

Adding Tree Rings to North America's National Forest Inventories: An Essential Tool to Guide Drawdown of Atmospheric CO₂

MARGARET E. K. EVANS¹, R. JUSTIN DEROSE², STEFAN KLESSE³, MARTIN P. GIRARDIN⁴, KELLY A. HEILMAN⁵, M. ROSS ALEXANDER⁶, ANDRÉ ARSENAULT⁷, FLURIN BABST⁸, MATHIEU BOUCHARD⁹, SEAN M. P. CAHOON¹⁰, ELIZABETH M. CAMPBELL¹¹, MICHAEL DIETZE¹², LOUIS DUCHESNE¹³, DAVID C. FRANK¹⁴, COURTNEY L. GIEBINK¹⁵, ARMANDO GÓMEZ-GUERRERO¹⁶, GENARO GUTIÉRREZ GARCÍA¹⁷, EDWARD H. HOGG¹⁸, JUHA METSARANTA¹⁹, CLÉMENTINE OLS²⁰, SHELLY A. RAYBACK²¹, ANYA REID²², MARTIN RICKER²³, PAUL G. SCHABERG²⁴, JOHN D. SHAW²⁵, PATRICK F. SULLIVAN²⁶, AND SERGIO ARMANDO VILLELA GAYTÁN²⁷

Tree-ring time series provide long-term, annually resolved information on the growth of trees. When sampled in a systematic context, tree-ring data can be scaled to estimate the forest carbon capture and storage of landscapes, biomes, and—ultimately—the globe. A systematic effort to sample tree rings in national forest inventories would yield unprecedented temporal and spatial resolution of forest carbon dynamics and help resolve key scientific uncertainties, which we highlight in terms of evidence for forest greening (enhanced growth) versus browning (reduced growth, increased mortality). We describe jump-starting a tree-ring collection across the continent of North America, given the commitments of Canada, the United States, and Mexico to visit forest inventory plots, along with existing legacy collections. Failing to do so would be a missed opportunity to help chart an evidence-based path toward meeting national commitments to reduce net greenhouse gas emissions, urgently needed for climate stabilization and repair.

Keywords: carbon accounting, carbon sinks, national forest inventory, negative emissions technologies, tree rings

We are at a crucial point in the Anthropocene: Industrialization and deforestation (FAO 2015) especially, among other factors, have altered and continue to alter the concentration of carbon dioxide (CO₂) in the atmosphere, the Earth's energy balance, and the climate system. These changes have far-reaching consequences for global economies, ecology, and human well-being (Reidmiller et al. 2018). In 2016, 195 nations agreed to limit the warming of global mean surface temperature to 2.0 degrees Celsius (°C) above the preindustrial baseline (www.cop21paris.org); atmospheric CO₂ concentration should not exceed 450 parts per million (ppm) to reach this goal. The current atmospheric CO₂ concentration is already over 415 ppm (Le Quéré et al. 2015), global mean surface temperature has

already increased 1.0 °C, and atmospheric CO₂ is increasing by approximately 2 ppm per year. On this trajectory, there are just a few decades left to achieve a net-zero emissions world, especially if nations fully commit to the target of 1.5 °C of warming (IPCC 2018).

Besides reducing emissions, recent attention has focused on enhancing and managing natural carbon sinks, including a portfolio of negative emissions technologies, in other words, influencing the carbon flux through terrestrial ecosystems to draw CO₂ out of the atmosphere and restore the climate system (National Academies of Sciences 2019). Two of these technologies, afforestation and reforestation plus changes in forest management, are focused on forests, which cover 30% of the Earth's land surface (MacDicken et al. 2016)

BioScience XX: 1–14. © The Author(s) 2021. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com <https://doi.org/10.1093/biosci/biab119>

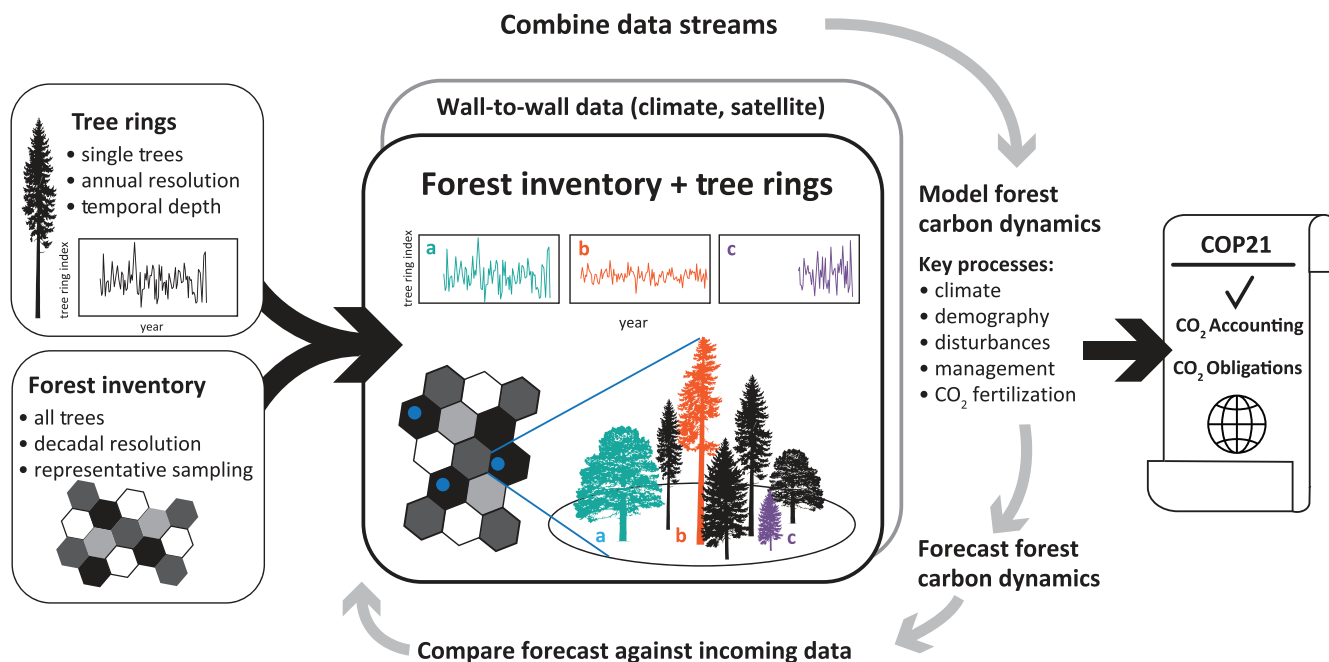


Figure 1. Conceptual model of how the collection of tree rings from NFIs would result in better carbon accounting to meet the obligations for the Conference of the Parties of the climate change convention, by better understanding a number of processes that are currently in question. In an ideal scenario, tree-ring data collected on NFIs would be consistent across regions and countries with a sampling design that was unbiased for all types of research questions and circumstances (e.g., among various stand-level disturbance regimes), across all forest types (tropical to temperate to boreal), for both managed and unmanaged stands, and providing robust information (in other words, quality control and sufficiently replicated data) that could be readily upscaled. The data and metadata associated with plots, trees, and cores should be well managed (in consistent formats with samples archived for new innovative research questions and techniques, including emerging genetic, isotopic and wood anatomy methodologies). In addition, future collections would benefit from a more formal recognition of the various disciplines that use tree-ring data, and the growing array of research and management questions that these data may someday inform (see box 1).

and have already acted as a major carbon sink, mitigating 25 to 35% of anthropogenic carbon emissions between 1959 and 2017 (Pan et al. 2011, Le Quéré et al. 2015). In fact, forests provide one quarter of the total planned greenhouse gas emissions reductions across all countries' commitments, made at the twenty-first session of the Conference of the Parties (COP21, or Paris Climate Accord; Grassi et al. 2017). However, the idea of relying on forest sinks to achieve these goals is set against a backdrop of divergent evidence regarding forest trends (Popkin 2019). Several lines of evidence suggest positive forest trends (and an overall increasing land carbon sink; Zhu et al. 2016), which we refer to collectively as the evidence for forest *greening*, contrasting other evidence for negative forest trends—drought-induced reductions in tree growth (Charney et al. 2016, Babst et al. 2017, Green et al. 2019) and increases in tree mortality—which we refer to as forest *browning*, as summarized in a recent comprehensive review (Allen et al. 2015). Indeed, future carbon sequestration by terrestrial ecosystems, forests in particular, is considered a major source of scientific uncertainty in earth system models (Winkler et al. 2019). Reliable

estimation of future carbon sequestration, which is critical for designing strategies to reach net-zero atmospheric CO₂ accumulation, requires a resolution between the evidence for forest greening versus browning.

We convened a conference of leading researchers on climate and tree rings collected in the context of forest inventory plots. Here we argue that tree-ring sampling in the permanent plots of existing national forest inventory (NFI) programs would greatly enhance the monitoring and forecasting of forest ecosystem carbon sequestration and earth system carbon dynamics (figure 1). The land carbon sink has historically been estimated by finding the difference between emissions, uptake by the world's oceans, and changes in atmospheric concentration—an indirect or inverse form of estimation (Le Quéré et al. 2015). Tree rings, in contrast, provide on-the-ground, direct records of aboveground carbon sequestration by individual trees and at critical temporal scales—annual or subannual resolution over multidecadal to centennial time frames. However, publicly available tree-ring data (the International Tree-Ring Data Bank) were often collected from trees selected for maximal climate

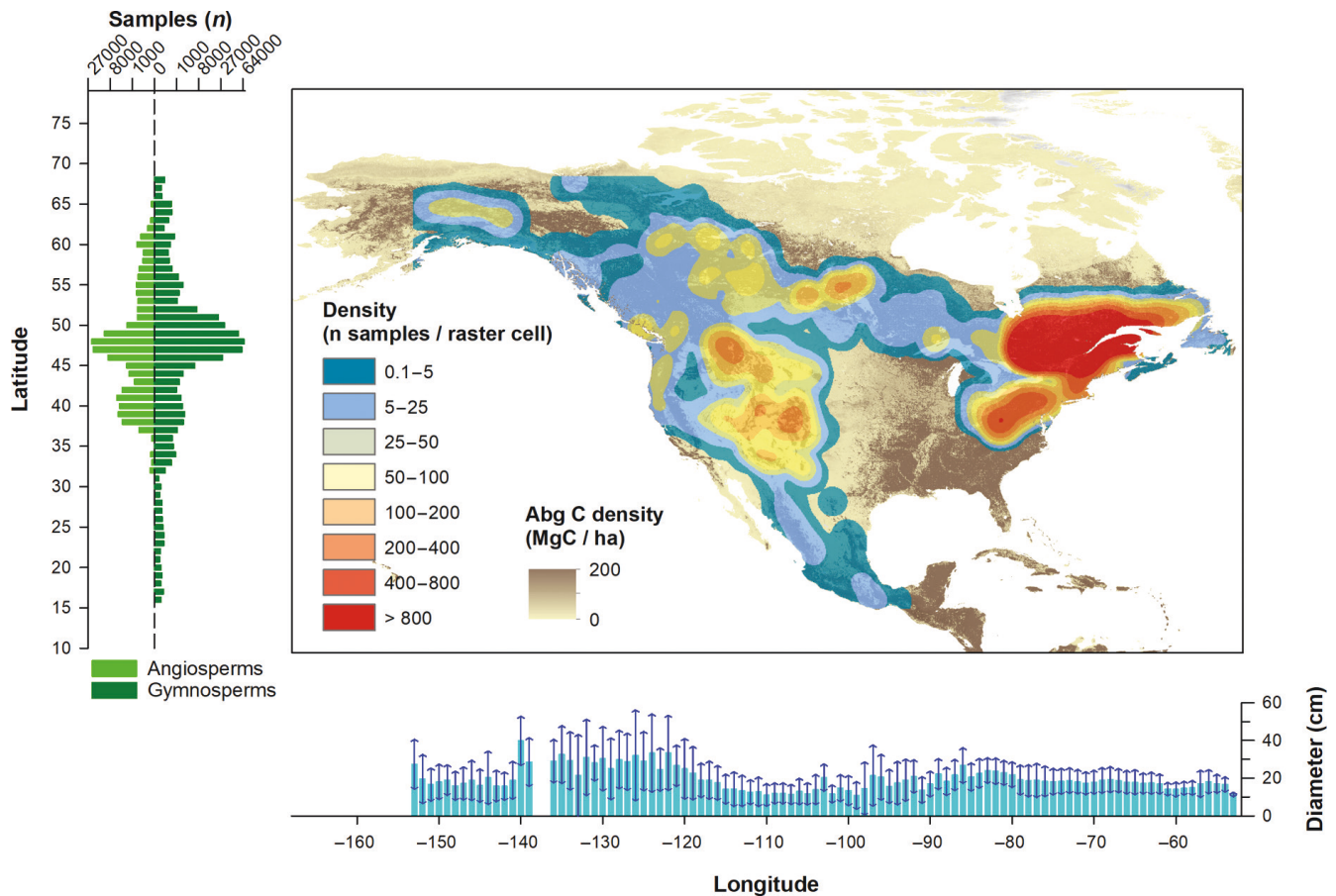


Figure 2. Density of increment cores collected per 0.1×0.1 degree ($^{\circ}$) raster cell (the unit area) over North America (when delimited in the south by the isthmus of Tehuantepec, in Mexico). A search radius of 2.5° was used to calculate density of cores. The mean diameter at breast height of samples (vertical histogram), and standard error (error bars), computed across 1° longitudinal bands are displayed at the bottom. The panel at left illustrates the frequency distribution of samples accordingly with their belonging to angiosperm and gymnosperm species computed across 1° latitudinal bands. The amount of aboveground biomass carbon (Abg C) density as of 2010 (Spawn et al. 2020) is displayed in the background to show that there are large areas of high biomass without known tree-ring collections.

sensitivity (for climate reconstruction), making them biased and not representative of the sensitivity of forest ecosystems to ongoing climate variation and change (Sullivan and Csank 2016, Zhao et al. 2019). These collections also lack the tree and forest information needed to quantify forest-level growth (for example, tree size and number per unit area), making it very difficult to scale up estimates of carbon sequestration. Recently, a regional dendroecological data network has been developed to address some of these issues (Rayback et al. 2020b), but thus far, it remains limited in extent. NFIs, by comparison, are systematic observatories of forest ecosystems designed specifically for large-scale inference—an appropriate basis for national-scale carbon monitoring, reporting, and verification (as required under the United Nations Framework Convention on Climate Change) and global-scale carbon accounting. NFI remeasurement intervals typically occur on a 5- or 10-year basis,

and the longest-running North American inventories have a temporal depth of several decades at best. We make the case for sampling tree rings in the forest inventories across North America to bring together the key data characteristics needed to quantify and better understand changes in forest biomass—spatial and ecological representativeness, annual resolution, and temporal depth.

The opportunity to build such a tree-ring data network across North America is near at hand. The field sampling could be achieved with relatively little additional investment, because the cost of revisiting NFI plots is already built into existing programs. Taking the modest additional time to bore trees when at a plot would make it possible to estimate annually resolved tree growth extending back decades or centuries (but see the “Challenges” section). The foundation for an NFI-based tree-ring network already exists in the form of legacy collections, totaling at least 405,092 increment cores

Table 1. Legacy tree-ring collections in North America's national forest inventories.

Country	Region	Number of cores with quality control ^a	Date of collection
Canada	Quebec ^b	332,290	1997–current
	NFI (CFS TRenD) ^c	19,645	1997–current
United States of America	Alaska	1,526 ^d	2014–current
	Western	23,824	1985–2001, 2011–current
	Eastern ^e	27,207	1980–1988
Mexico	National inventory (Inventario Nacional Forestal y de Suelos)	600 ^f	2013–2015
Total		405,092	

^aCrossdating or other statistical approaches. ^bComplete tree cores are sampled and measured for coniferous species, white birch, and poplars (a total of 21 species). For other deciduous species, only 10 cm segments or the 10 outermost rings are measured. ^cGirardin et al. 2021a. ^d2,074 more without quality control. ^eCanham et al. 2018. ^fFrom 33 species, includes 4,679 more cores from 759 species without quality control.

to date across North America (figure 2, table 1). It would be a missed opportunity not to build on this foundation when plots are revisited, but it requires planning and cooperation. To lay out the case for this effort we first explain the added value of such a tree-ring data network; second, we review the North American NFI tree-ring data that currently exist and discuss how they can be used to address monitoring challenges across diverse forest ecosystems; third, we consider the challenges associated with creating a continental-scale data network; fourth, we highlight the important unanswered C-cycling questions that tree rings can help address; and fifth, we chart key actions needed to build this network. Our suggestions are not limited to North America. Indeed, this is a call to action to more formally assemble, analyze, and archive tree-ring data collected in association with *any* forest inventory. Such an emerging global data set would present an unprecedented opportunity to resolve key scientific uncertainties in the global carbon cycle and address the climate crisis.

Why add tree ring collection to national forest inventories?

Large uncertainties plague our understanding of forest carbon dynamics. Which of several drivers are responsible for current forest growth trends? How will forest ecosystems respond to climate stress and feedback on the climate system? What are the effects of natural disturbances and forest management on carbon dynamics? It is unclear how much of the recent observed greening (increase in the land carbon uptake) is caused by forest recovery from disturbance versus positive effects of warming or increased atmospheric CO₂ in some regions. Indeed, we have a poor understanding of the limits of CO₂ fertilization: With atmospheric CO₂ and temperatures increasing together (the former causing the latter), at what point is the positive effect of CO₂ fertilization exceeded by the negative effect of increased evaporative stress, converting forests from a stabilizing feedback on the

climate system to a destabilizing feedback (Frank et al. 2015, Sullivan et al. 2017, D'Orangeville et al. 2018, Dannenberg et al. 2019, Gao et al. 2020)? These and many other open questions highlight the fact that many environmental factors simultaneously influence tree growth—climate, disturbances (including forest management), and CO₂ fertilization, in particular. Adding tree rings to NFIs will be critical to disentangling these drivers because tree-ring data are the single best source of information on the sensitivity of tree growth to interannual climate variability (Fritts 1976); when collected in an NFI context, they make it possible to quantify and disentangle these many influences, and they make the ideal basis for scaling up forest productivity (figure 1). In the following, we briefly flesh out these three core arguments for collecting tree-ring data in NFIs, delving into greater detail in the “Carbon cycle uncertainties, carbon accounting, and atmospheric CO₂ drawdown through forest management” section.

First, without tree-ring data, forest inventory-based estimates of the influence of climate on tree growth are limited to average growth in response to average climate over some number of years (usually 5–10). The annual resolution of tree-ring data makes it possible to detect the impact of climatic extremes, or more generally, nonlinear responses to interannual climate variation, as well as to disentangle responses to spatial versus temporal climate variation.

Second, when tree-ring data are collected in NFI (or other statistically designed) forest plot networks, multiple influences on tree growth can be captured in an unbiased and representative way—climate, competition, disturbance, and other environmental factors (DeRose et al. 2017)—which is critical to parse their effects. With attention to sampling design (see the “Challenges” section), tree-ring data sourced in an NFI context are representative of the forest population, both in the statistical and ecological sense. Forest inventories that incorporate permanent plots are specifically designed to capture forest trends (rates of tree growth, mortality, and

Table 2. Examples of existing and desired forest attributes (above and beyond existing) measured in the field for individual increment cores, trees, and associated plots.

Level	Existing	Desired
Core	One short core per tree	Less than one core per tree, full core, through-core
	Coring height	Sapwood length or area
	Unknown number of rings to stem center	Establishment date (pith date), pith offset
Tree	Stem diameter	Bark thickness
	Tree height	Wood density, biomass, or carbon
	Disturbance or damage agents	Crown radius, depth, and asymmetry
	Crown condition	Leaf area index, canopy health
	Common, vernacular name for species	Scientific name, if in doubt collect an herbarium specimen
	Status (live or dead)	Time and cause of death, if possible
Plot	Date of sampling, geographic coordinates, elevation	Stem mapping
	Competition	Hemispherical photographs
	Observations of disturbance	Coarse woody debris
		Soil water situation, pH, chemistry
		Method and motivation of tree selection

recruitment), and the influence of landscape-scale processes such as natural disturbances and land use. NFIs therefore provide a wealth of tree- and plot-level information (table 2). Sampling tree rings in NFIs would then create a record of tree growth across spatial and temporal scales, from microsite to macrosystem and from daily to centennial, with the necessary covariate data to disentangle the environmental and anthropogenic drivers of tree growth by their characteristic pattern and scale of influence. For example, consider temperature versus CO₂ as confounded drivers of tree growth: Temperature varies across a landscape (with topography and latitude), in addition to the intra-annual variability and global trends characteristic of both temperature and CO₂. Therefore for a given concentration of atmospheric CO₂, an NFI tree-ring network provides observations of tree growth across a range of mean temperatures and mean precipitation. A second example is that in contrast to the continuous trend of warming temperature, disturbance processes are discontinuous in onset, and in space (fire, insect outbreaks, droughts), with decade-scale impacts on tree growth that fade over time (Allen et al. 2015). Therefore, different drivers of forest growth have different temporal and spatial signatures. Although attribution of forest growth variation to these different drivers will not be an easy task, an NFI tree-ring network would greatly strengthen the empirical foundation for meeting this urgent challenge.

Third, NFIs are designed specifically for scaling up, precisely what is needed for carbon accounting and the deployment of forest-based negative emissions technologies. Without information on tree size, as in the case of the International Tree-Ring Data Bank, ring-width measurements must be detrended, creating a unitless ring-width index, before characterizing and attributing growth variation to specific drivers. Analyses are then limited to

relative rather than absolute growth. In a carbon accounting context, however, it is essential to analyze absolute growth (for example, carbon or biomass) on a per-area basis, therefore information on the size and per-area number of trees is critical. Tree-ring data sourced in NFI plots that were designed to represent a landscape can readily be used to aggregate and scale up existing forest estimators (Dye et al. 2016, Metseranta et al. 2018, Metseranta 2019, Ols et al. 2020). Joint tree-ring and NFI data would therefore allow for C-cycle dynamics in forested systems to be assessed and quantified to an unprecedented degree.

Existing NFI tree-ring data in North America

In North America, virtually all of the tree-ring data associated with NFIs to date have accumulated in an *ad hoc* manner, but these collections together make a strong foundation for a continental-scale data network (examples in box 1, figure 2, table 1). Tree-ring samples were collected from a subset of trees and species on a plot (figure 3), along with many other tree- and plot-level attributes (table 2), with the aim of determining tree age, estimating potential site productivity, and assessing growth. Some of these plots were designed to be temporary, whereas others are permanent and are therefore revisited. With subsequent visits, diameter remeasurements became the standard for estimating growth, and new cores were rarely collected (DeRose et al. 2017). As a result, a great deal of tree-ring samples exist from various inventories, with only some cores fully processed, cataloged and adequately stored (table 1). Some cores that were not discarded were later rediscovered by research scientists, who took the time and effort to measure samples, verify the quality of year assignments, and generate useful ring-width time series. However, there are substantial gaps in spatial, temporal, and species representation in the nascent

Box 1. Key issues in the climate sensitivity of tree growth: Local adaptation, reaction norms, assisted migration, and tree death.

A spatial network of unbiased, representative tree-ring data offers insight into a variety of critical issues about the climate sensitivity of tree growth. For example, legacy NFI tree-ring data networks have revealed spatial variation in productivity and climate sensitivity, with consequences for ecological forecasting, vulnerability assessment, and assisted migration. In an analysis of 14 species (Canham et al. 2018) across the eastern United States, and across the entire distribution of *Pseudotsuga menziesii* (Douglas-fir) in western North America (Klesse et al. 2020), average ring width increases with average annual temperature, even though warmer than average years generally lead to smaller than average growth rings. An analysis of the climate sensitivity of tree growth on the basis of forest inventory data (5- to 10-year averages) may not be able to distinguish between this kind of positive response to spatial variation in average temperature versus negative response to interannual temperature variability. An important implication of the contrasting positive versus negative responses to spatial versus temporal variation in temperature is that forecasting of future forest productivity cannot use space for time substitution: The productivity and climate sensitivity of trees at currently warmer locations cannot be expected of trees at currently cooler locations in a warmer future, because of genetic differentiation (local adaptation). Ecological forecasting of tree growth should follow norms of reaction inferred from ring-width time series data. Inference of these reaction norms is therefore a critical research priority.

Spatial variation in productivity and climate sensitivity detected through ecologically designed networks of tree-ring data further serve as a basis for identifying areas of high versus low vulnerability to climate change (Ols and Bontemps 2020, Ols et al. 2020). This information can then be used to target areas for management action (climate mitigation) as well as protection (refugia). Another solution to mitigate forest climate stress is to plant species or genotypes that are better adapted to projected future climate conditions—known as assisted migration. NFI tree-ring data make it possible to identify tree genotypes and phenotypes that are likely to thrive (grow and survive) in expected future climates, including tree-ring studies based in forestry provenance trials that have highlighted potential conflicts between cold versus drought adaptation and temporary carbon sequestration benefits (Housset et al. 2018, Girardin et al. 2021b).

Finally, tree-ring networks based in permanent sample plots can provide a better understanding of the sensitivity of tree mortality to ongoing environmental changes and discrete disturbance events (Neumann et al. 2017). NFIs track which trees die over time; the collection of increment cores from recently dead trees can pinpoint mortality timing, and the analysis of growth in the years preceding tree mortality can identify factors contributing to tree death (Cailleret et al. 2019), including reduced growth under climate extremes, extended drought events, defoliation, and other stressors. Recent efforts using tree-ring growth to understand and predict tree mortality (Dietze and Moorcroft 2011, Clark et al. 2016) would be greatly advanced by a large NFI-based tree-ring network that systematically cores both living and recently dead trees.

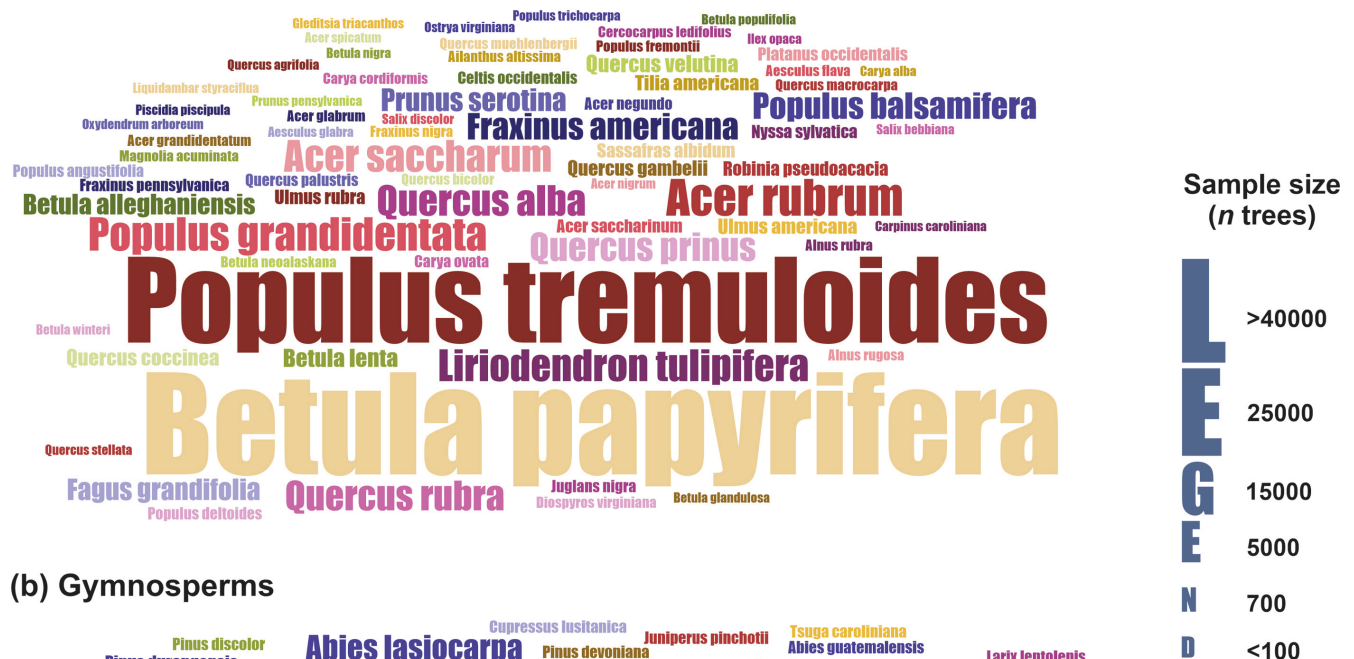
North American network of tree-ring data (figure 2). Future sample collection will likely continue to be *ad hoc*, unless a more cohesive, forward-looking approach is defined and pursued. The following overview of NFI-based tree-ring collections across Canada, Mexico, and the United States identifies differences among and within the collections, but also reveals the value added by incorporating region-specific tree-ring sampling.

Canadian Forest Inventory. Canada encompasses 223 million hectares of continuous boreal forest, representing 20% of the world's boreal forest biome, in addition to 45 million hectares of cool temperate forests (Brandt 2009). Boreal forests, in particular, have been identified as an important terrestrial carbon pool (Pan et al. 2011) and tipping point in the Earth's climate system (Lenton et al. 2008). Monitoring and forecasting the future behavior of this vast forested area is both critical and expensive. Canada's National Forest Inventory has achieved an unprecedented degree of homogeneous tree-ring sampling—6000 increment cores collected in a manner that is representative of the species and growing conditions across the managed forests of Canada. This inventory began in 2001, with anywhere from 1 to 10 cores per species collected in each plot. There

are also provincial- or territorial-level tree-ring collections, with substantial variation in sampling design. Québec, for example, has an unparalleled collection of over 300,000 increment cores sampled in approximately 130,000 temporary and permanent sampling plots (table 1; Duchesne et al. 2017). Tree-ring measurement and quality control procedures vary among these inventories and years, from more precise, time-consuming approaches in the federal system, to coarser automated methods in the high-volume inventory of southern Québec. Because the baseline cost of forest inventory sampling across Canada's vast landscape is already high, the addition of systematic tree-ring sampling, yielding historical depth and annual resolution at a low proportional cost, has great appeal.

US Forest Inventory and Analysis. The United States encompasses a substantial fraction of the world's temperate broad-leaf forests in the northern and eastern United States—which have been a carbon sink because of recovery from disturbance—along with a sizable fraction of the world's temperate coniferous forests in the western and southeastern United States. The US Forest Inventory system began in the 1930s with regional, periodic inventories. A nationally consistent annual Forest Inventory and Analysis program began in the

(a) Angiosperms



(b) Gymnosperms



Figure 3. Relative number (n) of tree samples from (a) angiosperm and (b) gymnosperm species in the tree-ring collections across North America (table 1). The figure shows 155 different species names, with frequencies ranging from 1 to more than 40,000.

late-1990s. Although tree-ring data were collected during plot establishment, there are currently no inventory-wide plans for sampling increment cores during plot remeasurement. Like in Canada, there is considerable variability in the representation of legacy increment core inventories across the four major US regions (Northern, Southern, Interior, and Pacific including Alaska). The archive of tree-ring data from inventories prior to the 2000s, combined with the current annual inventory, includes more than 24,000 cores from eight interior Western states (DeRose et al. 2017), with

1500–2000 new cores collected annually, another 20,000 or more from eight Northeastern states (Canham et al. 2018), a small nascent collection from the Pacific Northwest states, and a growing collection associated with initial plot installation in Alaska's vast boreal forest (Sullivan et al. 2016, Sullivan et al. 2017b, Cahoon et al. 2018). No known collections represent the Southeast (figure 2) or Midwest regions. Building a complete tree-ring data network on the Forest Inventory and Analysis grid would be facilitated by the 5-, 7-, or 10-year remeasurement cycles of this inventory

system—funding to revisit the plots is already included in the program.

Mexican National Forest and Soils Inventory (Inventario Nacional Forestal y de Suelos). Mexico has forest cover of 65.7 million hectares, which represents 33.6% of the national territory (CONAFOR 2018). With approximately 3,000 native tree species, diversity is high. For example, two of the most widely used genera in dendrochronology, *Pinus* and *Quercus*, are represented by 49 and 122 tree species, respectively (Gernandt and Pérez-de la Rosa 2014, Ricker et al. 2016). NFIs in Mexico started in the 1960s, with six inventories completed to date. The *Inventario Nacional Forestal y de Suelos* is carried out over a 5-year cycle, with field visits to over 26,000 sites, distributed on a national grid with distances between plots of 5–10 kilometers on forested land (CONAFOR 2012, 2018). Since 2013, field teams have collected (frequently short) cores from all tree species encountered in plots, primarily to develop a catalogue of wood density across this great diversity of species, with the goal of carbon accounting. There are currently 5,000 such samples, collected from 780 tree species, available at the National Herbarium. Furthermore, 600 cores from 33 conifer species have been crossdated (Gutierrez 2017). There are many angiosperm species from subtropical and tropical lowland areas which are not reliable for tree-ring analysis. Nevertheless, collection of full-length increment cores in many of Mexico's forests would yield annual-resolution, decades-long time series of growth in an inventory that is relatively young, building in a cost-effective manner on the existing investment to visit plots.

Challenges

Tree-ring science has been guided over the past century by sampling principles (site and tree selection criteria; Fritts 1976) aimed at climate reconstruction. Water- or temperature-stressed trees were targeted for their strong interannual ring-width variability. This leads to biased inference of the climate sensitivity of tree growth: Population-level sensitivity is overestimated (DeRose et al. 2017, Duchesne et al. 2017, Klesse et al. 2018a). The sourcing of tree-ring data from a network of locations designed to be representative of forested landscapes is a step forward, but a key remaining challenge is determining which trees to sample at those locations. Sampling in existing *ad hoc* NFI collections is biased toward canopy dominant and codominant trees. Because they represent the plurality of overstory species composition, and carbon stock and flux, these trees should be a major focus of sampling attention. However, sampling focused on canopy dominants can lead to biased estimates of growth rates—known as big tree selection bias (Brienen et al. 2012)—resulting in false inference of recent increases in growth (Morrongiello et al. 2012, Bowman et al. 2013, Nehrbass-Ahles et al. 2014, Duchesne et al. 2019, Hember et al. 2019). Moving forward, with carbon assessment and attribution questions in mind, multicohort sampling designs

will become increasingly important. Because coring all trees in all plots is impractical outside of a small-scale research context (for the time being), it would be wise to core all trees in a subset of forest inventory plots for validation and verification of tree selection guidelines, which have been shown to influence estimation of growth (Nehrbass-Ahles et al. 2014, Metsaranta et al. 2018, Cailleret et al. 2019). In remaining plots, stratified sampling across species and size classes will be important to strike a balance between sampling too many versus too few understory trees, and ultimately to disentangle the effects of year, age, size, climate, atmospheric CO₂, and disturbances (Bowman et al. 2013, Campbell et al. 2021). A further question is when and how to stratify repeated coring of individual trees—to find a balance between effort and information content. In practice, the selection process for recoring would depend on the shared information across trees in a plot, that is, how accurately and precisely the interannual growth of a tree that was not cored can be inferred on the basis of repeat diameter measurements, and what is learned from trees that were cored (Clark et al. 2007).

A second challenge is the inference of historical forest productivity from tree-ring time series, because of the fading record problem (Swetnam et al. 1999, Brienen et al. 2012, Dye et al. 2016). Trees that were once part of the forest but have died and decomposed cannot be sampled, causing systematic underestimation of historical forest carbon pools, a problem that exacerbates going backward in time (Dye et al. 2016). Furthermore, growth rates may be underestimated when estimated on the basis of surviving trees, because of a slow-grower survivorship bias (Brienen et al. 2012, Duchesne et al. 2019). The long-term monitoring of NFIs, in combination with tree-ring data collection, will improve our ability to quantify and correct this fading record bias. Until those long-term data accumulate, another solution is to upward-correct for the missing biomass, using expected forest stand trajectories (Andrews et al. 2018, Brienen et al. 2020) developed from observations in NFI permanent sample plot networks (Dr. Andria Dawson, Mount Royal University, Calgary, Alberta, Canada, personal communication, 27 October 2021).

A third challenge is that annual resolution, the assignment of a precise calendar year to each growth ring, a hallmark of tree-ring science—through crossdating (Black et al. 2016) or other techniques of quality control—may not always be feasible for forest inventory-based collections and can be quite time-consuming to achieve. The strength of correlations among tree-ring time series from forest inventory trees tends to be lower than the correlations among time series from trees at the more climate-limited locations usually selected by dendrochronologists (Girardin et al. 2021a), leaving potential uncertainty about year assignments. Strict adherence to traditional criteria for precise year assignments could lead to the rejection of many samples, limiting (and biasing) inference from NFI-based tree-ring data (Ricker et al. 2020). A mitigating influence is that missing rings are uncommon in trees

with the modest interannual ring-width variability that gives rise to low interseries correlation and therefore higher growth ring dating uncertainty (St. George et al. 2013), because these trees are less climate limited. The development of statistical methods for quantifying these patterns of uncertainty is a high priority, so that dating uncertainty can be propagated forward in projections of future forest state (Dietze 2017). A related point is that partially or fully automating the measurement of growth rings and their assignment to a year of formation would transform the tree-ring sciences—much as automated DNA sequencing and algorithmic alignment of sequences propelled studies of molecular evolution. It would then be possible, for example, to better take advantage of Quebec's massive southern inventory (approximately 400,000 cores; table 1), or to imagine sampling every tree during inventory or harvest activities. Machine learning approaches to identify growth ring boundaries are already in development (Dr. Kelly Swarts, Austrian Academy of Sciences, Gregor Mendel Institute of Molecular Plant Biology, Vienna, Austria, personal communication, 26 October 2021), which will also help expand the use of tree rings outside the temperate zone (for example, the great species and wood anatomical diversity of Mexico's trees).

A fourth challenge is scaling from measurements of ring widths to tree-level metrics of volume, biomass, and then carbon content, followed by scaling to forest stand-level carbon (via summation of all trees). This is a nontrivial task, as illustrated by LeBlanc (1990) and LeBlanc (1996) and as described by Babst et al. (2018). In particular, the allometric scaling that is necessary to estimate three-dimensional volume from one-dimensional measurements (radial or diameter increments, ideally combined with measurements of tree height) is subject to great uncertainty (Alexander et al. 2018), both because it is based on power-law relationships and because the destructively sampled data that scaling functions are estimated from are very difficult to obtain and therefore limited (Chojnacki et al. 2014). Improvement of these allometric scaling functions is an active area of research that is key for forest carbon accounting (Domke et al. 2012, MacFarlane 2015).

A final challenge is plot privacy and data accessibility. In Canada, the need for authorization from the various provinces and territories to disseminate and use NFI tree-ring data complicates research. In the United States, the exact locations of plots are guaranteed to be private under the 1998 Farm Bill and are therefore not available publicly without proper authorization. Without exact plot locations, climate data must be derived from approximate locations. In Mexico, there has been less federal institutional interest in NFI tree-ring analyses thus far. All the countries have limited financial resources to carry out this kind of research, suggesting a special need for stronger collaboration between government and research institutions. Ultimately, the greatest challenge is to spur the investment and coordination needed to make the idea of a continent-wide tree-ring data network sourced in forest inventories a reality.

Carbon cycle uncertainties, carbon accounting, and atmospheric CO₂ drawdown through forest management

Disentangling the effects of climate, natural disturbances, land use, endogenous forest demography, and CO₂ fertilization on forest growth is key to resolving the uncertainties surrounding forecasting of terrestrial carbon cycling—hence the forest greening versus browning debate. In the following, we highlight how the combined strengths of tree rings and NFIs would facilitate the detection and parsing of these drivers, improve models of carbon cycling, and clear a path for better carbon accounting and forest management aimed at the drawdown of atmospheric CO₂ levels.

Accurate and precise inference of climate effects on forest growth is essential, and tree rings are the best source of information on those climate effects. One important way that climate is changing is in the magnitude and frequency of extremes, and although forest inventories with remeasurement intervals of 5 to 10 years are excellent at detecting average growth rates in response to average conditions, they are less capable of resolving the effects of extreme events. Emerging phenomena such as heat waves are expected to become both more frequent and intense, including the compound effects of repeated events, with consequences for carbon cycling (Frank et al. 2015). Indeed, tree-ring data are already providing evidence that tree growth responses to interannual climate variability are asymmetric or nonlinear (D'Orangeville et al. 2016, 2018, Sullivan et al. 2017b, Dannenberg et al. 2019, Gao et al. 2020) implying that predictions of growth based on average climate conditions will be inaccurate, as well as the potential for threshold behavior. Annually resolved tree-ring data are further being used to characterize the time scale of recovery from drought events (Anderegg et al. 2020), and the spatial footprint of drought (the strength and extent of synchronized tree response to climate stress; Clark et al. 2016, Schurman et al. 2019), which are indicators of resilience over time and space, respectively. Legacy tree-ring data associated with NFIs are being used to address the key question of whether boreal tree growth is slowing in response to recent warming (Dietze and Moorcroft 2011, Housset et al. 2018, Isaac-Renton et al. 2018, Klesse et al. 2020). Additional considerations about the climate sensitivity of tree growth that would be detected by an inventory-based spatial network of ring-width time series are detailed in box 1.

In addition to detecting the effects of climate variability and stress, it is equally important to understand to what degree changes in forest growth are caused by endogenous forest demography, natural disturbances, forest management, and their interaction with climate. Both anthropogenic and natural disturbances (such as stand-replacing wildfires and insect outbreaks) have enormous impacts on forest ecosystem carbon budgets (Pugh et al. 2019a). Recent attention has been focused on understanding how much of the detected greening is due to regrowth after past forest disturbances, particularly harvest, because this aspect of the

forest carbon sink is strictly transient in nature (Zhu et al. 2016, Pugh et al. 2019b). With tree rings collected in NFIs, it would be possible to parse the nonstationary effects of changing climate from the transient effect of forest recovery, for example, by quantifying age-dependent growth. An NFI-based tree-ring collection further makes it possible to detect how changing climate may alter forest demography, such as tree recruitment following disturbances (Davis et al. 2019), or how forest responses to warming may be complicated by interactions with disturbances (Westerling et al. 2011, Dye et al. 2016, Danneyrolles et al. 2019).

A third crucial source of uncertainty regarding whether forests will have a stabilizing or destabilizing influence on the future global carbon cycle is the atmospheric CO₂ fertilization effect. CO₂ enrichment experiments, eddy flux measurements, and remote sensing observations all show that increased atmospheric CO₂ leads to increased water-use efficiency and net primary productivity, although the magnitude and duration of this fertilization effect varies (Walker et al. 2020). Evidence from tree rings also finds increased water-use efficiency (via stable isotope studies), although more recently these estimates have been shown to be influenced by tree size and environmental factors (Marchand et al. 2020, Rayback et al. 2020a). In contrast, tree-ring evidence for a fertilization effect on radial tree growth is limited (Hickler et al. 2008, Girardin et al. 2011, 2016, Frank et al. 2015, Giguère-Croteau et al. 2019, Hararuk et al. 2019). There are a variety of plausible reasons for the discord among these various lines of evidence; reconciling these differences is a high research priority (Walker et al. 2020) because of the significance of CO₂ fertilization uncertainty. A NFI tree-ring network offers a long-term archive of tree physiological responses on a cross-biome scale, which could be used for isotope sampling across geographic and environmental space (Correa-Díaz et al. 2019, Levesque et al. 2019).

With respect to all three of these sources of uncertainty—climate effects, disturbance and demographic processes, and CO₂ fertilization—adding tree rings to NFIs strengthens the empirical foundation for improving models and scaling of carbon dynamics from leaf to globe (Fisher et al. 2018, Kannenberg et al. 2019). At the scale of individual trees, tree rings form an obvious basis for parameterizing and validating next-generation mechanistic models of tree growth that explicitly represent wood formation—a key line of inquiry to help understand whether tree growth is controlled by photosynthesis (is source limited) or if in fact photosynthesis is controlled by the conditions needed to support growth, such as adequate turgor pressure (growth is sink limited; Körner 2013, Fatichi et al. 2014, Körner 2015, Sass-Klaassen 2015, Friend et al. 2019, Babst et al. 2020), the latter of which would fundamentally undermine the notion of CO₂ fertilization and the prediction of a strong forest carbon sink in the coming decades. Tree-ring data have been and are being used to estimate biomass increment at the forest stand level and forest ecosystem fluxes (Dye et al. 2016, Metsaranta et al. 2018, Metsaranta 2019), demonstrating the feasibility

of forest carbon scaling from tree rings. Assimilation of carbon pool and tree-ring growth data from NFIs could be used to improve ecosystem and dynamic vegetation models, which have been shown to overestimate sensitivity to climate and CO₂ fertilization (Rollinson et al. 2017, Klesse et al. 2018a). Iteratively confronting model predictions with a continuous stream of incoming data has led to improved skill in weather forecasting; with thousands of plots visited every year in NFI programs, iterative model–data comparisons could similarly improve prediction of forest ecosystems (figure 1; Evans et al. 2017, Dietze et al. 2018, Fer et al. 2018).

Finally, NFIs enhanced with tree-ring sampling make an ideal forest ecosystem monitoring system on which to base drawdown-oriented forest management and validated carbon accounting. Adaptive forest management aimed at a drawdown of atmospheric CO₂ concentrations will be greatly facilitated by incorporating the growth responses to warming climate recorded in tree rings into stand-level forest growth and yield simulators. These models are essential tools for local forest management, but have limited capacity to anticipate climate effects on forest stand development and response to silvicultural treatments. In terms of carbon accounting, NFIs already serve as the national instruments for carbon stock and flux assessment, including tracking progress toward COP21 commitments (Domke et al. 2018, 2020), and can contribute to the economic valuation of forest carbon sequestration as carbon markets emerge (Smith et al. 2019). Adding tree rings to the C-accounting process brings tangibility and accessibility in a way that has been shown to narrow the gap between scientists, managers, and communities living in and dependent on forests. That is, tree rings can be seen and understood intuitively, bringing immediacy and credibility to often indirect conclusions about climate change (Rice et al. 2009).

Key actions for moving forward

Building more formal national, continental, and global collaborations that promote NFI tree-ring networks is an important idea and its realization would benefit science, management, and society (figure 1). Continued collection of tree-ring data from NFIs represents an opportunity for increased temporal resolution, spatiotemporal coverage, population inference, and integration with other *in situ* data. Here we lay out key actions that could be taken to turn the idea of a systematic network of forest inventory-based tree-ring data into a reality.

In places such as Alaska and Mexico, where collections have just begun, developing and maintaining the financial support to continue sampling is paramount. Filling in gaps in the existing legacy collections (the southeastern United States; figure 2) and bolstering sampling in areas of sparse sampling (US Pacific Coast states; figure 2) are also high priority actions. At the same time, discussion of sampling design is needed, to balance the benefits of coordinated design versus meeting region-specific needs. Although the operations, funding, and scaffolding of the sampling process are probably best left to NFI programs, the development

of university–agency partnerships to process some cores, returning age, increment, and density data to the inventory programs, would accelerate the development of a complete data network. Furthermore, university–agency partnerships are a valuable path to address the challenges noted above, regarding the choice and assessment of sampling designs, the fading record problem, the development of automated quality control procedures, and assimilating tree-ring data into models. Public–private partnerships aimed at carbon accounting could also be considered a viable path forward, because there is growing interest from private foundations, corporations, and agencies at a variety of levels of government in nature-based solutions to the climate crisis.

The time is now to enhance existing forest monitoring to support negative emission technologies and climate mitigation. Considering that the vast majority of the cost of measuring forest inventory plots is incurred in travel, training, and logistics, with a little foresight (which trees to sample on a plot, which plots), substantially improved data to resolve the key scientific uncertainties surrounding forest ecosystem carbon sequestration becomes possible with limited additional investment. Failure to build on the existing legacy tree-ring collections in NFIs, by collecting increment cores during scheduled visits to plots, would be a massive missed opportunity. Both optimistic (Bastin et al. 2019) and pessimistic (Allen et al. 2015) views of the future of forests can be found in the scientific literature, begging the question, “How much can forests fight climate change?” (Popkin 2019). By adding tree rings to forest inventories, we can chart an evidence-based path forward to answer this question and more reliably deliver atmospheric CO₂ drawdown.

Acknowledgments

This article was prepared as an outcome of a joint meeting of the authors funded by the Interior West, Forest Inventory and Analysis Program of the USDA Forest Service and the Research, Innovation, and Impact Office of the University of Arizona. This article was prepared in part by employees of the USDA Forest Service as part of official duties and is therefore in the public domain. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US government determination or policy. RJD was further supported by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah, and is approved as journal paper no. 9414. MEKE was supported by the National Science Foundation under award no. DBI-1802893. CO acknowledges funding by the French National Research Agency (grants no. ANR-11-LABX-0002-01 and no. ANR-15-IDEX-04-LUE). Finally, we wish to thank Charlie Canham for contributions to the meeting, data, and ideas in this article.

References cited

- Alexander MR, Rollinson CR, Babst F, Trouet V, Moore DJ. 2018. Relative influences of multiple sources of uncertainty on cumulative and incremental tree-ring-derived aboveground biomass estimates. *Trees* 32: 1–12.
- Allen CD, Breshears DD, McDowell NG. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6: art129.
- Anderegg WRL, Trugman AT, Badgley G, Konings AG, Shaw J. 2020. Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change* 10: 1091–1095.
- Andrews T, Dietze M, Booth R. 2018. Climate or disturbance: Temperate forest structural change and carbon sink potential. *bioRxiv* 478693.
- Babst F, Friend AD, Karamihalaki M, Wei J, von Arx G, Papale D, Peters RL. 2020. Modeling Ambitions Outpace Observations of Forest Carbon Allocation. *Trends in Plant Science* 26: 210–219.
- Babst F, Poulter B, Bodesheim P, Mahecha MD, Frank DC. 2017. Improved tree-ring archives will support Earth-system science. *Nature Ecology and Evolution* 1: 0008.
- Babst F, et al. 2018. When tree rings go global: Challenges and opportunities for retro- and prospective insight. *Quaternary Science Reviews* 197: 1–20.
- Bastin J-F, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, Zohner CM, Crowther TW. 2019. The global tree restoration potential. *Science* 365: 76.
- Black BA, et al. 2016. The value of crossdating to retain high-frequency variability, climate signals, and extreme events in environmental proxies. *Global Change Biology* 22: 2582–2595.
- Bowman DMJS, Brien RJW, Gloor E, Phillips OL, Prior LD. 2013. Detecting trends in tree growth: Not so simple. *Trends in Plant Science* 18: 11–17.
- Brandt JP. 2009. The extent of the North American boreal zone. *Environmental Reviews* 17: 101–161.
- Brien RJW, Caldwell L, Duchesne L, Voelker S, Barichivich J, Baliva M, Ceccantini G, Di Filippo A, Helama S, Locosselli GM. 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature communications* 11: 1–10.
- Brien RJW, Gloor E, Zuidema PA. 2012. Detecting evidence for CO₂ fertilization from tree ring studies: The potential role of sampling biases. *Global Biogeochemical Cycles* 26: 2011GB004143.
- Cahoon SMP, Sullivan PF, Brownlee AH, Pattison RR, Andersen H-E, Legner K, Hollingsworth TN. 2018. Contrasting drivers and trends of coniferous and deciduous tree growth in interior Alaska. *Ecology* 99: 1284–1295.
- Cailleret M, et al. 2019. Early warning signals of individual tree mortality based on annual radial growth. *Frontiers in Plant Science* 9: 1964.
- Campbell EM, Magnussen S, Antos JA, Parish R. 2021. Size-, species-, and site-specific tree growth responses to climate variability in old-growth subalpine forests. *Ecosphere* 12: e03529.
- Canham CD, Murphy L, Riemann R, McCullough R, Burrill E. 2018. Local differentiation in tree growth responses to climate. *Ecosphere* 9: e02368.
- Charney ND, Babst F, Poulter B, Record S, Trouet VM, Frank D, Enquist BJ, Evans MEK. 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecology Letters* 19: 1119–1128.
- Chojnacki DC, Heath LS, Jenkins JC. 2014. Updated generalized biomass equations for North American tree species. *Forestry* 87: 129–151.
- Clark JS, et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology* 22: 2329–2352.
- Clark JS, Wolosin M, Dietze M, Ibáñez I, LaDeau S, Welsh M, Kloeppel B. 2007. Tree growth inference and prediction from diameter censuses and ring widths. *Ecological Applications* 17: 1942–1953.
- [CONAFOR] Comisión Nacional Forestal de México. 2012. Inventario Nacional Forestal y de Suelos: Informe de Resultados 2004–2009. CONAFOR.
- [CONAFOR] Comisión Nacional Forestal de México. 2018. Inventario Nacional Forestal y de Suelos: Informe de Resultados 2009–2014. CONAFOR.
- Correa-Díaz A, Silva LCR, Horwath WR, Gómez-Guerrero A, Vargas-Hernández J, Villanueva-Díaz J, Velázquez-Martínez A, Suárez-Espinoza J. 2019. Linking remote sensing and dendrochronology to

- quantify climate-induced shifts in high-elevation forests over space and time. *Journal of Geophysical Research: Biogeosciences* 124: 166–183.
- Dannenbergh MP, Wise EK, Smith WK. 2019. Reduced tree growth in the semiarid United States due to asymmetric responses to intensifying precipitation extremes. *Science Advances* 5: eaaw0667.
- Dannebrolles V, et al. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. *Nature Communications* 10: 1265.
- Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, Maneta MP. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences* 116: 6193.
- DeRose RJ, Shaw JD, Long JN. 2017. Building the Forest Inventory and Analysis Tree-Ring Data Set. *Journal of Forestry* 115: 283–291.
- Dietze MC. 2017. Prediction in ecology: A first-principles framework. *Ecological Applications* 27: 2048–2060.
- Dietze MC, et al. 2018. Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences* 115: 1424.
- Dietze MC, Moorcroft PR. 2011. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology* 17: 3312–3326.
- Domke G, Williams CA, Birdsey R, Coulston J, Finzi A, Gough C, Haight B, Hicke J, Janowiak M, de Jong B. 2018. Forests. Pages 365–398 in Cavallaro N, Shrestha G, Birdsey R, Mayes MA, Najjar RG, Reed SC, Romero-Lankao P, Zhu Z, eds. *Second State of the Carbon Cycle Report (SOCCR2): A Sustained Assessment Report*. US Global Change Research Program.
- Domke GM, Oswalt SN, Walters BF, Morin RS. 2020. Tree planting has the potential to increase carbon sequestration capacity of forests in the United States. *Proceedings of the National Academy of Sciences* 117: 24649–24651.
- Domke GM, Woodall CW, Smith JE, Westfall JA, McRoberts RE. 2012. Consequences of alternative tree-level biomass estimation procedures on U. S. forest carbon stock estimates. *Forest Ecology and Management* 270: 108–116.
- D'Orangeville L, Duchesne L, Houle D, Kneeshaw D, Côté B, Pederson N. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science* 352: 1452.
- D'Orangeville L, Houle D, Duchesne L, Phillips RP, Bergeron Y, Kneeshaw D. 2018. Beneficial effects of climate warming on boreal tree growth may be transitory. *Nature Communications* 9: 3213.
- Duchesne L, D'Orangeville L, Ouimet R, Houle D, Kneeshaw D. 2017. Extracting coherent tree-ring climatic signals across spatial scales from extensive forest inventory data. *PLOS ONE* 12: e0189444.
- Duchesne L, Houle D, Ouimet R, Caldwell L, Gloor M, Brien R. 2019. Large apparent growth increases in boreal forests inferred from tree-rings are an artefact of sampling biases. *Scientific Reports* 9: 6832.
- Dye A, Barker Plotkin A, Bishop D, Pederson N, Poulter B, Hessler A. 2016. Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests. *Ecosphere* 7: e01454.
- Evans MEK, Falk DA, Arizpe A, Swetnam TL, Babst F, Holsinger KE. 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. *Ecosphere* 8: e01889.
- [FAO] Food Agricultural Organization of the United Nations. 2015. *Global Forest Resources Assessment - Main Report* Rome, Italy. FAO.
- Fatichi S, Leuzinger S, Körner C. 2014. Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. *New Phytologist* 201: 1086–1095.
- Fer I, Kelly R, Moorcroft PR, Richardson AD, Cowdery EM, Dietze MC. 2018. Linking big models to big data: efficient ecosystem model calibration through Bayesian model emulation. *Biogeosciences* 15: 5801–5830.
- Fisher RA, et al. 2018. Vegetation demographics in Earth System models: A review of progress and priorities. *Global Change Biology* 24: 35–54.
- Frank DC, et al. 2015. Water-use efficiency and transpiration across European forests during the Anthropocene. *Nature Climate Change* 5: 579.
- Friend AD, Eckes-Shephard AH, Fonti P, Rademacher TT, Rathgeber CBK, Richardson AD, Turton RH. 2019. On the need to consider wood formation processes in global vegetation models and a suggested approach. *Annals of Forest Science* 76: 49.
- Fritts HC. 1976. *Tree Rings and Climate*. Academic Press.
- Gao S, Zhou T, Yi C, Shi P, Fang W, Liu R, Liang E, Julio Camarero J. 2020. Asymmetric impacts of dryness and wetness on tree growth and forest coverage. *Agricultural and Forest Meteorology* 288–289: 107980.
- Gernandt DS, Pérez-de la Rosa JA. 2014. Biodiversidad de Pinophyta (coníferas) en México. *Revista Mexicana de Biodiversidad* 85: 126–133.
- Giguère-Croteau C, Boucher É, Bergeron Y, Girardin MP, Drobyshév I, Silva LCR, Hélie J-F, Garneau M. 2019. North America's oldest boreal trees are more efficient water users due to increased [CO₂], but do not grow faster. *Proceedings of the National Academy of Sciences* 116: 2749.
- Girardin MP, Bernier PY, Raulier F, Tardif JC, Conciatori F, Guo XJ. 2011. Testing for a CO₂ fertilization effect on growth of Canadian boreal forests. *Journal of Geophysical Research: Biogeosciences* 116: 2010JG001287.
- Girardin MP, et al. 2016. No growth stimulation of Canada's boreal forest under half-century of combined warming and CO₂ fertilization. *Proceedings of the National Academy of Sciences* 113: E8406–E8414.
- Girardin MP, Guo XJ, Metsaranta JM, Gervais D, Campbell E, Arsenaault A, Isaac-Renton M, Harvey JE, Bhatti J, Hogg, Edward. 2021a. A national tree-ring repository for Canadian forests (CFS-TRenD): Structure, synthesis and applications. *Environmental Reviews* 29: er-2020-0099.
- Girardin MP, Isabel N, Guo XJ, Lamothe M, Duchesne I, Lenz P. 2021b. Annual aboveground carbon uptake enhancements from assisted gene flow in boreal black spruce forests are not long-lasting. *Nature Communications* 12: 1169.
- Grassi G, House J, Dentener F, Federici S, den Elzen M, Penman J. 2017. The key role of forests in meeting climate targets requires science for credible mitigation. *Nature Climate Change* 7: 220–226.
- Green JK, Seneviratne SI, Berg AM, Findell KL, Hagemann S, Lawrence DM, Gentile P. 2019. Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature* 565: 476–479.
- Gutierrez GG. 2017. Determinación taxonómica y análisis de crecimiento de especies forestales económicamente importantes para el aprovechamiento forestal sustentable e identificación de eventos climáticos extremos (sequías) en virutas procedentes de Inventario Nacional Forestal y de Suelos de los años 2013, 2014, y 2015. Ciudad de México: Reporte Técnico, FMCN-CONAFOR-USFS.
- Hararuk O, Campbell EM, Antos JA, Parish R. 2019. Tree rings provide no evidence of a CO₂ fertilization effect in old-growth subalpine forests of western Canada. *Global Change Biology* 25: 1222–1234.
- Hember RA, Kurz WA, Girardin MP. 2019. Tree Ring Reconstructions of Stemwood Biomass Indicate Increases in the Growth Rate of Black Spruce Trees Across Boreal Forests of Canada. *Journal of Geophysical Research: Biogeosciences* 124: 2460–2480.
- Hickler T, Smith B, Prentice IC, Mjöfors K, Miller P, Arneth A, Sykes MT. 2008. CO₂ fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Global Change Biology* 14: 1531–1542.
- Housset JM, Nadeau S, Isabel N, Depardieu C, Duchesne I, Lenz P, Girardin MP. 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. *New Phytologist* 218: 630–645.
- [IPCC] Intergovernmental Panel on Climate Change. 2018. Summary for Policymakers. IPCC. www.ipcc.ch/sr15/chapter/spm.
- Isaac-Renton M, Montwé D, Hamann A, Spiecker H, Cherubini P, Treydte K. 2018. Northern forest tree populations are physiologically maladapted to drought. *Nature Communications* 9: 5254.
- Kannenbergh SA, Maxwell JT, Pederson N, D'Orangeville L, Ficklin DL, Phillips RP. 2019. Drought legacies are dependent on water table depth,

- wood anatomy and drought timing across the eastern US. *Ecology Letters* 22: 119–127.
- Klesse S, Babst F, Lienert S, Spahn R, Joos F, Bouriaud O, Carrer M, Di Filippo A, Poulter B, Trotsiuk V. 2018a. A combined tree ring and vegetation model assessment of European forest growth sensitivity to interannual climate variability. *Global Biogeochemical Cycles* 32: 1226–1240.
- Klesse S, et al. 2020. Continental-scale tree-ring-based projection of Douglas-fir growth: Testing the limits of space-for-time substitution. *Global Change Biology* 26: 5146–5163.
- Klesse S, DeRose RJ, Guiterman CH, Lynch AM, O'Connor CD, Shaw JD, Evans MEK. 2018b. Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. *Nature Communications* 9: 5336.
- Körner C. 2013. Growth controls photosynthesis—mostly. *Nova Acta Leopoldina* 114: 273–283.
- Körner C. 2015. Paradigm shift in plant growth control. *Current Opinion Plant Biology* 25: 107–114.
- LeBlanc DC. 1996. Using tree rings to study forest decline: An epidemiological approach based on estimated annual wood volume increment. Pages 437–449 in [Dean JS](#), [Meko DM](#), [Swetnam TW](#), eds. *Tree Rings, Environment, and Humanity: Proceedings of the International Conference, Tucson, Arizona, 17–21 May 1994*. University of Arizona. 437–449.
- LeBlanc DC. 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. *Canadian Journal of Forest Research* 20: 1399–1407.
- Le Quéré C, et al. 2015. Global Carbon Budget 2015. *Earth System Science Data* 7: 349–396.
- Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, Rahmstorf S, Schellnhuber HJ. 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences* 105: 1786.
- Levesque M, Andreu-Hayles L, Smith WK, Williams AP, Hobi ML, Allred BW, Pederson N. 2019. Tree-ring isotopes capture interannual vegetation productivity dynamics at the biome scale. *Nature Communications* 10: 742.
- MacDicken K, Jonsson Ö, Piña L, Maulo S, Contessa V, Adikari Y, Garzuglia M, Lindquist E, Reams G, D'Annunzio R. 2016. Global Forest Resources Assessment 2015: How Are the World's Forests Changing? Food and Agricultural Organization of the United Nations.
- Marchand W, Girardin MP, Hartmann H, Depardieu C, Isabel N, Gauthier S, Boucher É, Bergeron Y. 2020. Strong overestimation of water-use efficiency responses to rising CO₂ in tree-ring studies. *Global Change Biology* 26: 4338–4558.
- McFarlane DW. 2015. A generalized tree component biomass model derived from principles of variable allometry. *Forest Ecology and Management* 354: 43–55.
- Metsaranta JM. 2019. Long-term tree-ring derived carbon dynamics of an experimental plantation in relation to species and density in Northwestern Ontario, Canada. *Forest Ecology and Management* 441: 229–241.
- Metsaranta JM, Trofymow JA, Black TA, Jassal RS. 2018. Long-term time series of annual ecosystem production (1985–2010) derived from tree rings in Douglas-fir stands on Vancouver Island, Canada using a hybrid biometric-modelling approach. *Forest Ecology and Management* 429: 57–68.
- Morrongiello JR, Thresher RE, Smith DC. 2012. Aquatic biochronologies and climate change. *Nature Climate Change* 2: 849.
- National Academies of Sciences E and Medicine. 2019. *Negative Emissions Technologies and Reliable Sequestration: A Research Agenda*. The National Academies Press.
- 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. *Global Change Biology* 20: 2867–2885.
- Neumann M, Mues V, Moreno A, Hasenauer H, Seidl R. 2017. Climate variability drives recent tree mortality in Europe. *Global change biology* 23: 4788–4797.
- Ols C, Bontemps J-D. 2020. Pure and even-aged forestry of fast growing conifers under climate change: On the need of a silvicultural paradigm shift. *Environmental Research Letters* 16: 024030.
- Ols C, Hervé J-C, Bontemps J-D. 2020. Recent growth trends of conifers across Western Europe are controlled by thermal and water constraints and favored by forest heterogeneity. *Science of the Total Environment* 742: 140453.
- Pan Y, et al. 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science* 333: 988.
- Popkin G. 2019. The forest question. *Nature* 565: 280–282.
- Pugh TAM, Arneth A, Kautz M, Poulter B, Smith B. 2019a. Important role of forest disturbances in the global biomass turnover and carbon sinks. *Nature Geoscience* 12: 730–735.
- Pugh TAM, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V, Calle L. 2019b. Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences* 116: 4382.
- Rayback SA, Belmecheri S, Gagen MH, Lini A, Gregory R, Jenkins C. 2020a. North American temperate conifer (*Tsuga canadensis*) reveals a complex physiological response to climatic and anthropogenic stressors. *New Phytologist* 228: 1781–1795.
- Rayback SA, Duncan JA, Schaberg PG, Kosiba AM, Hansen CF, Murakami PF. 2020b. The DendroEcological Network: A cyberinfrastructure for the storage, discovery and sharing of tree-ring and associated ecological data. *Dendrochronologia* 60: 125678.
- Reidmiller DR, Avery CW, Easterling DR, Kunkel KE, Lewis KLM, Maycock TK, Steward BC, eds. 2018. *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, vol. 2*. US Global Change Research Program, USGCRP.
- Rice JL, Woodhouse CA, Lukas JJ. 2009. Science and decision making: Water management and tree-ring data in the Western United States. *JAWRA Journal of the American Water Resources Association* 45: 1248–1259.
- Ricker M, Gutiérrez-García G, Juárez-Guerrero D, Evans MEK. 2020. Statistical age determination of tree rings. *PLOS ONE* 15: e0239052.
- Ricker M, Valencia-Avalos S, Hernández HM, Gómez-Hinostrosa C, Martínez-Salas EM, Alvarado-Cárdenas LO, Wallnöfer B, Ramos CH, Mendoza PE. 2016. Tree and tree-like species of Mexico: Apocynaceae, Cactaceae, Ebenaceae, Fagaceae y Sapotaceae. *Revista Mexicana de Biodiversidad* 87: 1189–1202.
- Rollinson CR, et al. 2017. Emergent climate and CO₂ sensitivities of net primary productivity in ecosystem models do not agree with empirical data in temperate forests of eastern North America. *Global Change Biology* 23: 2755–2767.
- Sass-Klaassen U. 2015. Tree physiology: Tracking tree carbon gain. *Nature plants* 1: 1–2.
- Schurman JS, et al. 2019. The climatic drivers of primary Picea forest growth along the Carpathian arc are changing under rising temperatures. *Global Change Biology* 25: 3136–3150.
- Smith JE, Domke GM, Nichols MC, Walters BF. 2019. Carbon stocks and stock change on federal forest lands of the United States. *Ecosphere* 10: e02637.
- Spawn SA, Sullivan CC, Lark TJ, Gibbs HK. 2020. Harmonized global maps of above and belowground biomass carbon density in the year 2010. *Scientific Data* 7: 1–22.
- St. George S, Ault TR, Torbenson MCA. 2013. The rarity of absent growth rings in Northern Hemisphere forests outside the American Southwest. *Geophysical Research Letters* 40: 3727–3731.
- Sullivan MJ, et al. 2017. Diversity and carbon storage across the tropical forest biome. *Scientific Reports* 7: 39102.
- Sullivan PF, Pattison RR, Brownlee AH, Cahoon SMP, Hollingsworth TN. 2017b. Limited evidence of declining growth among moisture-limited black and white spruce in interior Alaska. *Scientific Reports* 7: 15344.
- Sullivan PF, Csank AZ. 2016. Contrasting sampling designs among archived data sets: Implications for synthesis efforts. *Tree Physiology* 36: 1057–1059.
- Sullivan PF, Pattison RR, Brownlee AH, Cahoon SMP, Hollingsworth TN. 2016. Effect of tree-ring detrending method on apparent growth trends

- of black and white spruce in interior Alaska. *Environmental Research Letters* 11: 114007.
- Swetnam TW, Allen Craig D, Betancourt JL. 1999. Applied historical ecology: Using the past to manage for the future. *Ecological Applications* 9: 1189–1206.
- Walker AP, et al. 2020. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂. *New Phytologist* 229: 2413–2445.
- Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences* 108: 13165.
- Winkler AJ, Myneni RB, Alexandrov GA, Brovkin V. 2019. Earth system models underestimate carbon fixation by plants in the high latitudes. *Nature Communications* 10: 1–8.
- Zhao S, Pederson N, D'Orangeville L, HilleRisLambers J, Boose E, Penone C, Bauer B, Jiang Y, Manzanedo RD. 2019. The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global ecological representativity. *Journal of Biogeography* 46: 355–368.
- Zhu Z, et al. 2016. Greening of the Earth and its drivers. *Nature Climate Change* 6: 791.

Margaret E. K. Evans (mekevans@arizona.edu) is an assistant professor, Kelly A. Heilman is a postdoctoral researcher, David C. Frank is a professor and the director, and Courtney L. Giebkink is graduate student in the Laboratory of Tree-Ring Research at the University of Arizona, in Tucson, Arizona, in the United States. R. Justin DeRose (justin.derose@usu.edu) is an assistant professor in the Quinney College of Natural Resources at Utah State University, in Logan, Utah, in the United States. Stefan Klesse is a postdoctoral researcher in the Swiss Federal Institute for Forest, Snow, and Landscape Research, in Zürich, Switzerland. Martin P. Girardin is a research scientist for the Canadian Forest Service, Laurentian Forestry Centre, in Québec, Québec, Canada. M. Ross Alexander is an ecological and data scientist at the Argonne National Laboratory, in Lemont, Illinois, in the United States. André Arsenault is a forest ecologist for the Canadian Forest

Service, Atlantic Forestry Centre, Natural Resources Canada, in Corner Brook, Labrador, Canada. Flurin Babst is assistant research professor in the School of Natural Resources and the Environment at University of Arizona, in Tucson, Arizona, in the United States. Mathieu Bouchard is an assistant professor in the Department of Wood Science and Forestry, at Laval University, in Québec, Québec, Canada. Sean M.P. Cahoon is a research ecologist for the USDA Forest Service, Pacific Northwest Research Station, in Anchorage, Alaska, in the United States. Elizabeth M. Campbell is a research scientist for the Canadian Forest Service, Pacific Forestry Centre, in Victoria, British Columbia, Canada. Michael Dietze is professor in the Department of Earth and Environment at Boston University, in Boston, Massachusetts, in the United States. Louis Duchesne is forestry scientist at Direction de la Recherche Forestière, Ministère des Forêts, de la Faune, et des Parcs du Québec, in Québec, Québec, Canada. Armando Gómez-Guerrero is research professor in the Colegio de Postgraduados, Montecillo, Texcoco, Estado de México, in Mexico. Genaro Gutiérrez García is postdoctoral investigator in the Departamento de Ciencias Ambientales y del Suelo, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, in the Ciudad de México, in Mexico. Edward H. Hogg and Juha Metsaranta are research scientists in the Canadian Forest Service, Northern Forestry Centre, in Edmonton, Alberta, Canada. Clémentine Ols is a postdoctoral researcher at the Institut National de l'Information Géographique et Forestière, in Nancy, France. Shelly A. Rayback is an associate professor in the Department of Geography, University of Vermont, in Burlington, Vermont, in the United States. Anya Reid is a vegetation resource inventory specialist for the British Columbia Ministry of Forests, in Victoria, British Columbia, Canada. Martin Ricker is a senior researcher at the Instituto de Biología, Universidad Nacional Autónoma de México, in the Ciudad de México, in Mexico. Paul G. Schaberg is a research plant physiologist for the USDA Forest Service, Northern Research Station, in Burlington, Vermont, in the United States. John D. Shaw is a research forester for the USDA Forest Service, Rocky Mountain Research Station, in Ogden, Utah, in the United States. Patrick F. Sullivan is a research scientist in the Environment and Natural Resources Institute at the University of Alaska, in Anchorage, Alaska, in the United States. Sergio Armando Villela is a biologist for the Comisión Nacional Forestal, Sistema Nacional de Monitoreo Forestal, in San Juan de Ocotán, Jalisco, in Mexico.