**Title:** Joint effects of climate, tree size, and year on annual tree growth derived using tree-ring records from ten globally distributed forests

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# Abstract

Tree rings provide a uniquely valuable long-term record for understanding how climate and other environmental drivers shape individual tree growth and forest productivity. However, conventional tree-ring analysis methods are not designed to simultaneously account for the effects of climate, tree size, and other environmental drivers on individual tree growth, which has limited the potential to use tree rings to understand forest productivity, its climate sensitivity, and its global change responses. Here, we develop and apply a new method to simultaneously model non-linear effects of primary climate drivers, reconstructed tree diameter (DBH), and year in generalized least squares models that account for the temporal autocorrelation inherent to each individual tree’s growth. We analyze tree-ring data from 3811 trees representing 40 species at 10 globally distributed sites, showing that water, temperature, DBH, and time have additively, and often interactively, influenced annual growth over the past 120 years. Growth responses were predominantly positive to precipitation and negative to temperature, with both included in 78% of top models, and with non-linear responses prevalent (*##%* of relationships). Interactions between DBH and climate were common (44% of cases tested). Growth rates – expressed as ring widths, basal area increments, or biomass increments – varied non-linearly with DBH. Accounting for DBH, growth rate declined over time for 90% of species-site combinations. These trends were largely attributable to stand dynamics as cohorts and stands age, which remain challenging to disentangle from global change drivers. By providing a parsimonious approach for characterizing multiple interacting drivers of tree growth, our method reveals a more complete picture of the factors influencing tree growth than has previously been possible. *As global change pressures intensify and the need to understand changing forest dynamics becomes increasingly urgent, we expect that this approach will prove valuable to understanding drivers of tree growth and forest change.*

**Keywords**: climate sensitivity; tree diameter; environmental change; Forest Global Earth Observatory (ForestGEO); generalized least squares (GLS); nonlinear; tree rings

# Introduction

Tree rings provide a long-term record of annual growth increments that is invaluable for understanding forests in an era of global change (Amoroso et al., 2017; Fritts & Swetnam, 1989; Zuidema et al., 2013). Spanning time scales of decades to centuries or even millennia, they provide by far the most robust method for characterizing the interannual climate sensitivity of tree growth (Bräker, 2002; Fritts, 1976) and how it has changed through time (Au et al., 2020; Babst et al., 2019; Maxwell et al., 2016; Sniderhan & Baltzer, 2016; Wilmking et al., 2020). Combined with forest censuses, they can be used to estimate forest woody productivity (Davis et al., 2009; Dye et al., 2016; Graumlich et al., 1989; Teets, Fraver, Hollinger, et al., 2018) and its climate sensitivity (Helcoski et al., 2019; Klesse et al., 2018; Teets, Fraver, Weiskittel, et al., 2018). Tree rings also provide the long-term perspective critical to understanding how slowly changing environmental drivers including rising atmospheric carbon dioxide (CO2) concentrations, changing climate, and other anthropogenic and natural changes are influencing tree growth and forest productivity (e.g., Levesque et al., 2017; Mathias & Thomas, 2018; Walker et al., 2020). This information is critical to predicting forest responses to anthropogenic changes, particularly climate change, and thereby reducing the enormous uncertainty surrounding future contributions of Earth’s forests to the global carbon cycle (Arora et al., 2020).

Yet, collection and analysis of dendrochronological records has traditionally been optimized to detect climate signals rather than to understand variation among trees, including size-related variation in climate sensitivity (e.g., Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021), and predict forest productivity, its climate sensitivity, and how it may be changing (Babst et al., 2018; Cherubini et al., 1998; Klesse et al., 2018; Nehrbass-Ahles et al., 2014; Wilmking et al., 2020). As a result, prevailing approaches hold a number of limitations for using tree rings to address pressing questions concerning forest productivity in the current era of rapid environmental change. To realistically estimate forest woody productivity, it is necessary to measure or model the growth rate of the individual trees within the stand based on the primary biotic and environmental drivers. Needed is an analysis framework that can capture the additive and interactive effects of climate, tree size (most commonly diameter breast height, DBH), and other environmental drivers (e.g., Evans et al., 2017; Klesse et al., 2020; Rollinson et al., 2021), which may often be best described by nonlinear functions (REFS, Rollinson et al., 2021). While multifactorial and sometimes non-linear individual-based analysis frameworks have been applied (e.g., REFS, Evans et al., 2017; Rollinson et al., 2021), their use has been relatively limited, and as a result we lack synthetic, global-scale understanding of some of the key questions that may be addressed using this such an approach (Table 1). *Moreover, while tree-ring data has been used for benchmarking dynamic global vegetation models [DGVMs, e.g., REFS], an individual-based analysis approach focusing on multiple drivers including DBH would offer more opportunities for using tree-ring data as benchmarking tools for demographic DGVMs [*[*REFS?*](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/128)*].*

Understanding the climate sensitivity of tree growth is critical to predicting forest dynamics and productivity as the climate changes. Over the vast majority of Earth’s forested regions, water is the primary climatic factor limiting tree growth, whereas low temperatures are the strongest limitation in some high latitude or high elevation sites (Babst et al., 2019). The classic dendrochronological approach to characterizing the climate sensitivity of tree growth describes linear relationships between the main growth-limiting climate factor (moisture or temperature) and population-level growth responses captured in ring-width index chronologies [REFS]. While invaluable for applications such as reconstructing past climates [REFS], more in-depth characterization of climate sensitivity across a representative sample of all trees in a forest stand is desirable for efforts to understand forest productivity and its climate responses. To start, it is important to characterize the joint effects of temperature and moisture, which we hypothesize commonly act over different seasonal windows (Table 1) and therefore cannot be fully captured by commonly used drought metrics [e.g., PDSI or SPEI; REFS]. In addition, based on the predominance of nonlinear climate responses of tree growth over both smaller and larger spatiotemporal scales [REFS], we hypothesize that nonlinear climate responses, already known to be widespread within forest settings (Rollinson et al., 2021; Wilmking et al., 2020; Woodhouse, 1999), are in fact the predominant form of response in forests around the world [Table 1]. Finally, while the influence of DBH is typically removed through detrending (Edward R. Cook & Peters, 1997), thereby eliminating the potential to directly model interactive size-related variation in climate sensitivity, we hypothesize that such interactive effects are, in fact, quite common in forest settings (Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021; Table 1, Trouillier et al., 2019).

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Dendrochronological methods to characterize the climate sensitivity of tree growth have been optimized to obtain the strongest possible climate signal for climate reconstructions, but face limitations when it comes to characterizing the long-term climate sensitivity of individual tree growth or stand productivity. Traditional methods begin by fitting a function (commonly an exponential curve or a spline) to the growth record captured by each core, extracting residuals around the long-term trends, and then standardizing and averaging the residuals across cores to form a species-level ring-width index chronology (Fritts, 1976; Speer, 2010). Climate signals are then identified by examining month-by-month or seasonal correlations of the ring-width index chronology to one or more climate variables over the current year and, typically, previous growing season (e.g., Fritts, 1976; Meko et al., 2011; Zang & Biondi, 2015). Following identification of the top climate driver(s), statistical models describing their relationships to tree growth can be used for applications such as climate reconstruction (e.g., Buntgen et al., 2011) or projection of tree growth responses to climate change (e.g., Charney et al., 2016). An important caveat for the latter, however, is that the slopes of correlations between climate variables and ring-width index chronologies are not identical to the mean slope of the relationship among individuals within the population, as the process of building species chronologies obfuscates individual-level responses (Carrer, 2011; Pederson et al., 2020). Although population-level climate responses have been approximated based on climate sensitives derived from species chronologies (e.g., Charney et al., 2016; Helcoski et al., 2019), the removal of individual-level variation prior to analysis of climate sensitivity limits potential for using species chronologies to characterize the climate sensitivity of stand productivity. In particular, analysis of species-level chronologies does not allow the direct characterization of known variation in climate sensitivity in relation to tree height, canopy position, or microhabitat characteristics such as topographic wetness index (e.g., Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021).

Dendrochronological studies most commonly focus on linear climate responses to individual climate drivers, thereby missing nonlinearities and additive or interactive climate effects known to be widespread within forest settings (Wilmking et al., 2020; Woodhouse, 1999). Nonlinearities in climate sensitivities of tree metabolism and growth have been observed across a wide range of spatio-temporal scales. Over time frames of seconds to days, photosynthesis and respiration display unimodal relationships to temporal variation in temperature, typically peaking at temperatures reflective of the environment to which the plant is adapted and acclimated (Kumarathunge et al., 2019). Across broad climatic gradients, annual forest productivity generally increases with temperature, precipitation, and potential evapotranspiration (PET) up to a point, after which it plateaus or decreases (Banbury Morgan et al., 2021; M. J. P. Sullivan et al., 2020). Filling a critical gap between short-term physiological responses and the global gradients representing millennia of community assembly and species adaptation, the annual growth records of tree rings capture tree growth responses to interannual climatic variation. Yet, because non-linearities are problematic for reconstructing climate variables (Esper & Frank, 2009), systems exhibiting these are typically not the first focus for sampling. Many worked around the non-linearity issues by sampling at sites with characteristics that result in trees being more climate-limited, though not all (E. R. Cook, 1982). Importantly, traditional analysis methods are designed around first-order linear growth-climate relationships (Fritts, 1976). *Dendrochronological studies allowing for nonlinear or threshold responses of tree growth to climate are less common (Cavin & Jump, 2017; Edward R. Cook & Johnson, 1989; Ljungqvist et al., 2020; Rollinson et al., 2021; Tolwinski-Ward et al., 2013; Tumajer et al., 2017; Woodhouse, 1999)* ***one could say these were a lot of citation for it to be uncommon. Perhaps make it more clear what aspects are less common?****, and we therefore know little about the nonlinearities in tree growth responses to interannual variation in climate that occur for trees within forest settings.* Furthermore, temperature and moisture are known to jointly shape tree growth (Beedlow et al., 2013; Foster et al., 2016) and forest productivity (e.g., Alexander et al., 2018; Banbury Morgan et al., 2021), yet growth sensitivity to their additive or interactive effects, potentially operating over different seasonal windows, is not commonly considered (but see Foster et al., 2016; Meko et al., 2011; Sánchez-Salguero et al., 2015), **largely because dendroclimate studies sample in such a way as to isolate one or other of moisture or temperature limitation.**

Tree diameter at breast height (DBH) scales predictably with numerous traits affecting tree growth rate (e.g., height, crown size and position, root mass Enquist & Niklas (2002); Niklas (2004)] and therefore is itself linked to growth (e.g., Foster et al., 2016; Muller-Landau et al., 2006) and its climate sensitivity (e.g., Bennett et al., 2015; McGregor et al., 2020). However, for dendrochronological studies aimed at deciphering climate signals, DBH is not typically a variable of interest, and its influence, *along with the influence of stand dynamics in closed-canopy forests* , is removed through detrending (Edward R. Cook & Peters, 1997). Moreover, many studies constrain sampling to only trees in canopy positions or those that appear to be old (Fritts, 1976; Huckaby et al., 2003; Pederson, 2010). While convenient for developing long chronologies and identifying climate signals (Fritts, 1976), this approach is not optimal for subsequent inference of the climate sensitivity of forest productivity (Babst et al., 2018). Although climate correlations can be transformed to climate sensitivity (i.e., magnitude of response, *sensu* Charney et al., 2016) and scaled to characterize the climate sensitivity of stand productivity based on the scaling of ring width (RW) with DBH (Helcoski et al., 2019), they cannot be used to directly model known interactive effects of DBH and climate on tree growth (Trouillier et al., 2019). For example, drought sensitivity tends to increase with tree size (Bennett et al., 2015; Gillerot et al., 2020; McGregor et al., 2020), and responses to temperature can also vary with tree size or canopy position (Rollinson et al., 2021; Rossi et al., 2007). However, the removal of DBH signals via detrending makes it impossible to account for such size differences in climate sensitivity in a systematic, integrative way. To use tree rings to predict tree growth, ecosystem productivity, and forest dynamics, we need models that include DBH (e.g., Evans et al., 2017; Klesse et al., 2020) and its potential climate interactions (e.g., Rollinson et al., 2021).

Characterizing how tree growth and forest productivity are responding to slowly changing environmental drivers is challenging and uncertain. Directional climate change (as opposed to interannual variation), rising atmospheric CO2 concentrations, and changes in atmospheric deposition of sulfur dioxide (SO2) and nitrogen oxides (NOx) are all potentially influencing tree growth (Belmecheri et al., 2021; Levesque et al., 2017; Mathias & Thomas, 2018; Maxwell et al., 2019; Takahashi et al., 2020; Walker et al., 2020). At the same time, stand dynamics influence growth: tree growth rates are sensitive to competition, the intensity of which tends to increase as forests mature, and to canopy position, which can change directionally as trees overtop or are overtopped by their neighbors. Moreover, carbon allocation to woody growth – as opposed to leaf or fine root production, reproduction, defenses, etc. – is known to decline as individual trees and forest stands age (Goulden et al., 2011; Pregitzer & Euskirchen, 2004; Thomas, 2011). However, tree size and time are almost inextricably linked (because each cored individual increases in DBH through time) and difficult to disentangle due to various sampling and analysis biases (Bowman et al., 2013; Brienen et al., 2017, 2012; Cherubini et al., 1998; Hember et al., 2019; Nehrbass-Ahles et al., 2014; Peters et al., 2015; P. F. Sullivan et al., 2016). Continued improvement of analytical methods, in combination with sampling approaches that minimize potential biases, will be important to disentangling DBH from time and detecting directional growth trends.

Here, we develop, and apply to ten forested sites spanning 52 degrees latitude, a new method that allows simultaneous consideration of the effects of primary climate drivers (i.e., the most influential climate variables and the seasonal window over which they operate), tree size, and calendar year on annual tree growth. This approach allows us to address the following questions and associated hypotheses (Table 1) for a globally distributed tree-ring dataset: (1) How does interannual climate variation shape annual tree growth (ring width, RW)? (2) How does growth rate vary with DBH? (3) How have growth rates changed through time?

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