

Detecting trends in tree growth: not so simple

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Tree biomass influences biogeochemical cycles, climate, and biodiversity across local to global scales. Understanding the environmental control of tree biomass demands consideration of the drivers of individual tree growth over their lifespan. This can be achieved by studies of tree growth in permanent sample plots (prospective studies) and tree ring analyses (retrospective studies). However, identification of growth trends and attribution of their drivers demands statistical control of the axiomatic co-variation of tree size and age, and avoiding sampling biases at the stand, forest, and regional scales. Tracking and predicting the effects of environmental change on tree biomass requires well-designed studies that address the issues that we have reviewed.

Detecting trends in tree growth

Worldwide, forests represent half of the biospheric carbon sink. It is estimated that forest biomass is gaining > 2 Pg C (carbon) each year [1] due to increased growth of individual trees and greater abundance of trees. For instance, repeated measurements of permanent plots show a trend of increased biomass and growth in tropical [2–5] and temperate [6–8] forests, and remote sensing reveals rainforest expansion into savannas [9,10]. There is no consensus as to the ultimate cause of these changes [11–13]. Although snapshot inventory assessments and remote sensing can provide invaluable data of tree biomass, these techniques cannot provide insights into the growth of individual trees. Tree growth data are crucial to understand the mechanism underlying changes in tree biomass, and such data are difficult to acquire given the longevity and great size of trees. Here we review how tree growth is measured, and discuss the pitfalls and challenges in determining growth trends.

Patterns of tree growth

Tree growth can be defined as the increase in dimensions of an individual tree through time [14]. The most commonly measured dimensions are height and diameter, because these are convenient measures that are strongly correlated with wood volume and biomass. Stem basal area (the cross-sectional area of stems sometimes expressed per unit ground surface area) can be calculated from diameter, and is also useful in ecological and physiological studies. The rate of change of a dimension per unit

time, or ‘growth increment’ can be expressed in either absolute or relative terms. Relative growth rate (RGR, the change in a dimension per sampling interval relative to initial size) is commonly used in studies of short-lived plants, but is less useful for tree growth because there is an initial very rapid decline in RGRs with increasing tree size due to accumulation of non-photosynthetic material such as stems, branches, and roots (e.g., [15]).

The patterns of growth over the life span of a tree vary according to which dimension is measured (Figure 1). While patterns of growth vary according to tree species and growing conditions [16], in general height increases rapidly when a tree is young, but tends to level off when a tree attains maturity and height increment may approach zero. Stem diameter increases comparatively steadily over a tree’s lifespan [14,16,17]. By contrast, stem basal area increment and volume increment are initially small but increase until the tree becomes senescent (Figure 1; [18]). It is difficult to separate the effects of stem size and age on growth, because both increase together under natural conditions. **Experimental grafting of shoots from donor trees indicated that the age of the donor does not affect shoot growth rates, but that the size of the recipient does [15,19] suggesting that growth is most strongly influenced by tree size.** Growing conditions can affect tree growth patterns (Figure 1d), which is why foresters include site quality in their models of tree growth [14].

Tree diameter increment is a widely used proxy for whole tree growth, and is inherently self-scaling – while large trees produce more biomass than small trees, a specific diameter increment represents more absolute biomass in a large tree than in a small tree [20] (Figure 1b). In smaller trees the diameter increment varies less than basal area, biomass, and volume increment, which all increase markedly with size; the opposite tends to be true in larger trees (Figure 1c).

Approaches to measuring growth of individual trees

There are two main approaches to measuring growth of individual trees: repeated measurement of marked trees in permanent sample plots (PSPs), and measuring the width of annual rings in cores or discs taken from tree stems.

Permanent sample plots

Growth estimates from PSPs in theory require nothing more sophisticated than a tape measure and the ability to relocate and accurately remeasure a tree trunk. In practice

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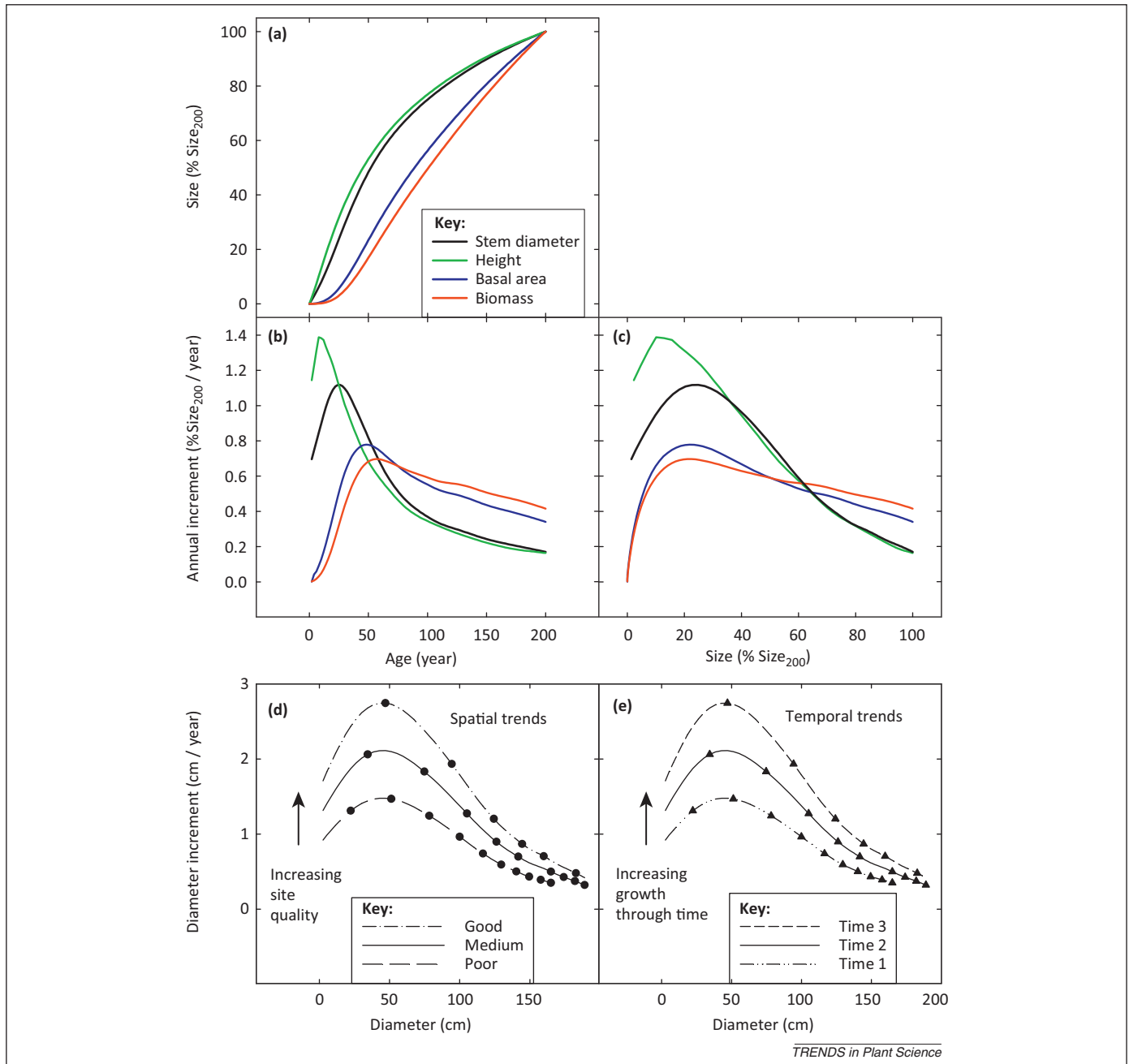


Figure 1. Measurements of tree size. There are various measures of tree size (a), and corresponding measures of growth, each displaying a subtly different pattern with age (b) and with size (c). Measurements have all been scaled to Size₂₀₀, the size at age 200 years, and are based on growth curves for *Pseudotsuga menziesii* var. *menziesii* [14] and an allometric equation relating aboveground biomass and diameter [50]. Height and diameter increment generally peak early in the life of a tree, whereas basal area and biomass increment peak later, and are small when the tree is young. The effect of site quality on the relationship between diameter growth and diameter is shown in (d). The symbols indicate 20-year intervals. Fast-growing trees achieve peak growth rates and generally die earlier than slow-growing trees. (e) It may be possible to detect consistent environmental change such as a CO₂ fertilization effect through an apparent increase in site quality with growth year, as in this hypothetical example showing diameter growth vs diameter increasing between Time 1 and Time 3. (Time refers to year of growth, and symbols indicate 20-year intervals). This assumes all other factors affecting growth are constant. Note that environmental changes such as increased CO₂ may induce reproductive maturation when trees have a smaller diameter, as well as at a younger age [51], and this may shift the growth-size relationship.

PSPs are very time-consuming to establish and logistically demanding because they are often located in remote species-rich forests, far from potential confounding anthropogenic disturbances. An advantage of PSPs for measuring tree growth is that the interval during which growth was measured is known precisely, providing growth rates from the time they are established (i.e., prospective growth measurements). Unlike dendrochronological approaches,

growth rates can be measured on trees that do not reliably form annual rings.

To representatively sample the range of sizes and species present, measurement of all trees above a minimum threshold (commonly 10 cm DBH, diameter at breast height, ~ 130 cm height) is required. This is because diameter increment tends to peak in the early- to mid-life of a tree, then gradually decline with size and age

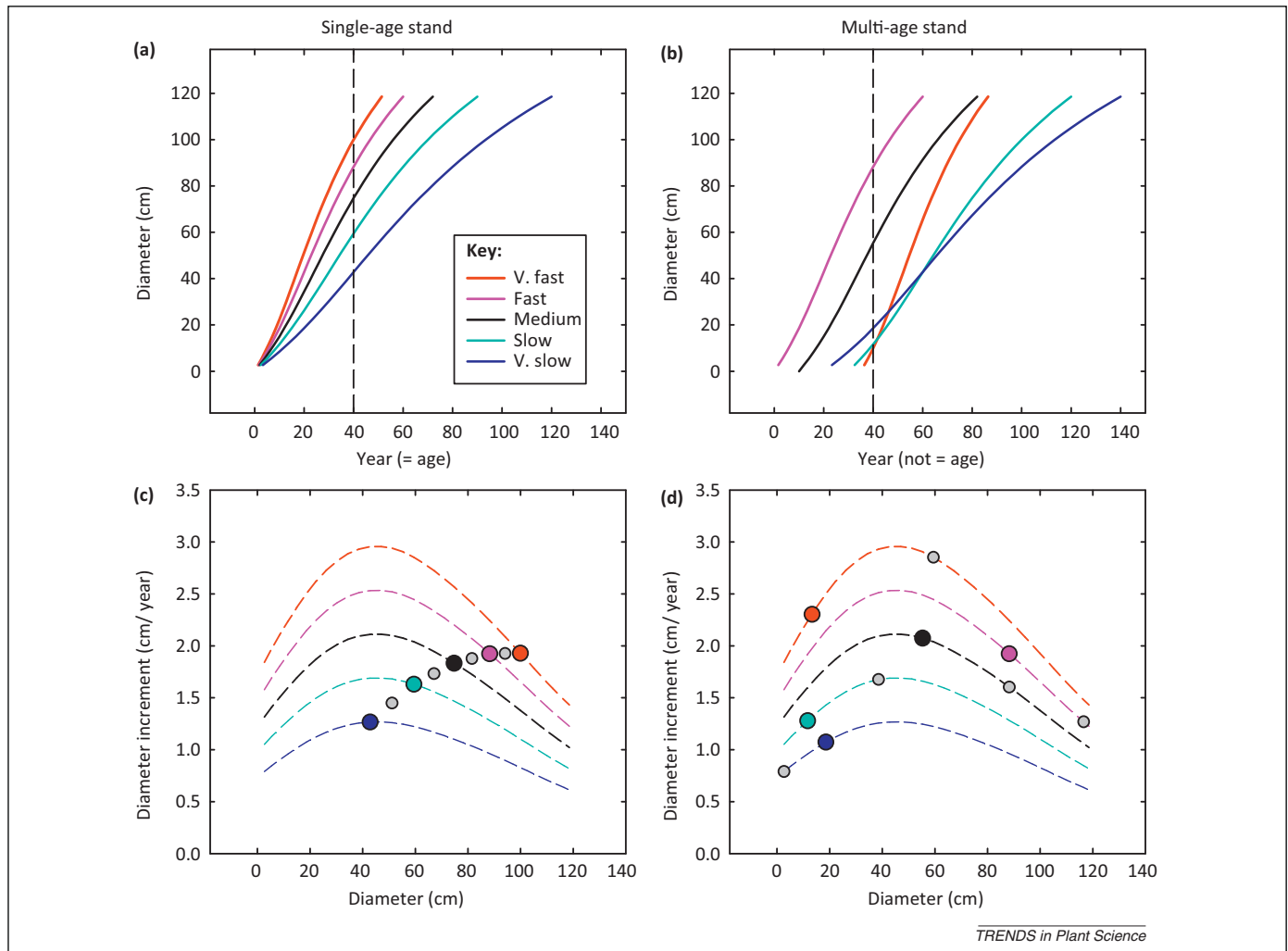


Figure 2. Idealized tree growth patterns in single-age stands, and in multi-age stands in which the same trees establish at different times (in a random order). The colored lines and corresponding symbols represent individual trees with growth rates varying from very slow (dark blue) to very fast (red). (a) The increase in stem diameter with time is shown for single-age, and (b) multi-age stands. The vertical dashed lines represent time of sampling (Year 40). Corresponding diameter increment vs diameter relationships are shown for (c) single-age and (d) multi-age stands. The broken lines represent diameter increment-diameter trajectories, and the colored circles, the relationship at the time of sampling in Year 40. The small gray circles represent additional trees, omitted from (a) and (c) for clarity.

[14,16,21] (Figure 2). As a consequence, in longitudinal studies of tree growth, average diameter increment of tagged trees will tend to decline unless new and therefore faster-growing trees are frequently added to the sampled population. Estimates of temporal growth trends will be biased if measurements are made only on the original tagged trees, so studies based on ageing cohorts of trees may mask long-term forest growth increases, or accentuate decreases, due to environmental drivers. Growth rates may also change systematically following disturbance, such as severe fires, insect outbreaks, and storms, after which growth of surviving trees may initially surge, but gradually slow as inter-tree competition for light, water, and nutrients increases [22]. In managed, single-age forests, canopy architecture changes and carbon allocation to stemwood declines following canopy closure, leading to reduced diameter growth [23]. To reliably assess growth trends in a region, many geographically representative stands need to be sampled over long time periods, weighted according to their successional stage (Box 1), or stand age, in the case of managed forests. Sampling over time intervals that are too short could miss rare catastrophic events,

and thus lead to positively biased estimates of biomass trends [12]. To be sufficiently representative of variation in tree growth across a region, PSPs also need to encompass the effect of site quality on tree growth and genetic differences within species [17,19]. A benefit of such broad-scale growth measurements is obtaining tree recruitment and mortality rates, which can be incorporated into demographic studies [24] and estimates of forest carbon fluxes [25].

Dendrochronology

The measurement and analysis of tree rings hinges on pattern matching of ring widths from cores taken from a population of trees, known as 'cross-dating' [26]. This approach relies on recognition of synchronized growth responses among trees, and consequently dendrochronologists have focused on specific environments and landscape settings where trees produce annual growth rings [27]. While techniques are being developed to apply dendrochronology to regions where growth is not reliably annual [28] or growth ring boundaries are not distinguishable [29–31], many of these methods are still experimental

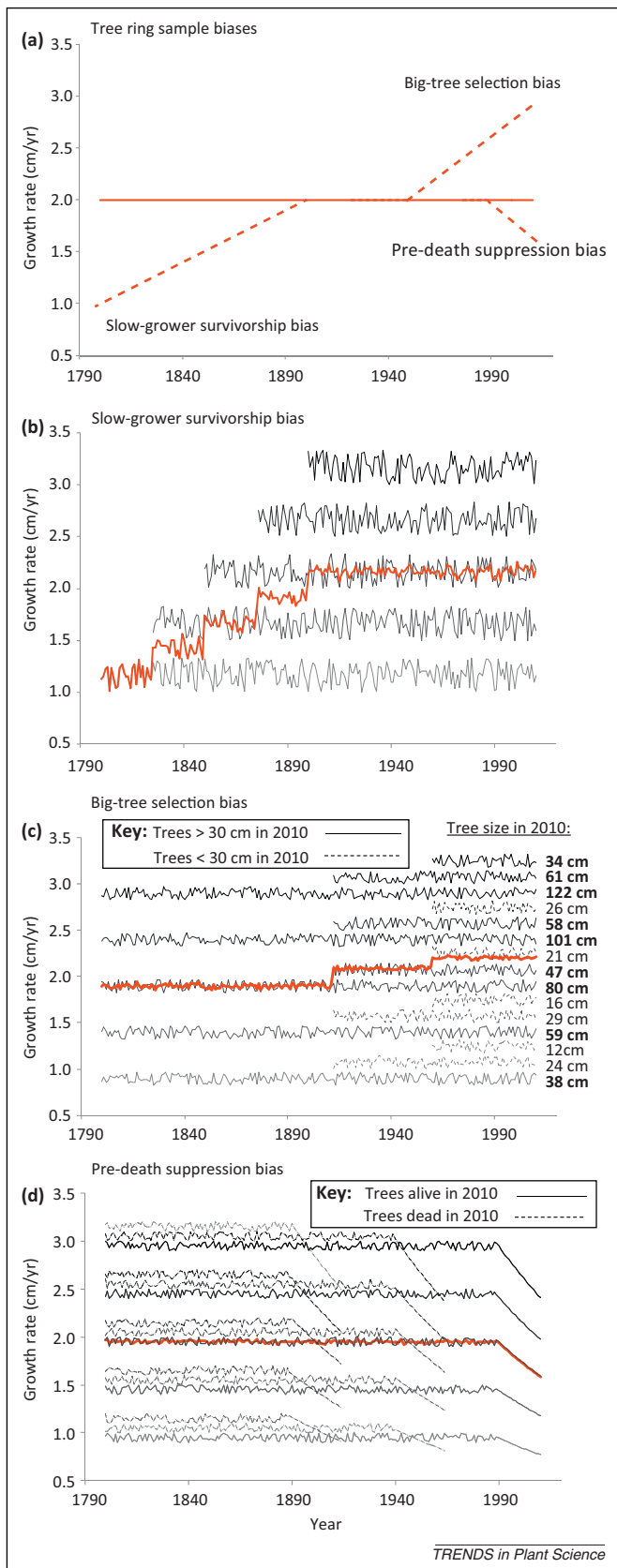


Figure 3. Tree ring studies. Hypothetical examples to illustrate three biases that may occur in tree ring studies, leading to artificial increases or decreases in growth rates towards the present (a). In panels (b) and (c), we assume that growth rates of individual trees (black lines) remain stable over time, with only minor stochastic variation, and that there are persistent differences between individual trees. Average width of sampled rings in each scenario is indicated by the red line. (b) The 'slow-grower survivorship bias' leads to lower reconstructed growth rates in the distant past, because slow-growing trees tend to live longer than

[29] and currently dendrochronology can be confidently applied to fewer regions than can PSPs. Dendrochronology also requires more equipment (such as dedicated microscopes and software), training and expertise than some permanent plot measurements. The great advantage of dendrochronology is that a single field sampling program can yield annual growth data dating back almost to the time a tree established (i.e., retrospective growth measurements). However, as outlined below, there are several sampling biases inherent to dendrochronology, which can lead to misleading estimates of growth trends within a stand (Figure 3): (i) The 'slow-grower survivor bias' [11], also termed the 'modern sample bias' [32] arises from sampling only those individuals in a population that are alive at the time of tree ring sampling, because there are persistent growth differences between individual trees [33–35], and slow-growing trees generally tend to live longer than fast-growing trees [36]. As a result, when cores are taken from a population of live trees, the oldest rings will be from the slowest-growing trees, because the faster-growing cohorts would not, on average, have survived long enough to be sampled. This bias strengthens the further back in time one goes. (ii) The 'big tree selection bias' [11] arises if dendrochronologists target the largest trees present in a population, so that only the fastest-growing of the recent recruits within a population will be large enough to be sampled. Slow-growing recent recruits will be too small, but slow-growing, older trees will be included in the sample, resulting in strong 'apparent' increases in growth over recent time periods [11]. (iii) The 'pre-death suppression bias' operates in the opposite direction and arises from a gradual loss of recent slow growth periods from the tree ring sample if only living trees are sampled. Due to the marked slowing in tree growth rates in the several years [37] to several decades [38] prior to tree death, widths of recent growth rings, which include those from individuals that are dying (but currently still alive) and have lower growth rates, may be smaller than those from the more distant past [11]. Such an effect has been observed in studies of both temperate and tropical trees, leading to recent, apparent growth decreases [33,39,40].

Collectively these sampling biases can result in misleading inferences about the effect of environmental changes. However, they can be minimized by well-designed studies that control for age, size, and tree competition.

Analysis of tree diameter growth trends

Analysis and interpretation of the tree diameter measurements from both PSPs and dendrochronology is

faster-growing ones (the longer lines at the bottom of the panel represent slow-growing trees). As a result, the oldest rings represented in sampled cores will be from slow-growing trees because the fast-growing trees of these old cohorts will have already died before samples were taken. (c) The 'big tree selection bias' occurs if dendrochronologists target the largest trees (here, > 30 cm diameter) in a population. Thus, fast-growing trees > 30 cm stem diameter were included in the sample, while smaller, slower growing trees from the same cohort (indicated by broken lines) were smaller than the sampling threshold and excluded, resulting in apparent recent increases in growth. (d) The 'pre-death suppression bias' arises because trees growth rates commonly decline prior to death. As a result of including suppressed trees with recently decreasing growth rates, there will be a negative bias in growth rates towards the present, while growth rates during earlier times are not affected because trees that died in the past (broken lines) were excluded by sampling only living trees.

Box 1. Designing and establishing permanent sampling plot networks

PSP networks provide a framework for understanding tree growth trends locally, regionally and globally. They also support additional studies such as intensive monitoring of carbon processes to construct the full carbon cycle and its short-term climate sensitivity, and assessing the carbon and biodiversity impacts of carbon sequestration schemes (e.g., REDD+) and evaluating forest management interventions against a robust baseline.

There are obvious trade-offs between replication, location, plot size, and cost of permanent plot networks. We favor a geographically widespread network of 0.5- to 1-ha plots in clusters of about ten. The geographic location of PSP clusters should be arranged across macro-ecological gradients and effort weighted by intensity of the carbon cycle (Gross Primary Productivity, Net Primary Productivity) and carbon storage. New plots should complement existing plots to reduce current biases toward the most highly accessible sites and so fill spatial gaps. Examples of such networks are RAINFOR [52] and, with a greater focus on biodiversity, CTFS [53], and TEAM [54]. Global networks of hundreds, perhaps thousands, of PSPs are required to monitor the effects of environmental change on all forest biomes.

Standardized protocols are required to ensure consistent measuring and recording of data. Core data should include (i) the identity, diameter, and other attributes of all trees ≥ 10 cm DBH; (ii) seedling establishment, growth, and mortality, charted using smaller sub-plots; and (iii) specific leaf area, leaf, and soil nutrients, and soil physical properties, measured using standardized sampling and analysis procedures, to provide ecological context for the plots. Trees should be permanently tagged, and the point of measurement needs to be chosen to avoid deformities, and marked. Trees should be remeasured on a 3–5 yearly cycle, with capacity for more frequent censuses if events require, such as following extreme droughts and fires. It is critical to ensure that plots are protected from habitat destruction.

Secure and accessible long-term data storage is critical to allow researchers worldwide to manage, analyze, check, and compare their data with those from other sites. Original field measurements must always be retained to provide an audit trail from the field notes through to analyses. There must be adequate support for training and the critical post field-work activities that precede any analysis: specimen drying, herbarium storage, identification, tree measurement data quality control procedures, data entry, and communication.

surprisingly complex, requiring statistical control for the intrinsic changes in tree diameter growth rates that occur as trees grow and age (Figure 2) and varying stand structures. Among trees of a single species growing in a common environment, tree diameter growth is typically positively related to stem diameter, but will decrease with age after peak growth has been attained [41–43] (Figure 2c). However, relationships between growth rate and size may appear to differ between single-age and multi-age stands, even when growth patterns of individual trees are identical (Figure 2c and 2d). Assuming individual trees follow similar growth trajectories but grow at different rates, and that slow-growing trees remain slow-growing [35], in a young, single-age stand there will be a clear positive relationship between diameter and diameter increment [42]; slow-growing trees are small and fast-growing trees are large (Figure 2c). However, this relationship is obscured in a multi-age stand, where slow-growing, large old trees coexist with fast-growing, small young ones because of different establishment dates (Figure 2d). Multi-age forests therefore present an additional layer of complexity in the sampling of tree growth.

Dendrochronologists typically control for developmental growth trends in individual trees by using regional curve standardization (RCS) [32]. Briefly, this analytical technique involves developing an average ring width-tree age relationship for a particular tree species in a specified region, and then scaling the widths of individual tree rings by the average ring width for that ring age, to remove the tree age trend in diameter growth [32]. A variant of this method can be used to remove the tree size trend in diameter growth [44]. Alternatively, statistical analyses can reveal the relationships between tree size, growth rate, and age. As discussed above, this can be achieved through sampling the full spectrum of tree ages and stem sizes in multi-age stands, or in the case of single-age stands, sampling a wide range of stands differing in establishment dates [45,46].

Drivers of growth trends are difficult to statistically quantify because they are confounded with covarying effects of anthropogenic environmental changes such as altered insolation, increased temperature, changes to precipitation patterns, nitrogen deposition, and CO₂ increases [47], which are closely correlated with calendar year. Likewise, calendar year is correlated with endogenous developmental (size- and age-related) changes in individual trees, which can further influence stand dynamics and inter-tree competition. Such close inter-correlations make it difficult to separate the effects of global and regional environmental change from tree age and size effects and local competitive trends, even in theory. Indeed, in the case of a single-age stand, tree age and calendar year are perfectly correlated and therefore inseparable. To break the nexus between tree age and calendar year requires many trees encompassing a wide range of establishment dates and sizes that are growing in similar environments, and where the date of the growth increment is known: either multi-age stands or many single-age stands where the growth history of individual trees is known. Changing environmental conditions, such as increasing CO₂, that may lead to increased growth rates may then be revealed in increases in the diameter increment vs diameter relationship (Figure 1f). Networks of plantations of single tree species are attractive model systems to investigate the effects of environmental change on tree growth because tree age and silvicultural practices are known. For example, Bontemps and colleagues used growth data derived from dendrochronological analyses of neighboring pairs of ‘young’ and ‘old’ single-age stands of common beech (*Fagus sylvatica*) to separate the effects of site, developmental stage, and calendar year on radial and height growth of dominant trees in two regions in France [44–46,48]. A similar approach is to compare growth rates of succeeding rotations of trees in plantations of the same species, in the same geographic location, and managed in the same way [6,49]. Such an approach would allow control for some of the biases inherent to dendrochronology discussed above.

Concluding remarks

Understanding how tree growth has been, and will be affected, by environmental change demands both retrospective and prospective studies. Thus both dendrochronological approaches and permanent plot studies are pivotal

in this quest. Ideally both approaches can be applied in the same forest systems to provide critical historical contextual information and to cross-validate them. Such joint studies will help resolve the relative importance of the potential biases inherent in both approaches. Nonetheless, dendrochronological studies are more geographically and floristically restricted given the need to sample trees with well-defined annual growth rings. A key objective of future research must be to control for effects of size and age in statistical analyses – this is especially important if sample sizes are small, or if specific size or age cohorts have been sampled, as is often the case in dendrochronological studies. Sampling designed to capture a range of individual sizes, ages, and establishment dates of particular tree species allows for separation of growth trends due to global or regional environmental change (e.g., warming and CO₂) from developmental effects. This is a crucial consideration in environments where stand-replacing disturbance is the norm. An alternative approach is to sample enough trees in enough plots for the size and age structure to be reasonably constant, and avoid introducing biases by changes in the size/age structure. This requirement can be met through extensive networks of PSPs (Box 1). Further, establishing regional clusters of PSPs across environmental gradients will also allow us to statistically analyze the effects of global and regional environmental effects on tree growth. A global system of plots in all major woody biomes is highly desirable because effects of global environmental changes interact with regional climatic trends and multiple other local factors, creating unexpected and complex outcomes.

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