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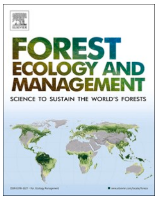

Evaluating the reliability of tree-ring-based estimates of aboveground biomass and biomass increment in managed forests

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A B S T R A C T

Forest biomass, as the major terrestrial reservoir of stored carbon, plays a key role in the global carbon cycle. Permanent plots are commonly used to estimate carbon stocks and net primary productivity (NPP). Because permanent plots are labor intensive, require prolonged field observations, and provide low temporal resolution, alternative methods have been developed. Dendroecological methods are commonly used to estimate forest growth, but most studies are often limited to the individual tree level rather than integrating growth estimates at the plot or stand level, which limits their use to understand forest-level biomass growth and productivity. Here, we evaluated the accuracy in estimating stand aboveground biomass (AGB) and annual AGB increments (AGBi) with two different approaches (dendroecological plots and repeated plot inventories) on a network of 40 permanent plots from managed forests representing four pine species across a wide environmental gradient in the Iberian Peninsula. Dendroecological AGB showed higher agreement with permanent plots than AGBi. For periods longer than 30 years, AGB and AGBi estimates significantly differed between methodologies. Low-productivity stands composed of drought-tolerant species showed better agreement than more productive and faster-growing forests. Recent disturbances or silvicultural treatments within the 20–30 years prior to sampling increased the deviations of dendroecological estimations compared to permanent plots. Carefully selecting sites with little past disturbance or management interventions increases the temporal range for which dendroecological estimates of forest biomass stocks and biomass growth are reliable. Our results show how dendroecological plots can complement the spatial distribution of permanent plots and provide high temporal resolution to assess the effects of climate variability on biomass dynamics in managed forests.

1. Introduction

Forest biomass plays a central role in the global carbon cycle as the major terrestrial reservoir of stored carbon (Houghton et al., 2009). Almost 80% of terrestrial carbon is stored in forest biomass, either aboveground or belowground (Dixon et al., 1994). The carbon contained in standing forest biomass constitutes long-term stocks that may be mobilized through natural or anthropogenic processes (Houghton, 2005). Biomass results from the accumulation of net primary production (NPP), which represents the balance between carbon uptake through photosynthesis and its release via autotrophic respiration. Forest NPP can be approximated by estimating aboveground biomass (AGB) increments and losses from successive estimations of stand-level biomass in permanent plots (Clark et al., 2001; Curtis and Marshall, 2005; Ohtsuka et al., 2009). Forest growth, as well as mortality, ingrowth and regeneration, can be accurately tracked and measured through multiple repeated full stand inventories in permanent plots. Allometric equations are then used to estimates biomass from in situ forest measurements (Clark et al., 2001; Houghton et al., 2009). Permanent plot analysis is the common reference standard for forest biomass, growth and aboveground net primary productivity (ANPP) estimations, despite its potential biases and uncertainties (Clark et al., 2001; Ohtsuka et al., 2009; Qin et al., 2021). Remeasurement intervals of 5–10 years reduce the temporal precision of permanent plot data, hindering the analysis of biomass dynamics and processes at interannual scales. This low temporal precision precludes the assessment of sensitivity of forest biomass to interannual climatic variability, which may be of particular interest in the current climate change context. Long measurement intervals may also increase errors in the estimation of AGB increments (AGBi), for example by not accounting for the growth of trees that died between remeasurements (Clark et al., 2001). Permanent plots also require long periods of time to obtain the data at decadal time scales relevant to

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analyze changes in ecological communities of long-lived individuals like trees and their biomass dynamics.

To overcome these limitations, other methods have been developed to estimate similar variables in a retrospective manner such as those based on tree rings (Babst et al., 2014a; Davis et al., 2009; Graumlich et al., 1989; Nehrbass-Ahles et al., 2014; Xu et al., 2019), satellite observations (Boisvenue and Running, 2006; Running et al., 2004) or eddy flux towers (Ouimette et al., 2018; Rocha et al., 2006). Despite the high temporal precision and detailed information on C-cycle processes of eddy flux towers and the large spatial scales of remote sensing observations, both are limited by their short temporal availability (<40 years). This limits the temporal scale and time periods of changes and processes that can be analyzed, particularly when compared with long-lived forest trees. Because they may only provide stand level estimates, but not tree level, they are also limited in their ability to assign C-fluxes to certain trees species, size or canopy class. Tree rings methods in contrast, allow extending the analyses back decades or centuries with annual precision and only require a single time of sampling. They can also provide additional information on the sampled trees such as species, age, past disturbances, and climatic sensitivity (Cook and Kairiukstis, 1990; Fritts, 1976). However, sampling designs commonly applied in dendroecological studies, which focus on either old-looking trees or dominant trees, fail to represent forest productivity because they inherently ignore biomass accumulation at the stand level as permanent plots do. In order to overcome these limitations, different sampling approaches have been used to estimate AGB and AGBi as proxies for ANPP from tree rings (Babst et al., 2014a; Davis et al., 2009; Graumlich et al., 1989; Nehrbass-Ahles et al., 2014). These dendrochronological methods to estimate forest productivity are based on three different sampling strategies within a certain area or plot: (i) sampling all trees within plots; (ii) random sampling; (iii) sampling based on a stratified selection of trees, in some cases prioritizing larger trees (Babst et al., 2014a; Davis et al., 2009; Graumlich et al., 1989; Nehrbass-Ahles et al., 2014; Xu et al., 2019). These three sampling strategies require different sampling efforts. Among them, variable-radius plots (or *k*-tree plots) include a fixed number of at least 30–60 trees show a good balance between sampling effort and accuracy compared to full-stand sampling (Babst et al., 2014a; Nehrbass-Ahles et al., 2014). However, as opposed to periodic inventory of permanent plots, tree-ring sampling with the objective of reconstructing forest biomass dynamics and stand growth may be biased through time because past tree mortality or harvest removes trees that cannot be captured at the time of tree ring sampling (Dye et al., 2016; Klesse et al., 2016). Thus, the effect of past mortality on AGB and AGBi is usually uncertain and has commonly been avoided or reduced by selecting forest stands without signs of past extensive mortality such as logs, stumps etc. Thus, the accuracy back in time to estimate NPP using tree-ring methods is reduced and limited by the mortality or extraction by management operations of trees before the time of sampling, the so-called *ghost* tree limitation (Swetnam et al., 1999), though some analytical solutions have been proposed (Foster et al., 2014; Gea-Izquierdo and Sánchez-González, 2022). The legacies of previous forest mortality can greatly affect the estimation of past NPP dynamics. Management-induced effects on forest AGB and AGBi dynamics introduce additional complexity when comparing dendroecological and permanent plot approaches, relative to unmanaged forests mainly driven by natural disturbances.

Despite these limitations, the use of dendroecological methods to analyze forest productivity increased over the last decade (Babst et al., 2014a; D'Amato et al., 2013; Foster et al., 2014; Gea-Izquierdo and Sánchez-González, 2022; Martin-Benito et al., 2021; Pérez-Luque et al., 2026; Teets et al., 2022, 2018). They are often used to analyze growth at the individual-tree level (Biondi, 1999; Foster et al., 2016) and less often to assess forest productivity at the stand level using complete dendrochronological sampling (D'Amato et al., 2013; Foster et al., 2014; Teets et al., 2018). Comparisons of past tree growth at the individual level from tree-ring time series and repeated inventories commonly show a good agreement in the temporal growth trends, but a low agreement in absolute individual growth values (Biondi, 1999; Foster et al., 2016) because the latter are greatly affected by stand dynamics. For estimates of stand-level AGB, previous studies suggest that tree-ring reconstructed AGB confidently reflects actual forest AGB for a maximum of around 30–40 years in forests dominated by natural disturbances (Dye et al., 2016) where frequent but low intensity disturbances tend to produce slow and gradual changes in forest structure, composition and growth, particularly in mixed-species forests compared to simpler, monospecific stands. However, most forests are subjected to some type of management or other human disturbances. Therefore, the question remains as for how long tree-ring estimates can be reliable substitutes of permanent plots to analyze biomass dynamics in forests under common management practices.

In this study, we aimed to evaluate and compare estimates of AGB and AGBi (as a proxy for ANPP) derived from two different methodologies with complementary spatial and temporal capabilities: (1) repeated inventories of permanent plots; and (2) full-sampling, tree-ring biomass-oriented plots (hereafter referred to as dendroecological plots). We analyzed a large network of both types of plots including 40 managed forests of four pine species along a wide environmental gradient in the Iberian Peninsula. These forests, monitored through inventory plots established in the 1960s, were managed using practices similar to those in surrounding forests. Specifically, we assessed whether: (1) these two methods yield significantly different estimates of aboveground biomass (AGB) and AGB growth (AGBi) for the common observational period (i.e. the last 70 years); (2) for how long can the AGB and AGBi from dendroecological plots reliably represent estimates from permanent plots. We specifically hypothesized that: (1) AGB shows better agreement between approaches than AGBi because a larger temporal scale of integration reduces its temporal variability; (2) recent disturbances, either natural or management-induced, reduce the reliability of stand-level dendroecological proxies as they increase the effect of 'ghost trees'; and (3) reliability of dendroecological estimates of forest biomass increases with decreasing stand productivity.

2. Material and methods

2.1. Study areas

This study was conducted in a wide network composed of 40 permanent plots in monospecific stands of four different native pine species (*Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* J.F. Arnold, and *P. sylvestris* L.) sampled across their entire distribution ranges in the Iberian Peninsula (Fig. 1A). They also cover the wide range of forest productivity for each pine species (Del Rio et al., 2025; Martin-Benito et al., 2008). These permanent plots were originally set up between 1963 and 1971 on even-aged forest stands (Figure S1A). Permanent plot areas ranged between 625 m^2 and 2500 m^2 and initial stem densities between 176 and 10,112 trees·ha^{-1} (Fig. 2). When permanent plots were originally set up, trees were individually tagged and the height of 1.3 m above ground (breast height) marked in each tree. Since the time of establishment, they were remeasured 6–9 times with a periodicity of 5–12 years. In total, we used over 40,000 measurements from 7604 trees. The years of last inventories ranged between 2006 for *P. nigra* and 2015 for *P. sylvestris* (Table 1). In each inventory, diameter at breast height (DBH) was always measured at the same height, and dead trees or trees no longer present in the plot were recorded as extracted. Separating between natural and management-induced mortality was not possible because the cause of death was not identified in these inventory plots. These stands were subject to management similar to that of the surrounding forests. As is commonly observed in most forest management practices, extracted trees where in general smaller than surviving trees (Figure S2).

To describe mean climate conditions at each site, we used monthly mean temperature and precipitation for the period 1960–2020 from the

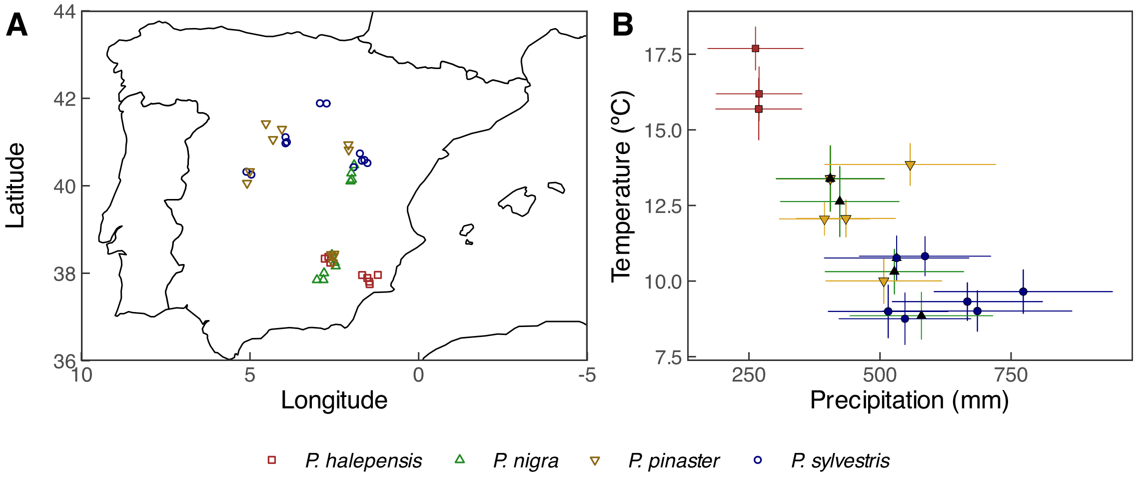

Fig. 1. Location and climate characteristics of all sampled plots for the four studied pine species. A) Map of the spatial distribution of plots. Points were jittered to decrease overlapping. B) Mean annual temperature and total precipitation (E-OBS v31.0e for the period 1960–2020). Error bars represent the standard deviations of mean annual variables. Note that in B some points overlap because they share the same E-OBS v31.0e grid point.

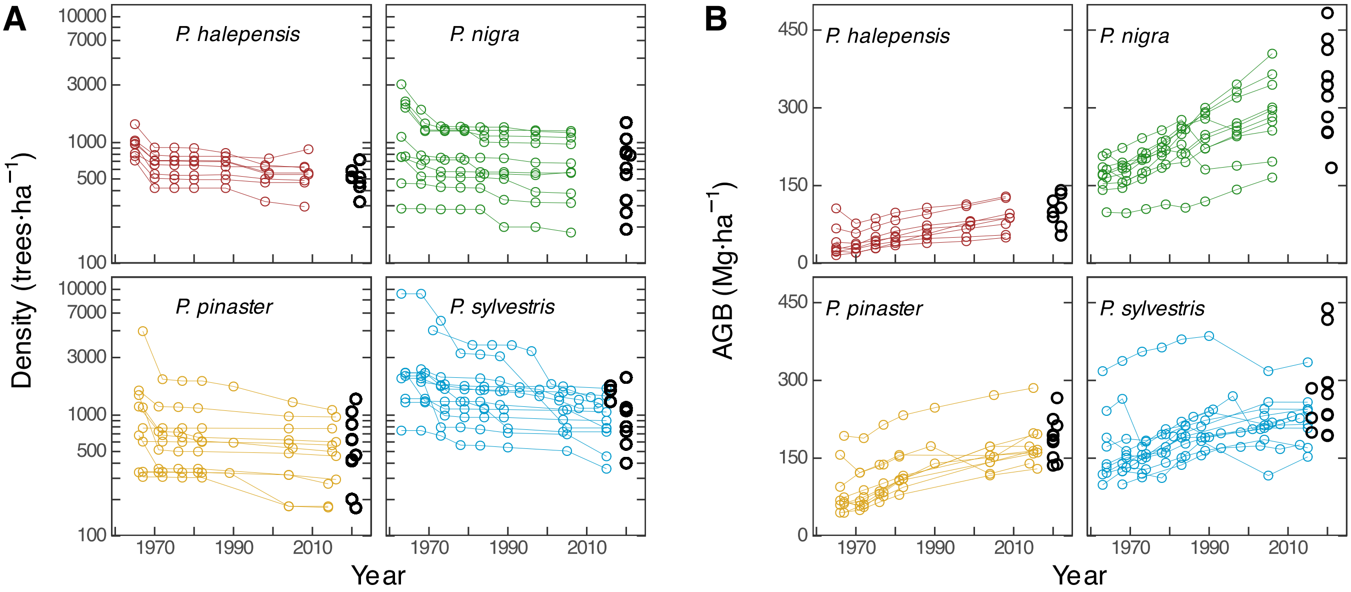

Fig. 2. Plot characteristics through time derived from repeated inventories (color lines and symbols). Open black symbols show values for each dendroecological plots at the time of sampling (2016, 2019 or 2020). (A) Stand density and (B) above ground biomass (AGB). Note the logarithmic scale in the y-axis of stand density in (A).

Table 1

Characteristics of the permanent plots at the last inventory. Mean values with ranges between parentheses except for AGBi where mean ± 1 SD is presented.

Species	Year of first inventory	Year of last inventory	N plots	Plot size (m^2)	Stem density (trees $\cdot ha^{-1}$)	BA ($m^2 \cdot ha^{-1}$)	AGB ($Mg \cdot ha^{-1}$)	AGBi ($Mg \cdot ha^{-1}$ $year^{-1}$)
P. halepensis	1965	2008–2009	8	1375 (1000–2000)	560.3 (295–880)	27.7 (16.8–39.0)	88.4 (49.8–129.1)	1.76 ± 0.73
P. nigra	1963–1964	2006	10	1591 (900–2500)	720.5 (180–1248)	57.1 (35.4–84.7)	288.4 (165.5–404.5)	5.08 ± 2.72
P. pinaster	1966–1967	2014–2016	10	1572 (625–2500)	570.7 (176–1104)	46.7 (31.7–67.9)	177.2 (129.5–285.4)	4.13 ± 2.69
P. sylvestris	1963–1971	2011–2015	12	1157 (625–2000)	999.3 (360–1667)	51.5 (37.5–62.0)	225.1 (152.6–334.9)	5.21 ± 4.70

BA, basal area at last inventory; AGB, aboveground biomass at last inventory; AGBi, aboveground biomass increment (for the entire period available (from 1963–1966 to 2006–2015 depending on the plot).

E-OBS v31.0e gridded data set (Cornes et al., 2018). We used monthly temperature and precipitation data from the closest grid point to each permanent plot location. Following species hydric and thermal requirements and species drought tolerance, temperature in this network showed a strong gradient (*P. sylvestris* < *P. nigra* < *P. pinaster* <*P. halepensis*) with precipitation showing an opposite, but less pronounced gradient (*P. sylvestris*> *P. nigra* >*P. pinaster* > *P. halepensis*) (Fig. 1B).

2.2. Field and dendrochronological methods

In 2019 and 2020, we established one *k*-tree circular plot (considering DBH ≥ 5 cm) collocated inside each permanent plot with *k* ranging between 35 and 48 trees per plot. Plot radius ranged between 8.4 m and 25.9 m (Table 2) which are considered sufficient to provide robust representations of carbon accumulations (Babst et al., 2014b; Nehrbass-Ahles et al., 2014). For each tree within these *k*-tree circular plots, we measured DBH and total height and collected two cores with increment borers (5-mm interior diameter). DBH distributions of trees sampled for tree rings were similar to those of all trees present at the last permanent plot inventory (Figure S1B). We used three additional dendroecological plots developed in 2016 for *P. sylvestris* following similar methods (Gea-Izquierdo and Sánchez-González, 2022). For a subsample of trees in each plot, we measured bark thickness with a bark probe to develop *ad hoc* allometric equations to estimate bark thickness based on measured DBH over bark (DBH_{ob}) and DBH under bark (DBH_{ub}) (Figure S3).

We sampled and used a total of 1642 trees from 40 dendroecological plots of the four species (Table 2). Increment cores were mounted onto wood boards, dried and progressively sanded until rings were visible. Rings were visually crossdated and later measured on a LINTAB measuring station (0.01 mm precision). Crossdating was verified with COFECHA (Holmes, 1983). When necessary, we adjusted ring widths so that their cumulative sum was equal or lower than the DBH under bark (DBH_{ub}) on the year of sampling (Bakker, 2005). For each tree, we reconstructed DBH back in time by subtracting ring widths from DBH_{ub}. We obtained DBH_{ob_recons} back in time by adding estimated bark thickness to DBH_{ub_recons}. This way reconstructed annual DBH over bark was estimated as $DBH_{ob\_recons}= DBH_{ub\_recons} + 2{\cdot}bark_{estimated}$ where DBH_{ub_recons} is the reconstructed annual DBH under bark for each tree and $bark_{estimated}$ is bark thickness estimated based on allometric equations and DBH_{ub_recons} (Figure S3B). Using bark thickness to reconstruct DBH and basal area increments (BAI) significantly reduces potential biases (Klesse and Bigler, 2025) such as negative growth value closer to the pith (Bakker, 2005). Because the size of *k*-tree plots of variable radius represent the minimum plot size containing *k* trees, they may overestimate stem density, basal area and above ground biomass (Kleinn and Vilčko, 2006). Thus, we corrected the field-measured radius of each plot by considering the distance to the a potential $k + 1$ tree by estimating the average distance from the plot center to all trees and adding it to the distance of the most distant tree as $r_{max} = d_k + \frac{\sum_{i=1}^{i=k} d_i}{k}$, where r_{max} is the maximum radius of the plot, d_i is the distance of tree *i* to the plot center and d_k is the distance of *k* tree to plot center (i.e. farthest tree measured within the plot). Thus, plot area for each *k*-tree plot was estimated as $Area = \pi{\cdot}r_{max}^2$, and areas of tree-ring plots ranged between 224 m^2 and 2498 m^2 (Table 2).

2.3. Aboveground biomass estimations

We used species-specific DBH-based allometric equations (Montero et al., 2005) to estimate total tree above ground biomass (AGB), i.e. including all components of the plant, both woody stems and the canopy. We used the same allometric equations for tree-ring based and permanent plot AGB estimates using DBH_{ob} either annually reconstructed from tree rings (DBH_{ob_recons}) or periodically measured in each inventory. Individual AGB of all trees sampled within each plot were summed to estimate plot-level AGB per unit area ($Mg{\cdot}ha^{-1}$) as $AGB = \sum_{i=1}^{i=k} AGB_i{\cdot}\frac{10{,}000}{Area}$, where AGB_i is the AGB for each *i* tree in the plot and *Area* is the surface area of each plot (in m^2). AGBi was used as a proxy of aboveground annual net primary productivity (ANPP). We estimated annual plot-level AGBi as the difference in tree-ring-based AGB between two consecutive years. For comparison with AGBi from permanent plots, we used the average tree-ring-based AGBi for the years between inventories of each permanent plots.

Annual AGBi from permanent plots was estimated as the difference between AGB of living trees between two consecutive inventories divided by the time elapsed between inventories (Clark et al., 2001): $AGBi = \sum_{i=1}^{n} AGBi_i = \sum_{i=1}^{n} \frac{AGB_{i,t} - AGB_{i,t-1}}{\Delta t}$, where $AGB_{i,t}$ is AGB of tree *i* at one inventory, $AGB_{i,\ t-1}$ is AGB of tree *i* at the previous inventory and Δt the time interval between inventories (in years), and *n* the total number of trees in the plot. This approach was selected because individual trees could not be tracked through time for some plots due to fading of painted tags and only stand-level biomass could be analyzed (Clark et al., 2001). The potential bias introduced by not analyzing the within-interval growth of all trees, including trees that died between inventories, for long intervals is minimized because management in these permanent plots extracted small or dead trees from most plots (Figure S2). However, large disturbance events such as increased mortality or timber extractions that affect large trees in combination with large inventory periods may introduce important biases in AGB and AGBi estimations from permanent plots (Clark et al., 2001).

2.4. Comparisons between inventory-based and tree-ring based estimates

Dendroecological plots were established entirely within the borders of permanent plots, but were smaller in size and of different shape (circular vs. rectangular) than permanent plots. To avoid scale-related biases, for comparisons between both types of data, from each inventory and permanent plot we generated 1000 random *k*-tree plots of equal *k* number of trees as those sampled for dendroecological plots. Because, tree location within each permanent plot was not recorded, we estimated the simulated sampled area for every simulated *k*-tree plot proportional to the density of permanent plots at the time of each inventory. We then calculated AGB and AGBi for these simulated plots to

Table 2
Characteristics of the dendroecological plots. Mean values with ranges between parentheses except for AGBi where mean ± 1 SD are presented.

Species	Time Span	N plots	Plot size (m^2)	Trees sampled per plot	DBH (cm)	Stem density (trees $\cdot ha^{-1}$)	BA ($m^2{\cdot}ha^{-1}$)	AGB ($Mg{\cdot}ha^{-1}$)	AGBi ($Mg{\cdot}ha^{-1}$ $year^{-1}$)
P. halepensis	1877–2020	8	819 (568–1238)	40 (35–48)	27.4 (7.9–56.6)	509.5 (323.1–721.4)	31.4 (17.8–42.0)	95.7 (43.9–133.4)	1.08 ± 0.17
P. nigra	1827–2020	10	839.1 (286.5–2091.2)	41 (39–43)	35.4 (5.8–78.2)	692.0 (191.3–1465.9)	63.3 (41.3–102.4)	318.9 (174.1–474.2)	3.62 ± 1.02
P. pinaster	1905–2020	10	1083.2 (301.7–2498.3)	41 (36–46)	34.9 (7.3–59.1)	580.7 (170.8–1358.9)	48.4 (31.2–64.6)	169.7 (55.2–251.3)	2.15 ± 0.78
P. sylvestris	1852–2020	12	455.4 (224.3–1098.6)	43 (38–48)	27.3 (5.7–69.8)	1139.0 (400.5–2050.7)	62.0 (47.7–80.2)	262.7 (186.2–432.3)	3.09 ± 1.42

Time span, period of tree ring data; tree-ring width data from three *P. sylvestris* plots ended in 2016. BA, basal area at the time of sampling; AGB, aboveground biomass; AGBi, aboveground biomass increment. BA and AGB at correspond to values at the time of sampling. AGBi corresponds to mean values for the last 10 years for each dendroecological plot.

compare with dendroecological-based estimates. We compared estimates of AGB and AGBi from both types of data using several metrics. We particularly focused on evaluating differences along different lengths of inventory-to-sampling intervals, i.e. the time interval between the dates of each periodic inventory of each permanent plot (between 1963 and 2016) and the time of sampling of dendroecological plots (2016, 2019 or 2020) (Figure S4). These comparisons offer the possibility to analyze how reliable dendroecological-based estimations are compared to inventory-based estimations across common periods. First, we used linear correlations between the estimates using dendroecological plots and the average of the 1000 simulated *k*-tree plots from each inventory of each permanent plot. Second, we estimated the mean differences between both AGB and AGBi for each plot and species along the full range of inventory-to-sampling intervals. Third, we used the nonparametric Mann–Whitney–Wilcoxon test with the *wilcox_test* function in the *rstatix* library in R (Kassambara, 2023) to assess whether the distributions of dendroecological and permanent plot AGB and AGBi estimates were identical without the assumption of normality. To analyze whether dendroecological derived AGB and AGBi underestimated or overestimated those derived from repeated inventories, we used the location parameter from the Mann-Whitney-Wilcoxon test and their confidence intervals (i.e. the median of the differences between both distributions). Location parameters represent shifts with respect to permanent plots used as reference group so that positive values indicate overestimation by dendroecological plots and negative values an underestimation. We also estimated root mean squared error (RMSE) and bias for each variable (AGB and AGBi) for different inventory-to-sampling intervals and for all intervals combined.

3. Results

3.1. Biomass dynamics from permanent plots and dendroecological plots

Across all species, plot density declined over time, with *P. sylvestris* showing the most pronounced decreases and *P. halepensis* the lowest decreases (Fig. 2). In contrast, AGB increased consistently for all species, particularly in *P. nigra* and *P. sylvestris*. As a result, over the period of permanent plot inventory data (1963–2019), plots tended towards lower stand density, but higher AGB as a result of higher individual tree biomass. In some plots, reduction in stand density also lead to decreases in AGB after management operations (e.g. thinning) or large natural disturbance events. For example, one *P. sylvestris* plot sharply reduced its density and AGB due to a snow storm in 1996 (Gea-Izquierdo and Sánchez-González, 2022).

Some of our tree-ring records go back to the 1820s and records in most plots started between 1900 and 1950 (Table 2; Figure S5). Our analyses focused on the common period for both dendroecological and permanent plot data (1964–2016). All species showed interannual and inter-plot variability in AGBi, particularly *P. nigra* and *P. sylvestris* (Fig. 3; Figure S5). Based on tree-ring reconstructed AGB (Table 2), *P. nigra* and *P. sylvestris* showed the highest AGBi values (3.62 ± 1.02 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ and 3.09 ± 1.42 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ respectively for the last 10 years of tree-ring data available), while *P. pinaster and P. halepensis* showed lower AGBi values (2.15 ± 0.78 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ and 1.08 ± 0.17 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$, respectively). At the species level, AGBi remained rather constant after the 1970s or 1980s (Fig. 3). Results from permanent plots showed larger mean species growth for all species for the entire period and similar interspecies gradients in AGB increments than those estimated using dendroecological plots: *P. halepensis* (1.76 ± 0.74 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$) < *P. pinaster* (4.12 ± 2.69 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$) < *P. nigra* (5.09 ± 2.72 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$) < *P. sylvestris* (5.23 ± 4.79 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$) (Table 1). These AGBi gradient from dendroecological and permanent plots were in general inversely related to the species drought tolerance (*P. sylvestris* < *P. nigra* < *P. pinaster* <*P. halepensis*).

3.2. Comparisons between AGB and AGBi from permanent and dendroecological plots

Aboveground biomass (AGB) from dendroecological plots were strongly correlated with permanent plots estimates along the entire range of inventory-to-sampling intervals (in all cases >10 years $R^2 \geq 0.67$, $P < 0.001$) (Fig. 4). The strength of the relationship was slightly lower at the shortest and longest inventory-to-sampling intervals and rather similar for intervals between 10 and 50 years (R^2 between 0.77 and 0.80). We note that the inventory-to-sampling interval < 10 years also had the lowest replication (22 plot-inventories). Despite strong agreements (slopes >0.75 for periods between 10 and 40 years), systematic differences were evident between AGB estimates derived from dendroecological plots and those from inventories across the four pine species (i.e. bias in estimates from dendroecological plots). In general, results from dendroecological plots slightly overestimated AGB at short times since inventory (positive location parameters and bias for <10 years; Table 3) and underestimated inventory-based AGB with increasing inventory-to-sampling intervals (negative location values and bias). These disagreements were more pronounced in the fastest growing plots (i.e. those at the more mesic sites including the least drought-

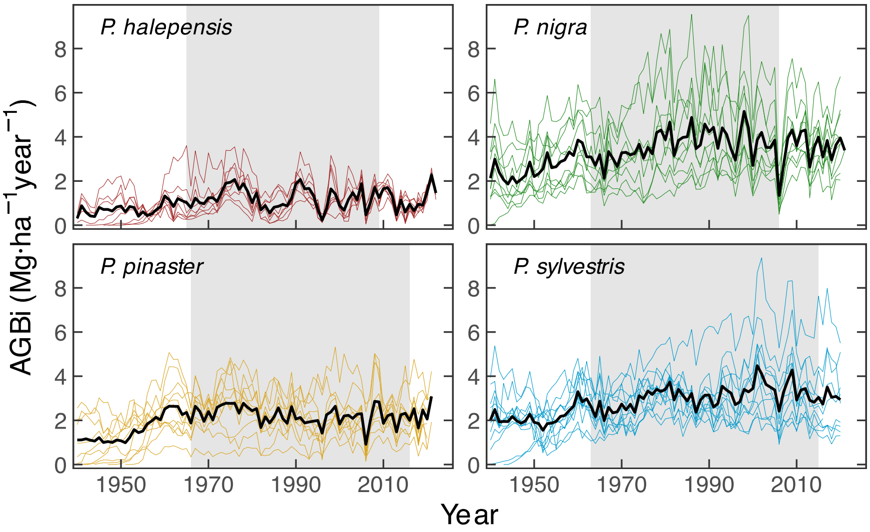

Fig. 3. Mean dendroecological derived above ground biomass increment (AGBi) for each plot for the four species analyzed. Color lines represent plot-level values and thick black lines represent species means. Grey shade shows the inventory period for each species. See Fig. S3 for full AGBi time series.

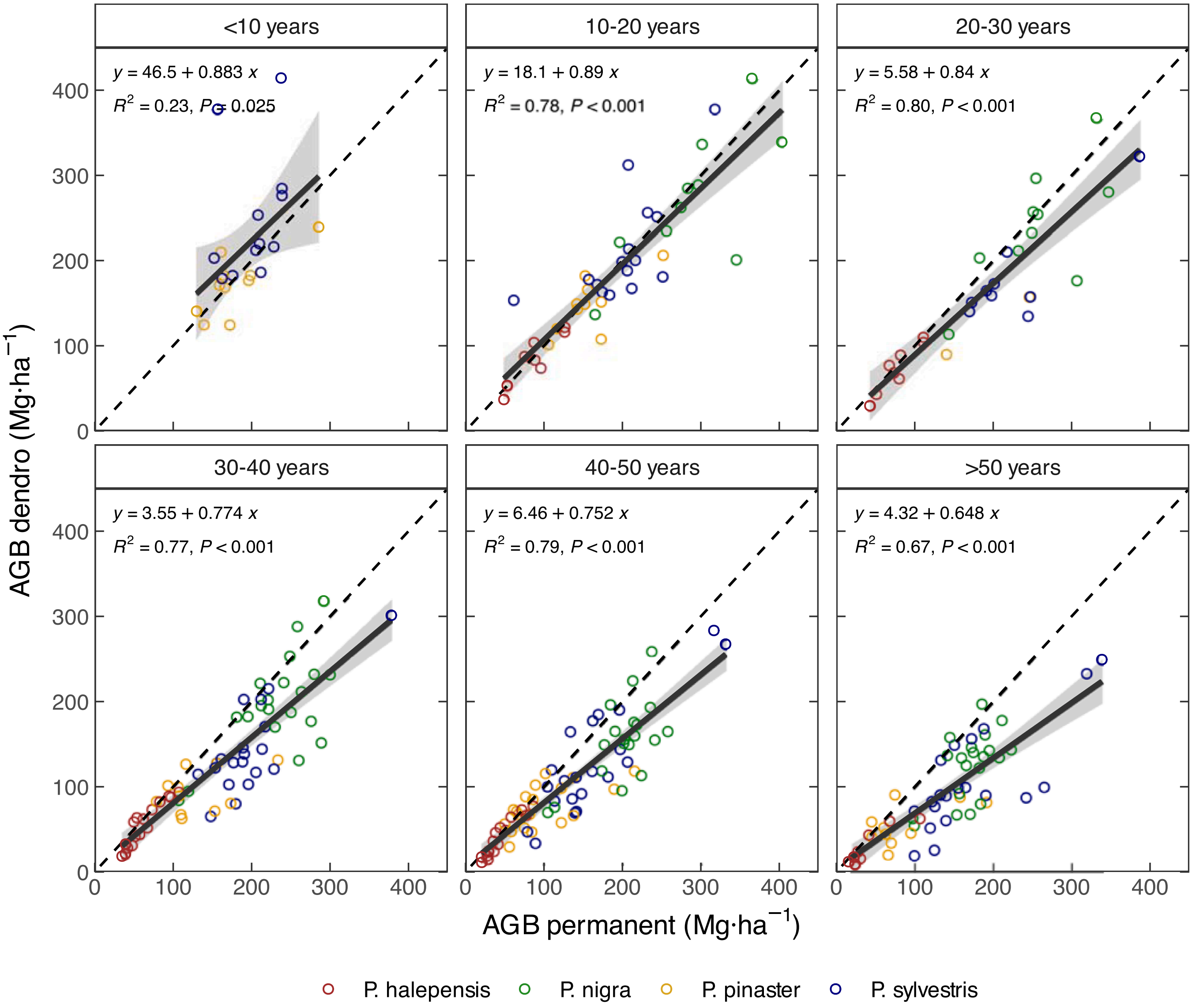

Fig. 4. Comparison between total above ground biomass (AGB) derived from permanent plots (x-axis) and from dendroecological plots (y axis) for different inventory-to-sampling intervals. Panels compare for different periods of time between tree-ring sampling year (2016, 2019 or 2020) and inventory year for both information sources. To make plot size comparable, AGB from inventories of permanent plots represent the mean from 1000 randomizations of all trees present at the time considered for an equal number of trees as those sampled for dendroecological plots and tree rings. Dashed line shows the identity relationship. Thick black lines present the linear relationships between both AGB estimates for all species within each period. Coefficients of determination (R^2) and p-values shown for each period.

tolerant species) such as those of *P. sylvestris* (Fig. 5). In general, differences in AGB between methodologies at the species level were < 7%-8% (ranging between −20% and 30%) for inventory-to-sampling intervals lower or equal than 30 years (Fig. 5). For these intervals below 30 years both estimates considering all species were within 30 Mg·ha^{-1} and not significantly different (Table 3). Despite the good general agreement in shorter inventory-to-sampling intervals, dendroecological plots may underestimate inventory based AGB by close to 100% for inventory-to-sampling intervals longer than 40 years (Fig. 5).

Differences between biomass increments (AGBi) estimates based on dendroecological plots and permanent plots showed moderate agreements and smaller than those for AGB, for different inventory-to-sampling intervals between 10 and 40 years with positive correlations ($R^2 = 0.13$–0.33, all $P < 0.028$), particularly for the period 20–30 years intervals (Fig. 6) which showed the lowest RMSE. The 10–20 years intervals showed the lowest correlations ($R^2 = 0.13$), in part due to some exceptionally high estimated AGBi from permanent *P. sylvestris* plots. Excluding this species from the analyses showed R^2 between 0.33 and 0.72 ($p < 0.001$, results not shown). In general, dendroecological-based AGBi estimates were similar to those from permanent plots for AGBi < 5Mg·ha^{-1}·year^{-1} but underestimated them (negative bias) for high growth rates from permanent plots (Fig. 6; Table 3). AGBi differences ranged between −100% and 100%, with some larger differences for individual plots and inventory periods. Both RMSE and bias for AGBi increased with inventory-to-sampling intervals (Table 3). Considering the entire period of data available, dendroecologically-derived AGBi underestimated permanent plot AGBi for all inventory-to-sampling intervals except < 20 years although differences were only significant for intervals > 30 years (Table 3). For shorter periods, the differences were within 0.3 Mg·ha^{-1}·year^{-1}. There were also some differences between species in AGBi estimates between the two data types. Less productive plots (i.e. lower permanent plot AGBi) showed better agreement in AGBi from both data sources (Figure S6). In general, the two species with slower growth rates and more drought-tolerance *P. halepensis* and *P. pinaster* showed better agreement and lower bias in contrast with the higher variability in *P. sylvestris* and *P. nigra*.

Table 3
Comparison between dendroecological and permanent plot aboveground biomass (AGB) and aboveground biomass increments (AGBi). Results of the Mann-Whitney-Wilcoxon test (Location, N1, N2 and *p*) and root mean square error (RMSE) and bias. Location parameters represents shift with respect to permanent plots used as reference group. Positive location indicates overestimation by dendroecological plots and negative values an underestimation. N1 and N2, represent sample sizes for tree-rings and permanent plots respectively. Significant differences are highlighted in bold.

Variable	Inventory-to-sampling interval (years)	Location (95% CI)	N1	N2	*p*	RMSE	Bias
AGB	< 10	14.67 (-17.07, 45.46)	22	22	0.211	66.7	24.3
	10–20	-4.31, (-41.00, 31.45)	43	43	0.790	40.8	-2.89
	20–30	-29.14 (-80.33–21.99)	29	29	0.272	47.3	-25.2
	30–40	-34.1 (-64.32, −7.82)	67	67	**0.013**	50.9	-33.6
	40–50	-24.22 (-47.48, −3.22)	76	76	**0.025**	42.5	-26.0
	> 50	-45.01 (-70.22, −20.90)	58	58	**< 0.001**	59.6	-44.2
	All	-26.78 (-39.88, −13.79)	295	295	**< 0.001**	50.5	-24.1
AGBi	< 10	0.15 (-1.40, 1.00)	22	22	0.825	3.46	-1.10
	10–20	0.15 (-0.51, 0.77)	43	43	0.612	3.02	-0.28
	20–30	-0.32 (-1.23, 0.50)	29	29	0.497	1.63	-0.29
	30–40	-1.07 (-1.83, −0.34)	67	67	**0.002**	3.64	-1.82
	40–50	-1.33 (-1.96, −0.77)	75	75	**< 0.001**	3.81	-2.09
	> 50	-2.93 (-5.34, −1.49)	19	19	**< 0.001**	4.89	-3.76
	All	-0.83 (-1.18, −0.50)	255	255	**< 0.001**	3.52	-1.55

3.3. Effects of disturbances and management on biomass estimation bias

A detailed comparison for all plots revealed varying levels of agreement between both estimates of AGBi, with some plots showing close correspondence and others notable discrepancies (Figure S7). In general, tree ring estimates of AGBi represented permanent plots estimates better in the absence of disturbances. Larger differences between both types of data were generally caused by large underestimations by tree rings (see for example *P. sylvestris* plots in Figure S7). In general, plots with large reductions in basal area showed larger differences in both AGB and AGBi (Fig. 8). Basal area reductions in inventory-to-sampling intervals between 10 and 30 years (i.e. recent disturbances or management operations) had the larger effect on the relative differences between estimations from dendroecological plots and permanent plots. In contrast, changes in basal area occurring either very recently (<10 years before dendroecological sampling) or long time before sampling (inventory-to-sampling intervals >30 years), showed lower effect on the differences between estimates.

4. Discussion

Understanding the role of forests in the global carbon cycle requires assessing how forests fix and store carbon and how environmental changes or management affect those processes. Combining permanent plots and dendroecological data have a great potential to better understand the role of forest management and its interactions with climate on terrestrial carbon sequestration. In this study, we combined both approaches on collocated plots to evaluate how each method captures stand-level carbon stocks (AGB) and productivity (AGBi as a proxy for ANPP). Despite certain discrepancies and temporal limitations, dendroecologically-based reconstructions captured major trends in both analyzed variables. Our results support their use for understanding carbon dynamics in managed forest ecosystems and provide recommendations on reliable temporal scales and limitations such as the need to carefully account for disturbance and management history.

4.1. Complementarity in biomass estimates between dendroecological plots and permanent plots

Combining forest permanent plots with retrospective tree-ring-based analyses offer invaluable opportunities to understand carbon fixation at different time scales. Permanent plots provide long-term observations of forest growth and productivity as well as regeneration and mortality through time at temporal scales commonly of 5 or 10 years (Clark et al., 2001; Curtis and Marshall, 2005). In contrast, most dendroecological approaches, which provide finer and longer temporal scales, are limited in their ability to analyze stand level growth because the fading record bias (‘ghost-tree’ effect) creates an artificial apparent growth decrease back in time caused by using only the growth of live trees at the time of sampling (Alexander et al., 2018; Bowman et al., 2013; Brienen et al., 2017; Foster et al., 2014). Combining permanent plots and tree ring data have a great potential to better understand the role of forest management and its interactions with climate on terrestrial carbon sequestration. Our comparisons of permanent research plots and collocated dendroecological plots on the same forest stands allowed to assess the reliability of tree-ring based reconstructions of ANPP in managed forests. Similar sizes of dendroecological and permanent plots (600–2500 m^2 in both approaches) reduced the potential selection bias of having just one dendroecological plot compared to a large inventory plot. Dendroecological-based reconstructions of stand-level AGB and AGBi provide a robust basis for analyzing the influence of climate and other environmental drivers compared to estimates derived from individual trees or standardized tree-ring indices (Nehrbass-Ahles et al., 2014) to be used, for example, in combination with process-based vegetation models (Gea-Izquierdo and Sánchez-González, 2022) or eddy-covariance based studies (Babst et al., 2014a; Ohtsuka et al., 2009). Stand-level reconstructions quantify growth in absolute units per unit area which are direct integrative proxies of carbon fixation such as

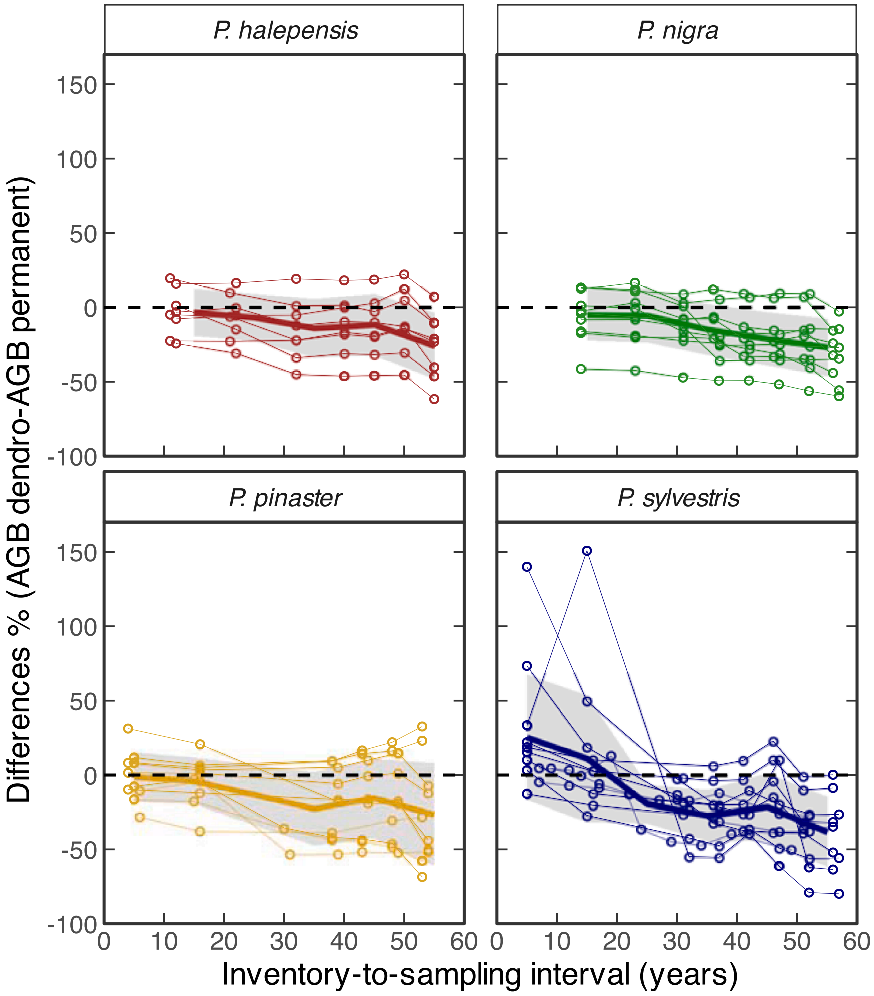

Fig. 5. Differences between total above ground biomass (AGB) derived from permanent plots and from dendroecological plots as a function of time between inventory and time of tree-ring sampling (2016, 2019 or 2020) for both information sources. AGB from inventories represents the mean from 1000 randomizations of all trees present at the time considered for an equal number of trees as those sampled for tree rings. Color lines represent the temporal trend of AGB differences with inventory-to-sampling intervals for each sampled plot. Thick color lines present species means whereas grey shaded areas representing mean ± standard deviation.

ANPP, but require either sampling of all trees or a randomized selection of trees within certain area (plot). Nevertheless, for larger forest stands, establishing sets of clustered dendroecological plots per stand may reduce the uncertainty with respect to estimations from single plots (Babst et al., 2014a; Dye et al., 2016; Foster et al., 2014; Martin-Benito et al., 2022) due to single plot idiosyncrasies and spatial heterogeneity of biomass in a forest landscape (Alexander et al., 2018).

4.2. Biases on biomass and biomass increment estimates from dendroecological plots

In general, the dendroecological approach underestimated AGB and more significantly AGBi compared to permanent plots, similar to previous studies of different types of forests, even in the absence of management interventions (Dye et al., 2016). We attribute the higher similarity between AGB estimates of both approaches to the fact that the studied stands were even-aged and their development resembles that of forest regrowth after harvest which limits the long-term effects of the fading-record bias. Estimating biomass increments is usually more challenging because it involves differencing consecutive AGB estimates which results in compounding underlying uncertainties. AGB estimations based on permanent plots are generally less biased by long measurement intervals than AGBi because measurement errors or errors in the corrections for mortality or recruitment compound over time (Clark et al., 2001). Analyses of forest productivity from permanent plot data is also prone to bias particularly when long measurement intervals are used (up to 12 years in our study) and there is significant mortality of large trees (Clark et al., 2001). Because AGBi was estimated based on living trees at the stand level only (i.e. not tracking individual trees) within-interval growth of trees that died between inventories is unknown, which may have resulted in underestimations of AGBi in our permanent plots (Clark et al., 2001). However, that bias was probably minor because most extracted trees were small and it would go in the same direction (underestimation) as the potential bias in dendroecological AGBi produced by the ghost-tree effect (i.e. trees that died before they could be sampled) which may have increased the similarity of results between both methodological approaches. Despite the differences observed in absolute AGBi magnitudes, the high correlations between estimates from both approaches evidence the high similarity in their variability both for AGB and AGBi. Our results thus further support that, in most cases, tree-rings can reliably be used to explore ANPP variability when they are integrated at the plot level and converted to biomass units (Alexander et al., 2018; Babst et al., 2014a; Gea-Izquierdo and Sánchez-González, 2022; Martin-Benito et al., 2021; McKenzie et al., 2021; Pérez-Luque et al., 2026) to, for example, analyze effects of climate on forest productivity.

Dendroecological studies are also subject to several types of biases (Brienen et al., 2012), although some can be reduced with appropriate

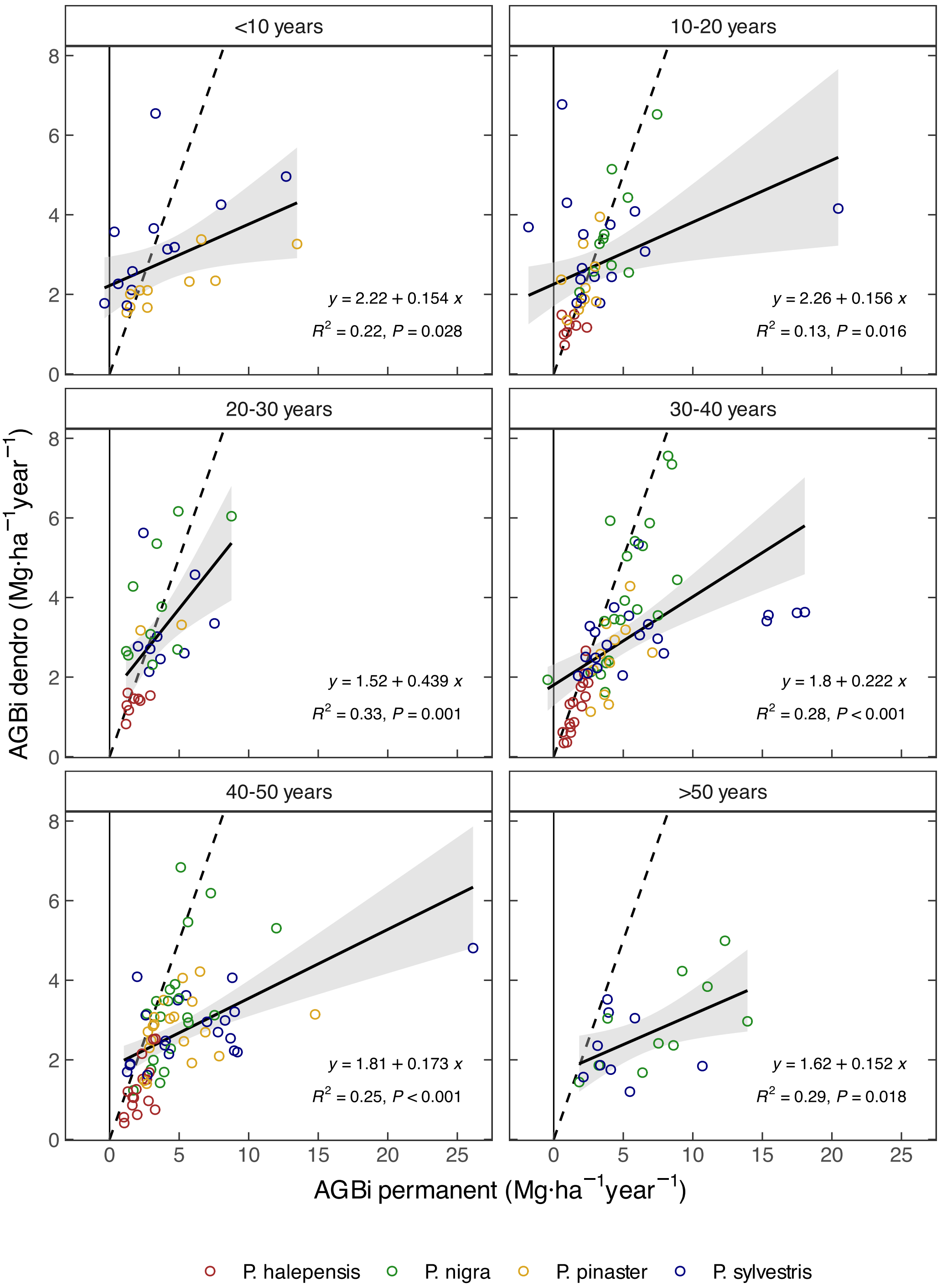

Fig. 6. Comparison between above ground biomass increments (AGBi) derived from permanent plots (x-axis) and from dendroecological plots (y axis). Panels compare for different periods of time between tree-ring sampling year (2016, 2019 or 2020) and inventory year for both information sources. AGB increments from inventories represent the mean from 1000 randomizations of all trees present at the time considered for an equal number of trees as those sampled for tree rings. Dashed line shows the identity relationship. Thick black lines present the linear relationships between both AGBi estimates for all species within each period. Coefficients of determination (R^2) and p-values shown for each period.

sampling protocols (Nehrbass-Ahles et al., 2014). By sampling trees across all diameter classes, including smaller diameters than commonly used in dendrochronological studies, our sampling avoided the “big-tree selection bias” (Brienen et al., 2012), which arises from sampling only large diameter trees which would preferentially select fast growing trees of the younger cohorts. Some biases common to dendroecological studies may be lower in managed forests than in forests subjected to natural disturbances. The “slow-grower survivor bias”, caused by different growth rates among individual trees with slower growth in older trees that are more likely to reach higher longevities (Bowman et al., 2013; Brienen et al., 2010), is probably lower in managed forests because tree growth tends to be more similar among individuals and fewer trees are suppressed or slow growing. In fact, dendroecological sampling in managed forests likely results in the opposite bias because slow-growing trees (small trees in even-aged stands) are more likely to be removed by intermediate treatments such as thinning from below during the development of the stand (Del Río et al., 2017), as observed in our permanent plots (Figure S3). This “fast-grower survivor bias” may

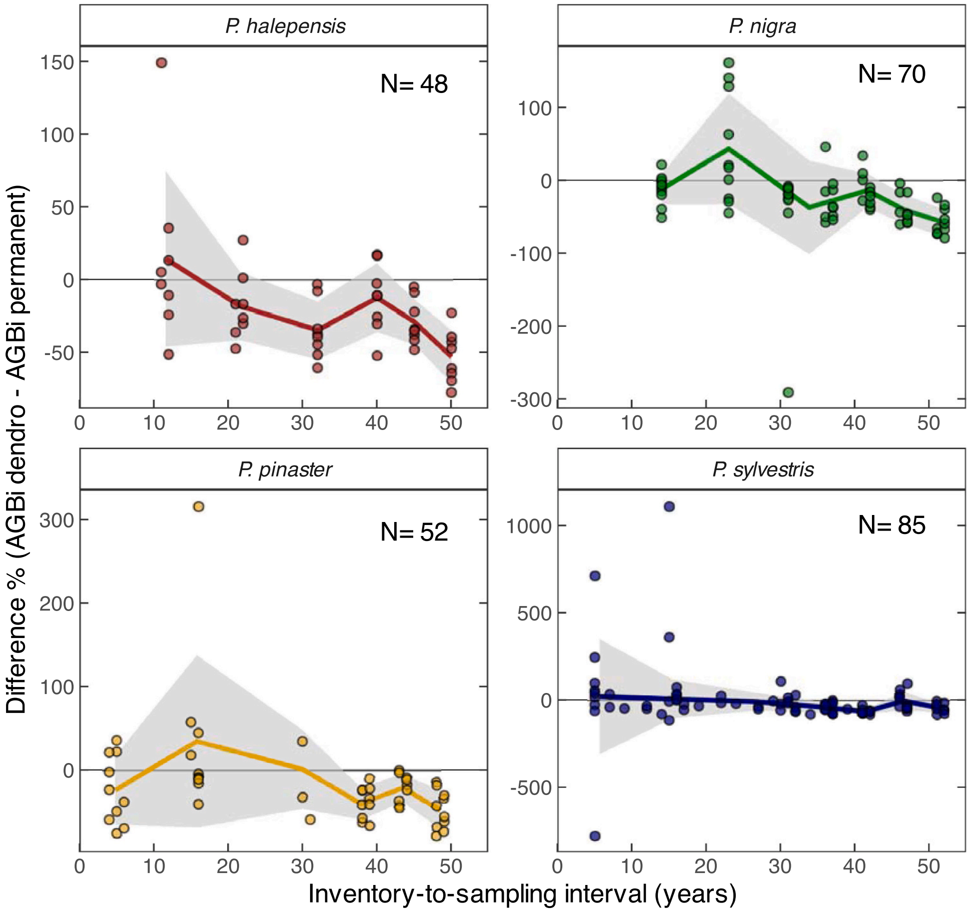

Fig. 7. Difference between above ground biomass increments (AGBi) derived from permanent plots and from dendroecological plots (in %). Thick color lines present species means whereas grey shaded areas representing mean ± standard deviation. AGB increments from inventories represents the mean from 1000 randomizations of all trees present at the time considered for an equal number of trees as those sampled for tree rings. Note different scales in each panel for clarity.

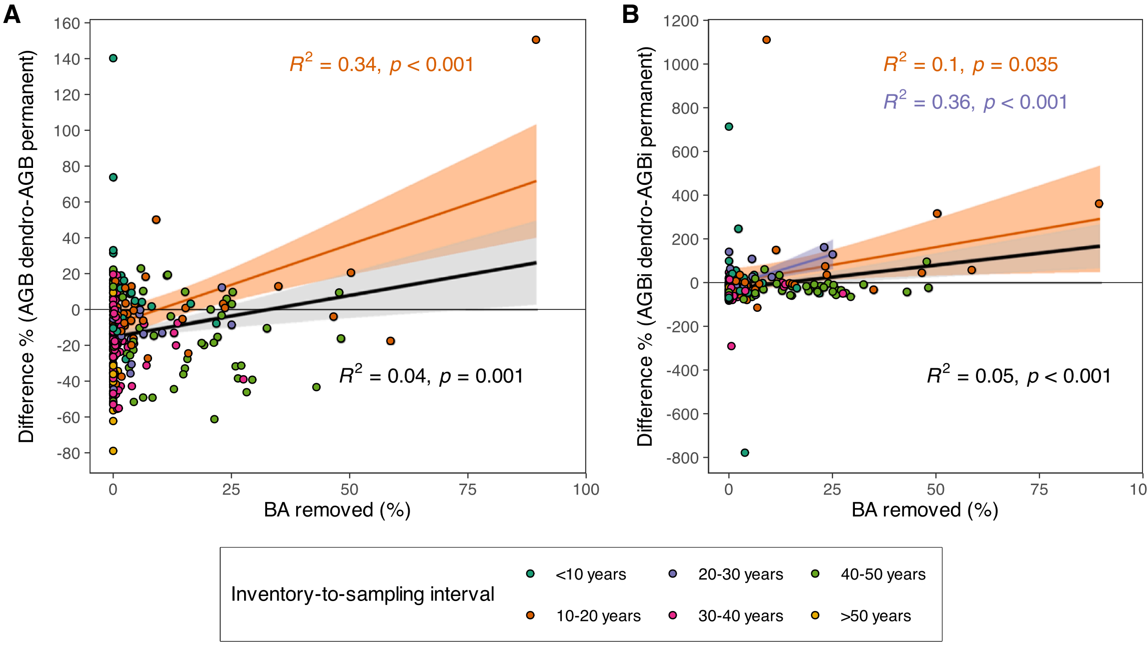

Fig. 8. Effect of reductions of basal area (BA) on the differences in (A) AGB and (B) AGBi using permanent plots and dendroecological plots during the study period. BA removed (%) represents the relative difference in basal area in each plot between two consecutive inventories. Only significant linear regression lines ($p < 0.05$) are shown. Black lines represent correlation for all plots and inventory-to-sampling intervals. Color lines represent correlations for different inventory-to-sampling intervals classes: A) 10–20 years for AGB; B) 10–20 years and 20–30 years for AGBi.

have contributed to reduce the differences in AGB and AGBi between approaches in our study. They may have also partly compensated for the fading record because dead “ghost trees” were most likely suppressed, slow growing trees and their contribution to AGB and AGBi would have been low (Lutz et al., 2018; Stephenson et al., 2014).

4.3. Effects of forest management and disturbances on biomass reconstructions

Although, most forests worldwide experience some type of management, many studies comparing permanent and dendroecological plots to reconstruct stand-level biomass as a proxy for ANPP focused on unmanaged forests (but see Gea-Izquierdo and Sánchez-González, 2022; Klesse et al., 2016) where dynamics are dominated by natural disturbances (Dye et al., 2016). In managed forests, logging operations with varying frequency and intensity present an increased challenge for the dendroecological reconstruction of forest productivity (Babst et al., 2014a). Despite these potential difficulties, our results showed that AGB and AGBi estimates from permanent and dendroecological plots in managed pine forests were rather similar for up to 30 years (Table 3). However, despite the high correlation between AGB estimated using both approaches ($R^2>0.79$ for up to 50 years) (Fig. 4), there was an important increase in bias beyond 30 or 40 years (Fig. 5). Our estimates of the temporal representativeness of the use of tree ring-based plots are comparable to those observed in other monospecific pine forests (Klesse et al., 2016), but lower than diverse and more complex temperate mixed forests subject to natural disturbances (Dye et al., 2016).

Unaccounted mortality is one of the largest sources of uncertainty of total biomass estimates using dendroecological approaches (Alexander et al., 2018; Foster et al., 2014; Gea-Izquierdo and Sánchez-González, 2022). Thinning interventions or extreme mortality events several decades before dendroecological sampling can reduce the ability of tree rings to capture changes in AGB or ANPP (Alexander et al., 2018; Babst et al., 2014a). Among our study plots, those which experienced lower changes in stem density or AGB losses (Fig. 2), such as those of *P. halepensis* or *P. nigra* (Fig. 2), showed better agreements than those where stem density was more strongly reduced during the period analyzed such as *P. sylvestris* plots (Fig. 2 and Figure S4). Larger changes in basal area in the two or three decades before dendroecological sampling (i.e. inventory-to-sampling intervals $\leq$30 years) in our managed forests resulted in larger differences between estimations of AGB or AGBi probably as a result of increased fading record bias. This may partly explain the larger differences observed in our study compared to previous studies of forests subject to natural disturbances (Dye et al., 2016) where stand level AGB and AGB may remain more stable and more similar for longer periods of time. Selecting sites without signs of recent disturbances or management may significantly reduce the mismatch between estimate using both approaches (Graumlich et al., 1989). Even in the absence of visible signs of recent tree mortality, carefully assessing potential disturbance from tree rings during the period of interest may be advisable for analyzing AGB dynamics. AGB and AGBi from sites where tree-ring series show large, abrupt growth increases that may indicate growth releases of surviving trees after mortality events (natural or human-induced) (Lorimer, 1985) may induce larger biases and not reliably represent past forest productivity.

4.4. Reliability in dendroecological biomass estimates improves with decreasing forest productivity

Disagreements between biomass increments using the two different methodologies were larger for the most productive sites and the least drought-tolerant species (Fig. 6) as previously reported for forests under natural disturbance regimes (Dye et al., 2016). The larger underestimations by dendroecological plots compared to permanent plots were observed at productive sites or during periods of faster growth (Fig. 6). ANPP of productive sites may be harder to capture in dendroecological plots than in permanent plots because management interventions, such as thinning, may increase individual tree growth at productive sites more than at less productive sites, but also reduce stand-level biomass more (Del Río et al., 2017; Pretzsch, 2020) particularly if larger trees are harvested. Because forest management aims to increase stand growth and concentrate it on fewer, larger trees by removing small, slow growing or less healthy trees and because large trees represent a disproportionate share of biomass and growth compared to their number (Lutz et al., 2018; Stephenson et al., 2014), the loss of any of these larger trees in managed forests may have large consequences in terms of biomass and biomass accumulation. Such loss of biomass may not be accurately captured by tree rings several decades afterwards or may do so with certain delays (Figure S7), increasing the fading record bias if the trees were lost in the recent decades. Additionally, interventions in managed forests such as thinning and harvesting may be more frequent and more intense in more productive sites. Thus, the structure and biomass at the less productive sites may remain more stable over time reducing the differences between both approaches to estimate AGB and AGBi. They are also more frequent than natural disturbances and introduce non-natural changes in structure. These changes further complicate the estimations of AGB and AGBi in permanent plots when these interventions occur within long remeasurement periods or soon after one of the remeasurement events (Clark et al., 2001). In unmanaged sites, tree-ring based biomass and productivity estimations may also be more accurate at low productivity sites because they may experience lower mortality, either natural or by management (Bigler and Veblen, 2009). Thus, in unmanaged forests, where disturbance history is mostly endogenous and gradual, estimates of AGB and AGBi from both dendroecological and inventory plots may better reflect true biomass changes and for longer periods of time.

5. Conclusions

Our study showed that dendroecological approaches can accurately reproduce patterns in absolute aboveground biomass (AGB) and variability patterns of aboveground biomass increments (AGBi) over periods of up to three decades in managed forests, particularly in the absence of major disturbances. Thus, our results support the use of dendroecologically derived AGB and AGBi to capture interannual and decadal dynamics of forest productivity even in stands where management interventions may potentially bias long-term reconstructions. Our results suggest potential biases that may arise when using dendroecological estimates, including an overall underestimation of biomass growth. However, we show that these biases are lower in slow growing, single-species forests with low productivity, particularly in stands not affected by recent disturbances or management operations at least for 20–30 years prior to sampling. Even in the absence of external signs of recent tree mortality, caution should be practiced when analyzing AGB dynamics for sites where tree ring series show large, sudden growth increases suggesting growth releases of surviving trees after some natural or human-induced mortality event. Integrating permanent inventory plots with tree-ring data improves our ability to monitor carbon dynamics in forests by combining the annual resolution and climate sensitivity of dendroecological approaches with the robust and long-term information derived from repeated inventories. The use of dendroecological plots may contribute to reduce some of the temporal limitations of permanent research plots and their labor intensity and enable generating more reliable stand-level reconstructions including inter-annual variability in carbon dynamics under climate change. Our study shows potential to enlarge the limited spatial distribution of inventory plots with dendroecological plots to assess biomass dynamics in forests.

CRediT authorship contribution statement

Dario Martin-Benito: Writing – original draft, Visualization,

Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Guillermo Gea-Izquierdo:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123652.

Data availability

Data will be made available on request.

References

Alexander, M.R., Rollinson, C.R., Babst, F., Trouet, V., Moore, D.J.P., 2018. Relative influences of multiple sources of uncertainty on cumulative and incremental tree-ring-derived aboveground biomass estimates. Trees 32, 265–276. https://doi.org/10.1007/s00468-017-1629-0.

Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I.A., Nikinmaa, E., Ibrom, A., Wu, J., Bernhofer, C., Kostner, B., Grunwald, T., Seufert, G., Ciais, P., Frank, D., 2014a. Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. N. Phytol. 201, 1289–1303. https://doi.org/10.1111/nph.12589.

Babst, Flurin, Bouriaud, O., Alexander, R., Trouet, V., Frank, D., 2014b. Toward consistent measurements of carbon accumulation: A multi-site assessment of biomass and basal area increment across Europe. Dendrochronologia 32, 153–161. https://doi.org/10.1016/j.dendro.2014.01.002.

Bakker, J.D., 2005. A new, proportional method for reconstructing historical tree diameters. Can. J. For. Res. 35, 2515–2520. https://doi.org/10.1139/x05-136.

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130–1138. https://doi.org/10.1111/j.1600-0706.2009.17592.x.

Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol. Appl. 9, 216–227.

Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Glob. Change Biol. 12, 862–882.

Bowman, D.M.J.S., Brienen, R.J.W., Gloor, E., Phillips, O.L., Prior, L.D., 2013. Detecting trends in tree growth: not so simple. Trends Plant Sci. 18, 11–17.

Brienen, R.J., Gloor, M., Ziv, G., 2017. Tree demography dominates long-term growth trends inferred from tree rings. Glob. Change Biol. 23, 474–484. https://doi.org/10.1111/gcb.13410.

Brienen, R.J.W., Zuidema, P.A., Martínez-Ramos, M., 2010. Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions. Oecologia 163, 485–496. https://doi.org/10.1007/s00442-009-1540-5.

Brienen, R.J.W., Gloor, E., Zuidema, P.A., 2012. Detecting evidence for CO fertilization from tree ring studies: The potential role of sampling biases. Glob. Biogeochem. Cycles 26, GB1025. https://doi.org/10.1029/2011gb004143.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: Concepts and field methods. Ecol. Appl. 11, 356–370. https://doi.org/10.1890/1051-0761(2001)011%255B0356:MNPPIF%255D2.0.CO;2.

Cook, E.R., Kairiukstis, L.A., 1990. Methods of dendrochronology. Kluwer, Dordrecht, The Netherlands.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. J. Geophys. Res. Atmospheres 123, 9391–9409. https://doi.org/10.1029/2017jd028200.

Curtis, R.O., Marshall, D.D., 2005. Permanent-plot procedures for silvicultural and yield research. No. PNW-GTR-634). U.S. Department of Agriculture, Forest Service. Pacific Northwest Research Station, Portland, OR. https://doi.org/10.2737/PNW-GTR-634.

D`Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol. Appl. 23, 1735–1742. https://doi.org/10.1890/13-0677.1.

Davis, S.C., Hessl, A.E., Scott, C.J., Adams, M.B., Thomas, R.B., 2009. Forest carbon sequestration changes in response to timber harvest. For. Ecol. Manag 258, 2101–2109. https://doi.org/10.1016/j.foreco.2009.08.009.

Del Rio, M., González, D., Calama, R., Cañellas, I., Guijarro, M., Sixto, H., Oliveira, N., Aldea, J., Bachiller, Á., Carrillo, C., De La Cruz, A.C., González, D., De La Iglesia, J.P., Fuertes, A., Hernando, C., López-Senespleda, E., Madrigal, G., Madrigal, J., Martín-Benito, D., Montes, F., Moreno-Fernández, D., Rodríguez-Alonso, J., Ruiz-Peinado, R., Viscasillas, E., Pardos, M., 2025. La Red de Parcelas Permanentes del ICIFOR-INIA: información para una gestión forestal sostenible ante el cambio global. Cuad. Soc. Esp. Cienc. For. 50, 111–138. https://doi.org/10.31167/csef.v0i50.19961.

Del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017. A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. For. Syst. 26, eR03S. https://doi.org/10.5424/fs/2017262-11325.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C., Wisniewski, J., 1994. Carbon Pools and Flux of Global Forest Ecosystems. Science 263, 185–190. https://doi.org/10.1126/science.263.5144.185.

Dye, A., Barker Plotkin, A., Bishop, D., Pederson, N., Poulter, B., Hessl, A., 2016. Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern US forests. Ecosphere 7, e01454.

Foster, J., D`Amato, A., Bradford, J., 2014. Looking for age-related growth decline in natural forests: unexpected biomass patterns from tree rings and simulated mortality. Oecologia 175, 363–374. https://doi.org/10.1007/s00442-014-2881-2.

Foster, J.R., Finley, A.O., D`Amato, A.W., Bradford, J.B., Banerjee, S., 2016. Predicting tree biomass growth in the temperate–boreal ecotone: Is tree size, age, competition, or climate response most important? Glob. Change Biol. 22, 2138–2151. https://doi.org/10.1111/gcb.13208.

Fritts, H.C., 1976. Tree rings and climate. Academic Press, New York.

Gea-Izquierdo, G., Sánchez-González, M., 2022. Forest disturbances and climate constrain carbon allocation dynamics in trees. Glob. Change Biol. 28, 4342–4358. https://doi.org/10.1111/gcb.16172.

Graumlich, L.J., Brubaker, L.B., Grier, C.C., 1989. Long-Term Trends in Forest Net Primary Productivity: Cascade Mountains, Washington. Ecology 70, 405–410. https://doi.org/10.2307/1937545.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. TreeRing Bull. 43, 69–78.

Houghton, R.A., 2005. Aboveground Forest Biomass and the Global Carbon Balance. Glob. Change Biol. 11, 945–958. https://doi.org/10.1111/j.1365-2486.2005.00955.x.

Houghton, R.A., Hall, F., Goetz, S.J., 2009. Importance of biomass in the global carbon cycle. J. Geophys. Res. 114. https://doi.org/10.1029/2009jg000935.

Kassambara, A., 2023. rstatix: Pipe-friendly framework for basic statistical tests. R package version 0.7.2.

Kleinn, C., Vilčko, F., 2006. A new empirical approach for estimation in k-tree sampling. For. Ecol. Manag 237, 522–533. https://doi.org/10.1016/j.foreco.2006.09.072.

Klesse, S., Bigler, C., 2025. Growth trends in basal area increments: The underlying problem, consequences for research and best practices. Dendrochronologia 90, 126296. https://doi.org/10.1016/j.dendro.2025.126296.

Klesse, S., Etzold, S., Frank, D., 2016. Integrating tree-ring and inventory-based measurements of aboveground biomass growth: research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. Eur. J. For. Res. 135, 297–311. https://doi.org/10.1007/s10342-015-0936-5.

Lorimer, C.G., 1985. Methodological considerations in the analysis of forest disturbance history. Can. J. For. Res. 15, 200–213. https://doi.org/10.1139/x85-038.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.-W., Chao, K.-J., Chao, W.-C., Chiang, J.-M., Chu, C., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau, B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.-F., Hu, Y.-H., Hubbell, S.P., Inman-Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson, A.J., Li, Y., Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.-R., Malhi, Y., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny, V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips, R.P., Reynolds, G., Sack, L., Song, G.-Z.M., Su, S.-H., Sukumar, R., Sun, I.F., Suresh, H.S., Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R., Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.-H., Xu, H., Yamakura, T., Yap, S., Zimmerman, J.K., 2018. Global importance of large-diameter trees. Glob. Ecol. Biogeogr. 27, 849–864. https://doi.org/10.1111/geb.12747.

Martin-Benito, D., Gea-Izquierdo, G., Río, M. del, Cañellas, I., 2008. Long-term trends in dominant-height growth of black pine using dynamic models. For. Ecol. Manag 256, 1230–1238.

Martin-Benito, D., Pederson, N., Férriz, M., Gea-Izquierdo, G., 2021. Old forests and old carbon: A case study on the stand dynamics and longevity of aboveground carbon. Sci. Total Environ. 765, 142737. https://doi.org/10.1016/j.scitotenv.2020.142737.

Martin-Benito, D., Molina-Valero, J.A., Pérez-Cruzado, C., Bigler, C., Bugmann, H., 2022. Development and long-term dynamics of old-growth beech-fir forests in the Pyrenees: Evidence from dendroecology and dynamic vegetation modelling. For. Ecol. Manag 524, 120541. https://doi.org/10.1016/j.foreco.2022.120541.

McKenzie, S.M., Pisaric, M.F., Arain, M.A., 2021. Comparison of tree-ring growth and eddy covariance-based ecosystem productivities in three different-aged pine plantation forests. Trees 35, 583–595.

Montero, G., Ruiz-Peinado, R., Munoz, M., 2005. Producción de biomasa y fijación de CO_2 por los bosques españoles. INIA-Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria.

Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M., Frank, D., 2014. The influence of sampling design on tree-ring-based quantification of forest growth. Glob. Change Biol. 20, 2867–2885.

Ohtsuka, T., Saigusa, N., Koizumi, H., 2009. On linking multiyear biometric measurements of tree growth with eddy covariance-based net ecosystem production. Glob. Change Biol. 15, 1015–1024. https://doi.org/10.1111/j.1365-2486.2008.01800.x.

Ouimette, A.P., Ollinger, S.V., Richardson, A.D., Hollinger, D.Y., Keenan, T.F., Lepine, L. C., Vadeboncoeur, M.A., 2018. Carbon fluxes and interannual drivers in a temperate forest ecosystem assessed through comparison of top-down and bottom-up approaches. Agric. For. Meteorol. 256–257, 420–430. https://doi.org/10.1016/j.agrformet.2018.03.017.

Pérez-Luque, A.J., Martin-Benito, D., Zamora, R., Gea-Izquierdo, G., 2026. Optimal carbon partitioning drives sink potential dynamics in large-scale pine reforestation under climate change. J. Appl. Ecol. 63, e70244. https://doi.org/10.1111/1365-2664.70244.

Pretzsch, H., 2020. Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning. For. Ecol. Manag. 460, 117879. https://doi.org/10.1016/j.foreco.2020.117879.

Qin, L., Meng, S., Zhou, G., Liu, Q., Xu, Z., 2021. Uncertainties in above ground tree biomass estimation. J. For. Res. 32, 1989–2000. https://doi.org/10.1007/s11676-020-01243-2.

Rocha, A.V., Goulden, M.L., Dunn, A.L., Wofsy, S.C., 2006. On linking interannual tree ring variability with observations of whole-forest CO_2flux. Glob. Change Biol. 12, 1378–1389. https://doi.org/10.1111/j.1365-2486.2006.01179.x.

Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M., Hashimoto, H., 2004. A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production. Bioscience 54, 547–560. https://doi.org/10.1641/0006-3568(2004)054%255B0547:acsmog%255D2.0.co;2.

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied Historical Ecology: Using the Past to Manage for the Future. Ecol. Appl. 9, 1189–1206. https://doi.org/10.1890/1051-0761(1999)009%255B1189:AHEUTP%255D2.0.CO;2.

Teets, A., Fraver, S., Weiskittel, A.R., Hollinger, D.Y., 2018. Quantifying climate–growth relationships at the stand level in a mature mixed-species conifer forest. Glob. Change Biol. 24, 3587–3602. https://doi.org/10.1111/gcb.14120.

Teets, A., Moore, D.J.P., Alexander, M.R., Blanken, P.D., Bohrer, G., Burns, S.P., Carbone, M.S., Ducey, M.J., Fraver, S., Gough, C.M., Hollinger, D.Y., Koch, G., Kolb, T., Munger, J.W., Novick, K.A., Ollinger, S.V., Ouimette, A.P., Pederson, N., Ricciuto, D.M., Seyednasrollah, B., Vogel, C.S., Richardson, A.D., 2022. Coupling of Tree Growth and Photosynthetic Carbon Uptake Across Six North American Forests. JGR Biogeosciences 127, e2021JG006690. https://doi.org/10.1029/2021JG006690.

Xu, K., Wang, X., Liang, P., Wu, Y., An, H., Sun, H., Wu, P., Wu, X., Li, Q., Guo, X., Wen, X., Han, W., Liu, C., Fan, D., 2019. A new tree-ring sampling method to estimate forest productivity and its temporal variation accurately in natural forests. For. Ecol. Manag. 433, 217–227. https://doi.org/10.1016/j.foreco.2018.10.066.