sequoia sempervirens</i>	2,980	-	California	
<i>Sequoia sempervirens</i>	3,280	-	California	
<i>Sequoia sempervirens</i>	3,300	-	California	

^aNumbers are in biomass units, rather than carbon (C). If aboveground C was reported, we converted C to AGB assuming a biomass:C ratio of 2:1

^bAge is given if reported by authors. Depending on the study, 'age' may refer to mean tree age, maximum tree age, or time since last stand-replacing disturbance

^cPanel number(s) in Fig. 14.2 in which old-growth AGB estimate appears. Based on reported species composition, each old-growth study was assigned to one or more FIA forest types. No panel number is given in cases where no matching FIA chronosequence was available (<250 FIA plots for the forest type in each soil class)

^dStands with age > 50 years and where *Populus tremulooides* comprised > 50% of total AGB are included here; authors state that *P. tremulooides* stands in their study area "attain at least some old-growth characteristics, such as fallen large trees and standing snags, by age 50–80"

^eRegeneration from 1880 stand-replacing fire

^fStand ages reported in Busing et al. (1993)

^gAGB range reflects different allometric assumptions for same stand

^hStands with age > 300 years are included here. Authors report total stand biomass (above- and below-ground) for all stands. We report AGB as 75% of total, based on the reported range across stands (70–80%)

ⁱAGB estimate is for stem biomass only

^jCited in Grier et al. (1992), who report AGB and age range from Meeuwig (1979)

^kThree communities identified in 52-ha tract: *Fagus grandifolia* (lower slope), *Acer saccharum/Tilia heterophylla* (middle slope), and *Quercus prinus/Acer rubrum* (upper slope). Brown et al. (1997) estimated mean AGB for the entire tract from the pooled dbh distribution reported by Muller (1982)

^lWe considered this 'wave-regenerated' stand to be old-growth because its age is close to the natural lifespan of *Abies balsamea* in the study area according to the author

^mBiomass calculated by Brown et al. (1997) by applying standard allometric equations to dbh distribution reported in original paper. All other AGB values were estimated by the original authors using allometric equations

ⁿSelectively logged or otherwise disturbed stands:

^{na}Part of study area (Carmean Woods) selectively logged for large *Quercus* until ~50 years prior to study

^{nb}Cattle and sheep grazing and small amount of fuel-wood removed

^{nc}Study area (21 ha) selectively cut until 1898, and 1.2 ha completely cleared in 1800s. No trees cut between and 1898 and time of survey (1964)

ndA few valuable *Betula alleghaniensis* removed in 1950s

^{ne}Selective logging of *Ulmus americana* and *Tilia americana* in early 1900s

^sSelective logging of *Quercus alba* around 1900

^tGrazed from mid-1800s to 1917. Up to 50 dead or damaged trees removed from 8-ha tract in 1940s–1950s. Theft of 3–4 *Juglans nigra* in 1960s. Surveyed in 1992

^uAbout 100 trees removed from 7-ha tract from 1800s to 1950s. Surveyed in 1967

^v*I* Alban and Perala (1992), 2 Binkley et al. (2003), 3 Binkley et al. (2004), 4 Brown and Parker (1994), 5 Busing (1998), 6 Busing and Fujimori (2005), 7 Cho and Boerner (1991), 8 Forcella and Weaver (1977), 9 Fujimori et al. (1976), 10 Goodale and Aber (2001), 11 Grier et al. (1992), 12 Grier and Logan (1977), 13 Grier et al. (1981), 14 Harmon et al. (2004), 15 Hooper et al. (2001), 16 Law et al. (2003), 17 Martin and Bailey (1999), 18 McClain and Ebinger (1968), 19 Meeuwig (1979), 20 Morrison (1990), 21 Mroz et al. (1985), 22 Muller (1982), 23 Ryan and Waring (1992), 24 Schmelz and Lindsey (1965), 25 Smithwick et al. (2002), 26 Spetich and Parker (1998), 27 Sprugel (1984), 28 Turner and Singer (1976), 29 Weaver and Ashby (1971), 30 Westman and Whittaker (1975)

14.3.2.3 Successional Changes in Biomass Associated with Species Turnover

We assembled FIA AGB chronosequences for early-, mid-, and late-successional forest types on mesic soils within restricted geographic and/or elevation ranges (Fig. 14.3; see figure legend for details of plot filtering). We used A_{μ} as the time axis to define the age classes; but because the emphasis here is on comparing AGB between, rather than within, chronosequences, our results do not depend strongly on how the age classes are defined. Our assignment of forest types to successional stages follows published accounts (Christensen and Peet 1981; Franklin and Hemstrom 1981; Heinzelman 1981; Burns and Honkala 1990; Bergeron and Dansereau 1993; Pacala et al. 1996), but some degree of subjectivity is unavoidable. We included forest types with ≥ 10 plots in at least three different age classes. Some of the included types are represented by fewer than 250 FIA plots and therefore do not appear in Fig. 14.2. If more than four types were available for a given successional class in a region, we present chronosequences only for the four types with the longest available chronosequences; this restriction does not qualitatively affect the results. It is most meaningful to base comparisons among successional stages on the older age classes or on the overall mean across age classes; i.e., it does not make sense to compare AGB in old age classes of early-successional types to young age classes of late-successional types.

Among the seres we examined (Fig. 14.3), the *Pseudotsuga-Tsuga* transition in the Cascade Mountains of the Pacific Northwest provides the strongest evidence for an AGB decline associated with species turnover. In the upper Midwest, the mid-successional temperate forest types of relatively high AGB (*Acer rubrum*, *Quercus rubra*, *Pinus strobus*) are most likely to be replaced by the late-successional temperate types (*Acer saccharum*/*Fagus/Betula* or *Tsuga canadensis*) with similar AGB, rather than the late-successional boreal types (*Picea glauca*, *Abies balsamea*) with relatively low AGB (Burns and Honkala 1990). In all of the comparisons in Fig. 14.3, it is possible to identify transitions that could result in AGB declines; e.g., *Liquidambar/Liriodendron* to *Quercus/Carya* in the Piedmont, *Quercus rubra* to succeeding types in New England, or *Betula/Populus* to *Picea/Abies* in the upper Midwest. However, with the exception of the *Pseudotsuga-Tsuga* transition, these declines are small, and the overall impression is that species turnover is not associated with substantial AGB declines.

Unlike the FIA chronosequences within forest types (Fig. 14.2, Table 14.2), there was no evidence for late-successional AGB increases across forest types; i.e., except for the *Pseudotsuga-Tsuga* transition, mean and maximum AGB appeared relatively constant across successional stages in the seres we examined (Fig. 14.3).

For most forest types, the chronosequences in Fig. 14.3 are similar to those in Fig. 14.2 (which pools data across all geographic locations), although in some cases, small sample sizes in Fig. 14.3 result in chronosequences with few age classes and large standard errors (e.g., Rocky Mountain *Pseudotsuga*). AGB is somewhat

higher for coastal *Pseudotsuga* in Fig. 14.3 compared to Fig. 14.2 (panel 62), perhaps because the former was restricted to elevations 400–1,200 m, whereas the latter included all elevations (up to 1,866 m). For *Abies lasiocarpa*, the sharper decline in AGB in Fig. 14.3 compared to Fig. 14.2 (panel 56) may reflect sampling errors in the smaller dataset used in Fig. 14.3, violation of the space-for-time substitution assumption in Fig. 14.3 (e.g., if older stands tend to be at higher elevation), or a genuine effect that is masked in Fig. 14.2 by pooling over too large a geographic area.

The coastal *Pseudotsuga-Tsuga* AGB decline from ~ 800 to 500 Mg ha^{-1} suggested by the FIA data (Fig. 14.3) is greater than that suggested by the old-growth literature data (Fig. 14.2, panels 62, 63), which have a mean of 878 and 809 Mg ha^{-1} for coastal *Pseudotsuga* and *Tsuga*, respectively. However, all but three of the literature values for *Tsuga* are from coastal *Tsuga/Picea sitchensis* sites (Smithwick et al. 2002). The three old-growth *Tsuga* literature values from the Cascades have a mean AGB of 678 Mg ha^{-1} . This brings the mean decline suggested from the literature ($\sim 200 \text{ Mg ha}^{-1}$) closer in line with that suggested by the FIA data ($\sim 300 \text{ Mg ha}^{-1}$).

14.4 Discussion

14.4.1 Late-Successional AGB Trajectories

Three lines of evidence suggest that, in most US forest types, AGB will stabilize or increase late in succession: (1) in the FIA chronosequences that controlled for successional changes in species composition (Fig. 14.2), late-successional AGB declines were rare, whereas late-successional AGB increases were relatively common (Table 14.2); (2) for a given forest type, old-growth AGB estimates from the literature tend to be higher than AGB in the oldest FIA age classes (Fig. 14.2); and (3) only one of the six regional seres we examined (Fig. 14.3), which account for successional changes in species composition, provides evidence for a substantial late-successional AGB decline. We now examine each of these lines of evidence and discuss the validity of our results.

14.4.1.1 FIA Chronosequences Within Forest Types

FIA data for only six of 79 forest-type/soil-class combinations provided statistical evidence for a late-successional AGB decline (Table 14.2). The true number of declines may be even smaller, because we did not correct for multiple testing (e.g., Bonferroni correction). Mechanisms that could lead to late-successional AGB declines within forest types (i.e., in the absence of major changes in species composition) are reviewed in Sects. 14.2.1–14.2.3. Either these mechanisms are not very important in the US, or our approach masked their effects. We now address three factors that could bias our FIA chronosequence results within forest types:

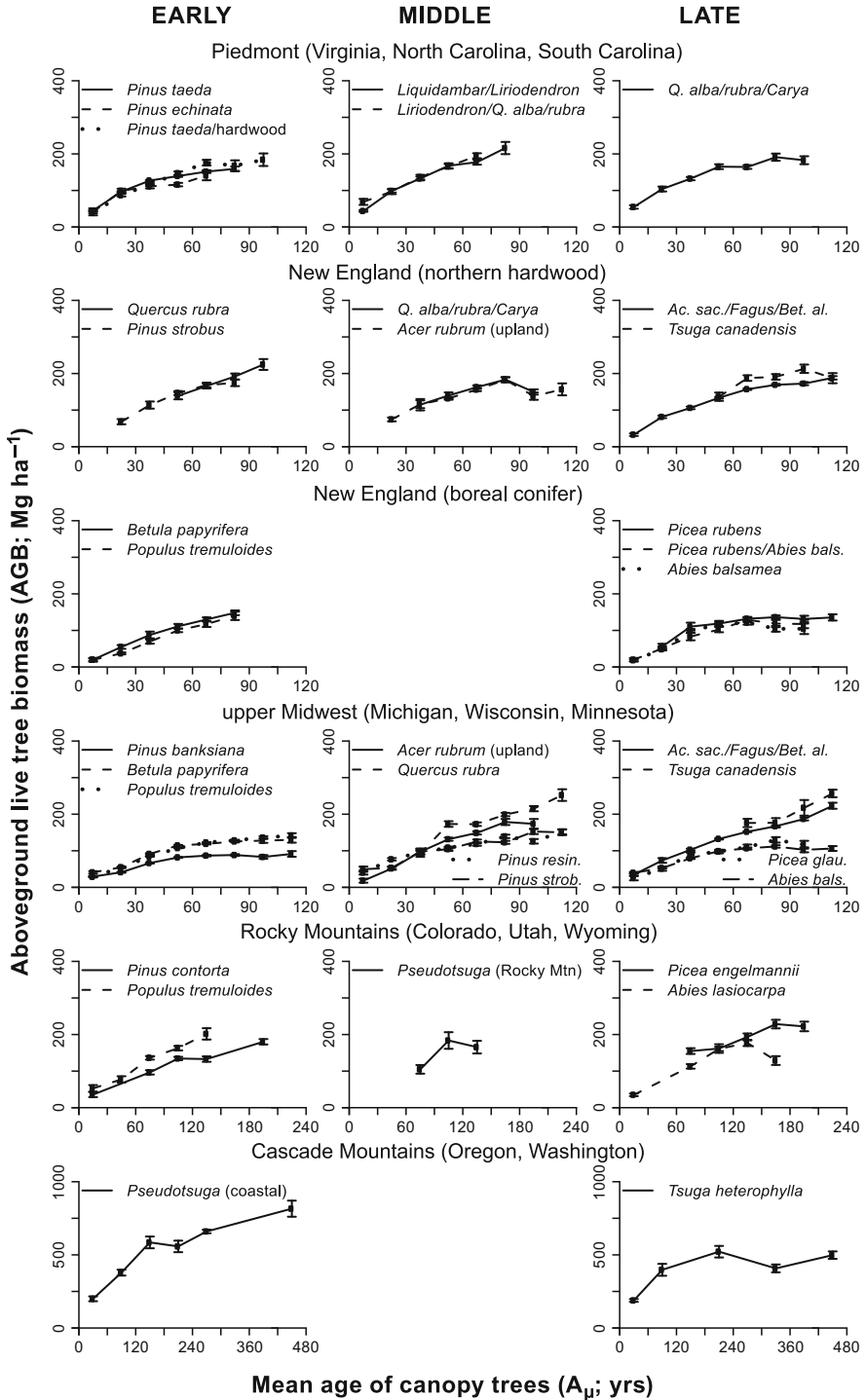


Fig. 14.3

(1) violation of the space-for-time substitution assumption, (2) inadequate proxies for stand age, and (3) limited chronosequence lengths.

Space-for-Time Substitution

The key assumption of the space-for-time substitution approach (Pickett 1989) is that stands that are currently in older age classes are informative about the future condition of stands (in other locations) that are currently in younger age classes. There are many reasons why this assumption might be false. We mention three that seem particularly important. (1) Beginning in the late 1800s, agricultural abandonment followed by forest regrowth would likely have occurred first on the least productive soils (Williams 1989; Birdsey et al. 2006). This would bias the older FIA age classes towards being on poorer sites than the younger age classes, and could potentially bias our results towards detecting ‘false’ late-successional declines. (2) Unlogged forests tend to be on unproductive and/or inaccessible sites (Stahle 1996), which would again bias the older age classes towards being on poor sites. (3) Since the most productive sites, supporting the most massive forests, would have been logged first, they may now host relatively old second-growth, while the poorest sites (logged later) may now host relatively young second-growth. This would bias the older age classes towards being on the richest sites. We do not know the relative importance of these different factors, but taken together, they seem as likely to bias our results in favor of detecting ‘false’ AGB declines as to prevent us from detecting ‘true’ ones.

Stand-Age Proxies

Because stand age (time since the last stand-replacing disturbance) is not available for FIA plots, we used three proxies – A_{μ} , D_1 , and D_2 (Table 14.1) – as the time axes

Fig. 14.3 AGB chronosequences from FIA data for typical early- (*left column*), mid- (*middle column*), and late-successional (*right column*) forest types in several US regions. Only in the Cascade Mountains is there strong evidence for a substantial AGB decline associated with successional changes in species composition. In the upper Midwest, the mid-successional forest types with the highest AGB (*Acer rubrum*, *Quercus rubra*) are likely to be replaced by late-successional types of similar AGB (*Acer saccharum*/*Fagus grandifolia*/*Betula alleghaniensis* or *Tsuga canadensis*), rather than the boreal types of lower AGB (*Picea glauca*, *Abies balsamea*). Means and standard errors are shown at the midpoint of each age class with $n \geq 10$ plots. All data are from plots classified as being on mesic soils. ‘New England’ includes New York, Massachusetts, Connecticut, Rhode Island, Vermont, New Hampshire, and Maine. Data for other regions are restricted to the states indicated in the figure labels. Additional restrictions are as follows: Piedmont plots are east of the Appalachian Mountains; Rocky Mountains plots are at 2,500–3,500 m elevation; Cascade Mountains plots are at 400–1,200 m elevation and 121–123° W longitude. Abbreviations: *Abies bals.* *A. balsamea*; *Abies lasio.* *A. lasiocarpa*; *Ac. sac.* *Acer saccharum*; *Bet. al.* *Betula alleghaniensis*; *Pic. engel.* *Picea engelmannii*; *Picea glau.* *P. glauca*; *Pinus resin.* *P. resinosa*; *Pinus strob.* *P. strobus*

for AGB chronosequences within FIA forest types. A_{μ} is the time axis for the chronosequences presented in Fig. 14.2, whereas all three indexes were used in the analyses presented in Table 14.2. As discussed in Sect. 14.3.1.3 (see Stand Age) in most cases, mean AGB should decline with at least one of these indexes if in fact mean AGB declines with stand age. We acknowledge that there is no real substitute for knowing the true stand ages, but the fact that we detected significant late-successional AGB declines in only six of 79 chronosequences (Table 14.2) suggests that such declines are rare in the US.

Chronosequence Lengths

In some forest types, there may be insufficient FIA data in old age classes to quantify late-successional AGB trajectories. This is likely the case, for example, in some of the *Pinus* types in the eastern US (Fig. 14.2, panels 11–20). The proportion of chronosequences showing late-successional AGB declines was lower in the east than in western or boreal regions, regardless of which stand-age proxy was used to define the age classes (Table 14.2). Nevertheless, AGB declines were neither common nor severe in any region. Comparing the three regions in terms of late-successional AGB increases is less straightforward: using A_{μ} as the stand-age proxy, relatively more increases were observed in the east compared to western or boreal regions (Table 14.2). In contrast, if we take D_1 or D_2 as the stand-age proxy, relatively fewer increases were observed in the east. Because of the circularity in testing for AGB increases using age classes defined by D_1 or D_2 , the results based on A_{μ} are perhaps more credible. In this case, we would conclude that the relatively greater number of AGB increases in the east might be due to limited chronosequence lengths in this region.

“In summary, the conclusion that late-successional AGB declines are rare in US forests appears to be robust, despite limited chronosequence lengths in the eastern US. In contrast, this data limitation may have inflated the observed frequency of late-successional AGB increases in the eastern US.”

14.4.1.2 Comparison of Literature and FIA Data

We were unable to locate old-growth literature AGB estimates for most forest types, so that literature values were available for comparison with only 27/79 FIA chronosequences (Fig. 14.2). The paucity of old-growth literature estimates reflects at least three factors: (1) Most studies of old-growth structure do not report AGB estimates. We hope that our work will encourage more researchers to include AGB estimates in their published work. If local biomass-allometry equations are not available, generalized equations (e.g., Jenkins et al. 2003) can be used. (2) The concept of old-growth is difficult to apply to forest types dominated by short-lived pioneer species (e.g., *Populus* spp. and some *Pinus* spp.) and to ecosystems where

the expected return time of stand-replacing disturbances (e.g., fire) is shorter than the time required for forests to reach quasi-equilibrium (Johnson et al. 1998). (3) Examples of old-growth are rare or nonexistent for some US forest types, particularly in the eastern US. This reflects the young age of most forests in this region (Fig. 14.2, histograms), as well as the elimination of the conditions needed to create or maintain some old-growth communities. For example, old-growth *Pinus palustris* (Platt et al. 1988, Means 1996) and *Pinus taeda/echinata* (Bragg 2002) forests – which are maintained by frequent, low-intensity fires in the southeastern US – have been mostly replaced by more shade-tolerant hardwoods due to disruption of natural fire-regimes (Means 1996; Gilliam and Platt 1999; Bragg 2004).

Old-growth literature AGB estimates were higher, on average, than mean AGB in the oldest FIA age class in 26/27 cases, and higher than the largest mean AGB of any FIA age class in 25/27 cases (see triangles in Fig. 14.2 for mean literature values). Other studies have also found that AGB estimates from FIA plots tend to be lower than those reported in the literature (Brown et al. 1997; Van Tuyl et al. 2005). One possible explanation for higher AGB in the old-growth literature is that these studies may sample older forests than the oldest FIA age classes, and that AGB tends to increase late in succession. This explanation is consistent with the observation that late-successional AGB increases are common relative to declines in FIA chronosequences (Table 14.2). Another explanation for higher AGB in the literature is sampling. Researchers, particularly those interested in old growth, may introduce sampling biases when selecting study sites; e.g., by (perhaps unintentionally) selecting sites with few gaps and unusually large trees (Busing et al. 1993). In contrast, the FIA is a systematic (unbiased) inventory. Thus, aside from any differences in stand age, FIA plots may be on poorer sites and may be more impacted by both natural and anthropogenic disturbances (e.g., selective logging, edge effects) compared to old growth described in the literature. On the other hand, because unlogged forests tend to be on unproductive sites (Stahle 1996), there could be a poor-site bias in the old-growth literature. In light of the unknown impacts of the above sampling effects, the observation that AGB in the old-growth literature tends to be higher than AGB in the oldest FIA age classes cannot be taken as strong evidence for late-successional AGB increases. However, this observation is at least consistent with our conclusions from the FIA chronosequences that late-successional AGB declines are rare in US forests, whereas increases are relatively common.

Associated with the differences in mean AGB between the old-growth literature and the oldest FIA plots are structural differences, with large trees (e.g., dbh >70 cm) comprising a smaller proportion of total AGB in the FIA compared to the literature, particularly in the eastern US (Sect. 14.3.2.2). The extensive literature review of eastern US old-growth by Tyrrell et al. (1998) does not include biomass estimates, but does include data on size (dbh) distributions that could be compared with FIA data. We expect that such a comparison would show that the density of large trees is higher in the old-growth literature compared to the oldest FIA age classes. As with comparisons of mean AGB, it would be difficult to know if

structural differences between the literature and the FIA are due to differences in stand age or other sampling effects.

14.4.1.3 Impact of Successional Changes in Species Composition

Our results are consistent with previous reports that, in some systems, changes in species composition result in late-successional AGB declines (Franklin and Hemstrom 1981; Shugart 1984; Pastor et al. 1987; Pare and Bergeron 1995). However, our results suggest that in the US, such declines typically represent less than 10% of peak AGB (Fig. 14.3). Among the seres we examined, the largest AGB decline associated with species turnover was in the Cascade Mountains in the Pacific Northwest, where FIA data suggest that a transition from old-growth *Pseudotsuga menziesii* to old-growth *Tsuga heterophylla* would result in a mean AGB decline from ~ 800 to 500 Mg ha^{-1} (Fig. 14.3). This decline is most likely due to the stature of the dominant species in these forest types (Franklin and Hemstrom 1981; Chap. 5 by Wirth and Lichstein, this volume). AGB estimates from the Cascade Mountains sites in Smithwick et al. (2002) lead to a qualitatively similar result (decline from 878 to 678 Mg ha^{-1}) for an old-growth *Pseudotsuga-Tsuga* transition. It is important to note that the successional transition resulting in this AGB decline of $200\text{--}300 \text{ Mg ha}^{-1}$ may occur over millennia (Franklin and Hemstrom 1981), a time scale that is not particularly relevant to forest management. In contrast, conversion of an old-growth *Pseudotsuga* landscape to a managed landscape with a 50–100 year rotation length releases $\sim 250\text{--}350 \text{ Mg C ha}^{-1}$ (equivalent to $500\text{--}700 \text{ Mg biomass ha}^{-1}$) into the atmosphere, after accounting for storage in wood products (Harmon et al. 1990; Harmon and Marks 2002). In terms of forest management aimed at C storage in the Pacific Northwest, stand-replacing fires, though infrequent (Franklin and Hemstrom 1981), seem a more relevant concern than the possible loss of biomass over millennial time scales due to species turnover.

Unlike the FIA chronosequences within forest types (Sect. 14.4.1.1), the seres we examined provided no evidence for late-successional AGB increases across forest types (i.e., due to species turnover; Fig. 14.3). Thus, late-successional AGB increases, when they occur, are not expected to depend on late-successional changes in species composition.

14.4.2 Summary and Validity of Results

In summary, our results suggest that substantial late-successional AGB declines are rare in US forests. In contrast, late-successional AGB increases are relatively common, particularly in the eastern US. This may be due to the fact that many ‘old’ eastern forests are still accruing AGB as they transition from mature second-growth to old-growth. The largest decline we identified involves replacement of

Pseudotsuga menziesii in the Pacific Northwest by a late-successional species, *Tsuga heterophylla*, of smaller stature. Our approach may have underestimated the importance of late-successional AGB declines due to major windthrow or insect outbreaks, because the stand-age proxies available to us for FIA plots would not be meaningful if all large trees in a stand died within a short period of time (Sect. 14.3.1.3, Stand Age). Even so, it is unlikely that this situation is common in US forests, and our conclusion that AGB of most US forests will not, under current conditions, decline with age should be robust. Paludification and other mechanisms involving late-successional nutrient depletion (Sect. 14.2.3) appear to be of minor importance in most of the coterminous US; this is not surprising, since these mechanisms have been described primarily in boreal regions (e.g., Van Cleve and Viereck 1981; Harper et al. 2005). The boreal forests at the northern fringes of the coterminous US may not be representative of those at higher latitudes.

14.4.3 Implications

Among the proposed mechanisms for late-successional AGB declines that we reviewed, the most generic is the demographic transition from an even-aged forest of large trees to an uneven-aged forest of different-sized trees (Bormann and Likens 1979). The AGB chronosequences we present for different US forests types, together with the old-growth AGB estimates we compiled from the literature, suggest that this demographic transition does not typically result in AGB declines in US forests. This finding is consistent with the biome-wide biomass chronosequences that Pregitzer and Euskirchen (2004) assembled from literature data, which show a small live biomass decline in the oldest age class for boreal forests, but an increase in temperate and tropical forests. This suggests that late-successional biomass declines tend to occur in particular environments for particular reasons (e.g., insect outbreaks in boreal forests; MacLean 1980; Bergeron et al. 1995), rather than as an inevitable result of successional dynamics (see also Chap. 5 by Wirth and Lichstein, this volume). While not discounting the possibility that the demographic hypothesis of Bormann and Likens (1979) may be correct in some cases, we note that the evidence originally presented in support of this hypothesis was based not on data, but on the JABOWA forest simulator (Botkin et al. 1972). Other forest simulation models, including FORET (Shugart 1984), FORCLIM (Bugmann 1996), and SORTIE (Pacala et al. 1996), also show mid-successional biomass peaks, followed by a decline to an asymptote. Pacala et al. (1996) attributed the biomass peak in SORTIE to an overly simplistic mortality submodel that failed to cause sufficient self-thinning of large saplings.

For all forest types, the age distribution of FIA plots in our sample peaked at either early- or mid-successional age classes (Fig. 14.2, histograms). In some boreal and western ecosystems, where natural return times for stand-replacing disturbances are relatively short, the age distributions in Fig. 14.2 may be similar to those expected in unmanaged landscapes. In contrast, in most of the eastern US

and in productive forests of the Pacific Northwest (e.g., Fig. 14.2, panels 62 and 63), the observed age distributions largely reflect landuse history (e.g., extensive clearing followed by agricultural abandonment in the east) and forest management (Williams 1989; Van Tuyl et al. 2005; Birdsey et al. 2006). The age distributions in Fig. 14.2 are not rigorous descriptions of the age distributions of US forest types because we did not correct for inaccessible land or for regional variation in sampling intensity and coverage prior to implementation of the FIA's national standard protocol in 1999. Nevertheless, the age distributions in Fig. 14.2 should be good approximations of the true distributions for most US forest types.

Because landuse and management have shifted the age distribution of US forests on productive sites towards younger age classes, and because our results do not support the notion of widespread late-successional declines in AGB, a substantial amount of additional carbon could probably be stored in US forests if large tracts of second growth were reserved from future harvest. This conclusion is consistent with previous studies of carbon storage in US forests (Heath and Birdsey 1993; Brown et al. 1997; Jenkins et al. 2001; Smithwick et al. 2002). It is well known that recovery of US forests from past landuse plays an important role in the northern hemisphere terrestrial carbon sink (Birdsey et al. 1993; Heath and Birdsey 1993; Houghton et al. 1999; Caspersen et al. 2000; Pacala et al. 2001; Birdsey et al. 2006). Our results suggest that projections of future carbon storage in US forests (e.g., Birdsey et al. 1993, 2006; Heath and Birdsey 1993) can reasonably assume that, in most cases, AGB will stabilize or increase, rather than peak and decline, as succession proceeds. Clearly, this conclusion applies to biomass accumulation in the absence of major disturbance such as stand-replacing fire.

The expected increase in US forest carbon stores under a reduced harvest regime does not translate directly into a prescription for forest management, which must balance socio-economic, carbon sequestration, and biodiversity objectives at different spatial and temporal scales. Forest management aimed at preservation of biodiversity and old-growth habitat must look beyond local and regional landscapes (Messier and Kneeshaw 1999; Berlik and Kittredge 2002); e.g., reduced harvest of US forests may be harmful for global conservation unless US consumption of wood products is also decreased. While recognizing the need to balance the goals of US forest management with those of global conservation, we note that there is so little old growth remaining on productive lands in the US that preserving these remnants would have little impact on available national harvest. Indeed, there is so little old growth left in the eastern US (< 1%) that increasing its current area by an order of magnitude is not incompatible with maintaining or increasing total harvest from US forests.

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References

- Alban DH, Perala DA (1992) Carbon storage in Lake States aspen ecosystems. *Can J For Res* 22:1107–1110
- Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel JT (2002) Ecological restoration of Southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl* 12:1418–1433
- Bechtold WA, Scott CT (2005) The Forest Inventory and Analysis plot design. In: Bechtold WA, Patterson PL (eds) The enhanced Forest Inventory and Analysis program – National sampling design and estimation procedures. USDA Forest Service Gen Tech Rep SRS-80, Southern Research Station, Asheville, NC, pp 27–42
- Bergeron Y, Dansereau PR (1993) Predicting the composition of Canadian southern boreal forest in different fire cycles. *J Veg Sci* 4:827–832
- Bergeron Y, Leduc A, Morin H, Joyal C (1995) Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Can J For Res* 25:1375–1384
- Berlik MM, Kittredge DB (2002) The illusion of preservation: a global environmental argument for the local production of natural resources. *J Biogeogr* 29:1557–1568
- Bessie WC, Johnson EA (1995) The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76:747–762
- Binkley D, Olsson U, Rochelle R, Stohlgren T, Nikolov N (2003) Structure, production and resource use in some old-growth spruce/fir forests in the front range of the Rocky Mountains, USA. *For Ecol Manag* 172:271–279
- Binkley D, White CS, Gosz JR (2004) Tree biomass and net increment in an old aspen forest in New Mexico. *For Ecol Manag* 203:407–410
- Birdsey RA, Plantinga AJ, Heath LS (1993) Past and prospective carbon storage in United States forests. *For Ecol Manag* 58:33–40
- Birdsey R, Pregitzer K, Lucier A (2006) Forest carbon management in the United States, 1600–2100. *J Environ Qual* 35:1461–1469
- Bormann FH, Likens GE (1979) Catastrophic disturbance and the steady state in northern hardwood forests. *Am Sci* 67:660–669
- Botkin DB, Wallis JR, Janak JF (1972) Some ecological consequences of a computer model of forest growth. *J Ecol* 60:849–872
- Bragg DC (2002) Reference conditions for old-growth pine forests in the Upper West Gulf Coastal Plain. *J Torrey Bot Soc* 129:261–288
- Bragg DC (2004) Composition, structure, and dynamics of a pine-hardwood old-growth remnant in southern Arkansas. *J Torrey Bot Soc* 131:320–336
- Brown MJ, Parker GG (1994) Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can J For Res* 24:1694–1703
- Brown RT, Agee JK, Franklin JF (2004) Forest restoration and fire: principles in the context of place. *Conserv Biol* 18:903–912
- Brown S, Schroeder P, Birdsey R (1997) Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *For Ecol Manag* 96:37–47
- Bugmann HKM (1996) A simplified forest model to study species composition along climate gradients. *Ecology* 77:2055–2074
- Burns RM, Honkala BH (1990) *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC
- Busing RT (1998) Composition, structure and diversity of cove forest stands in the Great Smoky Mountains: a patch dynamics perspective. *J Veg Sci* 9:881–890
- Busing RT, Fujimori T (2005) Biomass, production and woody detritus in an old coast redwood (*Sequoia sempervirens*) forest. *Plant Ecol* 177:177–188

- Busing RT, Clebsch EEC, White PS (1993) Biomass and production of southern Appalachian cove forests reexamined. *Can J For Res* 23:760–765
- Canham CD, Loucks OL (1984) Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65:803–809
- Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290:1148–1151
- Cho DS, Boerner REJ (1991) Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. *Vegetatio* 93:9–18
- Chojnacky DC, Rogers P (1999) Converting tree diameter measured at root collar to diameter at breast height. *West J Appl For* 14:14–16
- Christensen NL, Peet RK (1981) Secondary forest succession on the North Carolina Piedmont. In: West DC, Shugart HH, Botkin DB (eds) *Forest succession: concepts and application*. Springer, New York, pp 230–245
- Cooper CF (1960) Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol Monogr* 30:130–164
- Davis MB (1996) Extent and location. In: Davis MB (ed) *Eastern old-growth forests*. Island, Washington DC, pp 18–32
- Debell DS, Franklin JF (1987) Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. *West J Appl For* 2:111–114
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- Dunham RA, Cameron AD (2000) Crown, stem and wood properties of wind-damaged and undamaged Sitka spruce. *For Ecol Manag* 135:73–81
- Fang JY, Chen AP, Peng CH, Zhao SQ, Ci L (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292:2320–2322
- Flora of North America Editorial Committee (1993+) *Flora of North America North of Mexico*. 12+ vols. Oxford University Press, New York
- Forcella F, Weaver T (1977) Biomass and productivity of subalpine *Pinus albicaulis* – *Vaccinium scoparium* association in Montana, USA. *Vegetatio* 35:95–105
- Foster DR (1988) Species and stand response to catastrophic wind in central New England, USA. *J Ecol* 76:135–151
- Franklin JF, Hemstrom MA (1981) Aspects of succession in the coniferous forests of the Pacific Northwest. In: West DC, Shugart HH, Botkin DB (eds) *Forest succession: concepts and application*. Springer, New York, pp 212–229
- Franklin JF, Cromack J, Denison KW, McKee A, Maser C, Sedell J, Swanson F, Juday G (1981) Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service Gen. Tech. Rep. PNW-118. Pacific Northwest Forest and Range Experimental Station, Portland, OR
- Freedman B (1984) The relationship between the aboveground dry weight and diameter for a wide size range of erect land plants. *Can J Bot* 62:2370–2374
- Fujimori T, Kawanabe S, Saito H, Grier CC, Shidei T (1976) Biomass and primary production in forests of three major vegetation zones of the northwestern United States. *J Jpn For Soc* 58:360–373
- Gilliam FS, Platt WJ (1999) Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. *Plant Ecol* 140:15–26
- Goodale CL, Aber JD (2001) The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol Appl* 11:253–267
- Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. *Trends Ecol Evol* 11:378–382
- Greenberg CH, McNab WH (1998) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *For Ecol Manag* 104:179–191
- Greene S (1988) Research Natural Areas and protecting old-growth forests on federal lands in Western Oregon and Washington. *Nat Areas J* 8:25–30

- Grier CC, Logan RS (1977) Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol Monogr* 47:373–400
- Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above-ground and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can J For Res* 11:155–167
- Grier CC, Elliott KJ, McCullough DG (1992) Biomass distribution and productivity of *Pinus edulis*–*Juniperus monosperma* woodlands of north-central Arizona. *For Ecol Manag* 50:331–350
- Harmon ME (2001) Carbon sequestration in forests – addressing the scale question. *J For* 99:24–29
- Harmon ME, Marks B (2002) Effects of silvicultural practices on carbon stores in Douglas-fir-western hemlock forests in the Pacific Northwest, USA: results from a simulation model. *Can J For Res* 32:863–877
- Harmon ME, Ferrell WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702
- Harmon ME, Bible K, Ryan MG, Shaw DC, Chen H, Klopatek J, Li X (2004) Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga-Tsuga* forest ecosystem. *Ecosystems* 7:498–512
- Harper KA, Bergeron Y, Drapeau P, Gauthier S, De Grandpre L (2005) Structural development following fire in black spruce boreal forest. *For Ecol Manag* 206:293–306
- Heath LS, Birdsey RA (1993) Carbon trends of productive temperate forests of the coterminous United States. *Water Air Soil Pollut* 70:279–293
- Heinselman M (1981) Fire and succession in the conifer forests of northern North America. In: West DC, Shugart HH, Botkin DB (eds) *Forest succession: concepts and application*. Springer, New York, pp 374–405
- Hicke JA, Sherriff RL, Veblen TT, Asner GP (2004) Carbon accumulation in Colorado *ponderosa pine* stands. *Can J For Res* 34:1283–1295
- Hooper MC, Arai K, Lechowicz MJ (2001) Impact of a major ice storm on an old-growth hardwood forest. *Can J Bot* 79:70–75
- Horn HS (1971) *The adaptive geometry of trees*. Princeton University Press, Princeton, NJ
- Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land-use change. *Science* 285:574–578
- Janisch JE, Harmon ME (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiol* 22:77–89
- Jenkins JC, Birdsey RA, Pan Y (2001) Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecol Appl* 11:1174–1193
- Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. *For Sci* 49:12–35
- Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *For Ecol Manag* 140:227–238
- Johnson EA, Miyanishi K, Weir JMH (1998) Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. *J Veg Sci* 9:603–610
- Kaipainen T, Liski J, Pussinen A, Karjalainen T (2004) Managing carbon sinks by changing rotation length in European forests. *Environ Sci Policy* 7:205–219
- Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jpn J Ecol* 17:70–87
- Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol Appl* 9:526–547
- Law BE, Sun OJ, Campbell J, Van Tuyl S, Thornton PE (2003) Changes in carbon storage and fluxes in a chronosequence of *ponderosa pine*. *Glob Change Biol* 9:510–524
- Liski J, Pussinen A, Pingoud K, Mäkipää R, Karjalainen T (2001) Which rotation length is favourable to carbon sequestration? *Can J For Res* 31:2004–2013
- Loucks OL (1970) Evolution of diversity, efficiency, and community stability. *Am Zool* 10:17–25

- Lugo AE, Brown S (1992) Tropical forests as sinks of atmospheric carbon. For Ecol Manag 54:239–255
- MacLean DA (1980) Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For Chron 56:213–221
- Marland G, Marland S (1992) Should we store carbon in trees? Water Air Soil Pollut 64:181–195
- Marland G, Schlamadinger B (1997) Forests for carbon sequestration or fossil fuel substitution? A sensitivity analysis. Biomass Bioenerg 13:389–397
- Martin CW, Bailey AS (1999) Twenty years of change in a northern hardwood forest. For Ecol Manag 123:253–260
- McClain WE, Ebinger JE (1968) Woody vegetation of Baber Woods, Edgar County, Illinois. Am Midl Nat 79:419–428
- Means DB (1996) Longleaf pine forest, going, going, . . . In: Davis MB (ed) Eastern old-growth forests. Island, Washington, DC, pp 210–229
- Meeuwig RO (1979) Growth characteristics of pinyon-juniper stands in the western Great Basin. USDA Forest Service, Research Paper INT-238., Intermountain Forest and Range Experiment Station, Ogden, UT
- Messier C, Kneeshaw DD (1999) Thinking and acting differently for sustainable management of the boreal forest. For Chron 75:929–938
- Morrison I (1990) Organic matter and mineral distribution in an old-growth *Acer saccharum* forest near the northern limit of its range. Can J For Res 20:1332–1342
- Mroz GD, Gale MR, Jurgensen MF, Frederick DJ, Clark A (1985) Composition, structure, and above-ground biomass of two old-growth northern hardwood stands in Upper Michigan. Can J For Res 15:78–82
- Muller RN (1982) Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. Ecology 63:1901–1917
- Odum EP (1969) The strategy of ecosystem development. Science 164:262–270
- Oliver CD, Larson BC (1996) Forest stand dynamics. Update edition. Wiley, New York
- Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66:1–43
- Pacala SW, Hurr GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, Moorcroft P, Caspersen JP, Shevliakova E, Moore B, Kohlmaier G, Holland E, Gloor M, Harmon ME, Fan SM, Sarmiento JL, Goodale CL, Schimel D, Field CB (2001) Consistent land- and atmosphere-based US carbon sink estimates. Science 292:2316–2320
- Pare D, Bergeron Y (1995) Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J Ecol 83:1001–1007
- Pastor J, Gardner RH, Dale VH, Post WM (1987) Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. Can J For Res 17:1394–1400
- Peet RK (1981) Changes in biomass and production during secondary forest succession. In: West DC, Shugart HH, Botkin DB (eds) Forest succession: concepts and application. Springer, New York, pp 324–338
- Peet RK (1992) Community structure and ecosystem function. In: Glenn-Lewin DC, Peet RK, Veblen TT (eds) Plant succession: theory and prediction. Chapman and Hall, London
- Peterson CJ (2000) Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. For Ecol Manag 135:237–252
- Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed) Long-term studies in ecology: approaches and alternatives. Springer, New York, pp 110–135
- Platt WJ, Evans GW, Rathbun SL (1988) The population dynamics of a long-lived conifer (*Pinus palustris*). Am Nat 131:491–525

- Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob Change Biol* 10:2052–2077
- Reams GA, Smith WD, Hansen MH, Bechtold WA, Roesch FA, Moisen GG (2005) The Forest Inventory and Analysis sampling frame. In: Bechtold WA and Patterson PL (eds) The enhanced Forest Inventory and Analysis program – National sampling design and estimation procedures. USDA Forest Service Gen. Tech. Rep. SRS-80. Southern Research Station, Asheville, NC, pp 11–26
- Ryan MG, Waring RH (1992) Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology* 73:2100–2108
- Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. *Adv Ecol Res* 27:213–262
- Schmelz DV, Lindsey AA (1965) Size-class structure of old-growth forests in Indiana. *For Sci* 11:258–264
- Schroeder P, Brown S, Mo JM, Birdsey R, Cieszewski C (1997) Biomass estimation for temperate broadleaf forests of the United States using inventory data. *For Sci* 42:424–434
- Schulze ED, Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science* 289:2058–2059
- Schulze ED, Valentini R, Sanz MJ (2002) The long way from Kyoto to Marrakesh: implications of the Kyoto Protocol negotiations for global ecology. *Glob Change Biol* 8:505–518
- Shugart HH (1984) A theory of forest dynamics: the ecological implications of forest succession models. Springer, New York
- Smithwick EAH, Harmon ME, Remillard SM, Acker SA, Franklin JF (2002) Potential upper bounds of carbon stores in forests of the Pacific Northwest. *Ecol Appl* 12:1303–1317
- Spetich MA, Parker GR (1998) Distribution of biomass in an Indiana old-growth forest from 1926 to 1992. *Am Midl Nat* 139:90–107
- Spies TA, Franklin JF (1988) Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Nat Areas J* 8:190–201
- Sprugel DG (1984) Density, biomass, productivity, and nutrient-cycling changes during stand development in wave-regenerated balsam fir forests. *Ecol Monogr* 54:165–186
- Sprugel DG, Bormann FH (1981) Natural disturbance and the steady state in high-altitude balsam fir forests. *Science* 211:390–393
- Stahle DW (1996) Tree rings and ancient forest history. In: Davis MB (ed) Eastern old-growth forests. Island, Washington, DC, pp 321–343
- Strang RM (1973) Succession in unburned subarctic woodlands. *Can J For Res* 3:140–143
- Taylor SL, MacLean DA (2005) Rate and causes of decline of mature and overmature balsam fir and spruce stands in New Brunswick, Canada. *Can J For Res* 35:2479–2490
- Thomas JW, Ruggiero LF, Mannan RW, Schoen JW, Lancia RA (1988) Management and conservation of old-growth forests in the United States. *Wildl Soc Bull* 16:252–262
- Turner J, Singer MJ (1976) Nutrient distribution and cycling in a sub-alpine coniferous forest ecosystem. *J Appl Ecol* 13:295–301
- Tyrrell LE, Nowacki GJ, Crow TR, Buckley DS, Nauertz EA, Niese JN, Rollinger JL, Crow TS, Zasada JC (1998) Information about old growth for selected forest type groups in the eastern United States. USDA Forest Service Gen. Tech. Rep. NC-197. North Central Forest Experiment Station, St. Paul, MN
- USDA (2005) Forest Inventory and Analysis national core field guide. Vol 1: Field data collection procedures for phase 2 plots, version 3.0, Forest Inventory and Analysis Program, US Department of Agriculture, Forest Service
- USDA (2006) Users guide to the Forest Inventory Snapshot Database Version 2.1, Forest Inventory and Analysis Program, US Department of Agriculture, Forest Service
- Van Cleve K, Viereck LA (1981) Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West DC, Shugart HH, Botkin DB (eds) Forest succession: concepts and application. Springer, New York, pp 185–211
- Van Tuyl S, Law BE, Turner DP, Gitelman AI (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. *For Ecol Manag* 209:273–291

- Veblen TT, Kulakowski D, Eisenhart KS, Baker WL (2001) Subalpine forest damage from a severe windstorm in northern Colorado. *Can J For Res* 31:2089–2097
- Vitousek PM (1991) Can planted forests counteract increasing atmospheric carbon dioxide? *J Environ Qual* 20:348–354
- Weaver GT, Ashby WC (1971) Composition and structure of an old-growth forest remnant in unglaciated southwestern Illinois. *Am Midl Nat* 86:46–56
- Westman WE, Whittaker RH (1975) The pygmy forest region of northern California: studies on biomass and primary productivity. *J Ecol* 63:493–520
- Whittaker RH (1966) Forest dimensions and production in the Great Smoky Mountains. *Ecology* 47:103–121
- Williams M (1989) *Americans and their forests: a historical geography*. Cambridge University Press, New York
- Wirth C, Czimczik CI, Schulze E-D (2002) Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. *Tellus* 54B:611–630
- Zahner R (1996) How much old growth is enough? In: Davis MB (ed) *Eastern old-growth forests*. Island, Washington, DC, pp 344–358