AGU Advances

RESEARCH ARTICLE
10.1029/2024AV001188

Carbon-Water Tradeoffs in Old-Growth and Young Forests of the Pacific Northwest

Michael D. Farinacci[1], **Julia Jones**[2], and **Lucas C. R. Silva**[3]

[1]Department of Geography, University of Oregon, Eugene, OR, USA, [2]Geography, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA, [3]Environmental Studies, Department of Biology, Institute of Ecology & Evolution, University of Oregon, Eugene, OR, USA

Peer Review The peer review history for this article is available as a PDF in the Supporting Information.

Key Points:

- Forest carbon and water balances scale with tree growth depending on forest history
- Old-growth forests produce more biomass per unit water evapotranspired than young forests
- Tree growth is more sensitive to climate variability in planted than in old-growth stands

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

L. C. R. Silva,
lsilva7@uoregon.edu

Citation:

Farinacci, M. D., Jones, J., & Silva, L. C. R. (2024). Carbon-water tradeoffs in old-growth and young forests of the Pacific Northwest. *AGU Advances*, *5*, e2024AV001188. https://doi.org/10.1029/2024AV001188

Received 22 JAN 2024
Accepted 23 MAY 2024

Author Contributions:

Conceptualization: Lucas C. R. Silva
Data curation: Michael D. Farinacci
Formal analysis: Lucas C. R. Silva
Investigation: Michael D. Farinacci
Supervision: Lucas C. R. Silva
Validation: Julia Jones
Visualization: Michael D. Farinacci, Julia Jones, Lucas C. R. Silva
Writing – original draft: Michael D. Farinacci
Writing – review & editing: Julia Jones, Lucas C. R. Silva

Abstract

Despite much interest in relationships among carbon and water in forests, few studies assess how carbon accumulation scales with water use in forested watersheds with varied histories. This study quantified tree growth, water use efficiency, and carbon-water tradeoffs of young versus mature/old-growth forest in three small (13–22 ha) watersheds in the H.J. Andrews Experimental Forest, Oregon, USA. To quantify and scale carbon-water tradeoffs from trees to watersheds, tree-ring records and greenness and wetness indices from remote sensing were combined with long-term vegetation, climate, and streamflow data from young forest watersheds (trees ~45 years of age) and from a mature/old-growth forest watershed (trees 150–500 years of age). Biomass production was closely related to water use; water use efficiency (basal area increment per unit of evapotranspiration) was lower; and carbon-water tradeoffs were steeper in young forest plantations compared with old-growth forest for which the tree growth record begins in the 1850s. Greenness and wetness indices from Landsat imagery were not significant predictors of streamflow or tree growth over the period 1984 to 2017, and soil C and N did not differ significantly among watersheds. Multiple lines of evidence show that mature and old-growth forest watersheds store and accumulate more carbon, are more drought resistant, and better sustain water availability compared to young forests. These results provide a basis for reconstructions and predictions that are potentially broadly applicable, because first-order watersheds occupy 80%–90% of large river basins and study watersheds are representative of forest history in the Pacific Northwest region.

Plain Language Summary

Our analysis combines experimental studies of old-growth and young Douglas-fir forests, along with history of disturbance, as significant predictors of watershed-scale productivity and streamflow in Pacific Northwest landscapes. By integrating geophysical and ecological measurements, we calculated differences in water use efficiency among managed and unmanaged watersheds since the 1850s, providing evidence for carbon-water tradeoffs in forests of varying ages from 1984 to 2017. Our data show that forest carbon-water balance scales with tree growth depending on forest history, with old-growth forests producing more biomass per unit water evapotranspired than planted forests; and greater sensitivity to climate fluctuations in planted than in old-growth forests.

1. Introduction

Forest ecosystems play a central role in climate change mitigation and adaptation. They remove carbon dioxide from the atmosphere and provide a range of cultural and socioeconomic benefits to communities worldwide (H. Lee et al., 2023). Forest conservation and restoration represent a large share of climate change mitigation potential (~7.3 $GtCO_2$-eq yr^{-1}, Shukla et al., 2022). However, tradeoffs with water and nutrient use limit ecosystem carbon sequestration (Baldocchi & Penuelas, 2019), and land use history affects carbon storage through disturbances such as logging, fire, and tree planting. While the broader theme of carbon and resource-use tradeoffs has been well explored, its integration into predictive functions that work across different forest histories remains a challenge. The vast majority of ecological observations are made at resolutions ≤ 1 m^2, either unreplicated or infrequently repeated (Estes et al., 2018), and few studies have attempted to link changes in tree productivity and water use to broader patterns in ecosystem structure and function. The present study seeks to fill this gap by combining tree growth data with long-term climate and streamflow data to develop reconstructions and predictions at the landscape scale. This linkage is important for understanding multi-scale interactions in complex landscapes, particularly those managed for multiple uses, which have been increasingly recognized for their role in climate change mitigation and adaptation strategies (Chafe et al., 2024; Novick et al., 2024; Silva, 2022).

Forests of the Pacific Northwest (PNW) play a key role in the US carbon balance (Gray et al., 2016), and serve as a model for the nation and beyond (Silva et al., 2022). Throughout the region, intensively managed Douglas-fir plantations over the past century have replaced most of the area formerly in mature and old-growth forest (Spies et al., 2019), shifting the age distribution and structure of PNW forests toward denser and younger stands (Johnson & Swanson, 2009). At the same time, declining summer precipitation and increasing evapotranspiration (ET) driven by rising temperatures (Abatzoglou et al., 2014) brought some PNW forests to "the verge of switching from carbon sinks to carbon sources" (Baldocchi et al., 2018). These compounding pressures impact people and ecosystems across the PNW and other regions where rapid expansion of forest plantations correlates with decreases in streamflow (Iroumé et al., 2021; Lara et al., 2021), potentially contributing to global reductions in land water availability (Zhang et al., 2023), and resurfacing long-standing questions about the water cost of carbon sequestration (Jackson et al., 2005).

Understanding the interconnected changes in tree growth, forest productivity, streamflow, and ET is important for maintaining the ecological and hydrological integrity of forested landscapes, even in water-rich areas of the PNW. Young forests, which require more nutrients and water than older stands, often lead to significant reductions in landscape-scale water yields and dry-season streamflow due to intensive plantation forestry focused on rapid tree growth (Crampe et al., 2021; Liles et al., 2019; Perry & Jones, 2017). This reduction in dry-season streamflow can lead to persistent decreases in fish habitat availability, with modeled impacts ranging from 20% to 50% during summer low-flow periods (Gronsdahl et al., 2019). Additionally, intensive forestry practices in young, dense forests increase the risk of severe wildfires, influenced by homogenized fuels rather than pre-fire biomass, affecting wildfire risk and fire management strategies (Deak et al., 2024; Zald & Dunn, 2018). Moreover, forest interactions with climate change have increased uncertainties in hydropower supply predictions (Markoff & Cullen, 2008) and have led to modifications in reservoir management throughout the region (Jones & Hammond, 2020).

Recent research has generated considerable debate over whether old or young forests sequester more carbon and how carbon sequestration in forests with differing histories is affected by climate and drought. A recent study leveraging the Global Forest Age Database found a larger carbon sink in young stands regenerating after disturbance than in old-growth stands and noted that nearly half the sink in regrowth stands could be attributed to demographic changes (Pugh et al., 2019). However, contrary to the long-held view that tree growth rates decline with age, Stephenson et al. (2014) found that a tree's growth can accelerate throughout its lifetime, over many hundreds of years. Additionally, a recent study involving over 20,000 trees across five continents found that old-growth trees exhibit a higher drought tolerance than their younger counterparts (Au et al., 2022). In many cases, tree growth rate can decline over time for tree species in secondary or disturbed stands, whereas growth trends can increase in older forests as shown in a study of >3,800 trees of >40 species (Anderson-Teixeira et al., 2022). So, our ability to predict tree growth patterns and their influence on the carbon stocks of young and old forests is still quite limited.

Remote sensing offers the potential for broader scale assessments of aboveground carbon stocks. It has been used to scale up carbon dynamics from plots to landscapes, using for example Landsat-derived indices of greenness and wetness to discriminate young, mature, and old-growth forest age classes in the PNW (Cohen et al., 1996; Lefsky et al., 2005). However, it remains unclear whether greenness and wetness indices also enable tracking year to year variations in live biomass accumulation. Uncertainties inherent in remotely sensed data can significantly impact the accuracy of these estimates. For example, satellite-derived data products often face challenges such as the saturation effect, which can result in the underestimation of gross primary productivity or net primary productivity (NPP) in densely vegetated areas over time (Xiao et al., 2019). According to these authors, uncertainties in satellite-derived canopy cover can lead to significant errors in the output produced by prognostic process-based models, requiring additional information on historical disturbances, such as land cover changes, forest age, and fire history, to improve predictions of terrestrial carbon stocks. As another example, the response of canopies to changes in water availability is a major source of uncertainty in satellite-derived data, which can lead to systematic underestimation of ecosystem sensitivity to drought, in some cases misrepresenting carbon and water budgets in Earth System Models (Green et al., 2024). So, it is important that we focus on fundamental processes operating at intermediate scales, from trees to ecosystems, to advance basic understanding and improve predictions in this field.

Long-term watershed and vegetation studies provide intermediate spatial and temporal scales for testing hypotheses and for quantitatively reconstructing or predicting relationships among tree growth, water use, and forest

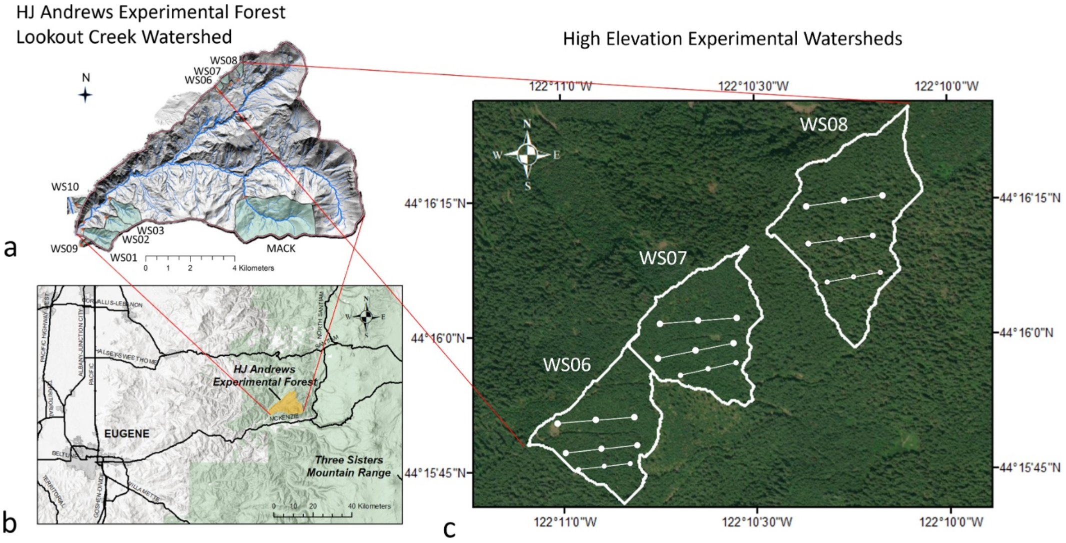

Figure 1. Location of (a) the H.J. Andrews Experimental Forest, (b) relative to Eugene, Oregon, and (c) sampling transects in WS06, WS07, and WS08. Source of map in Panel (a): Adapted from *andrewsforest.oregonstate.edu*.

history. Building on long-term research at the H.J. Andrews Experimental Forest, this study combines new data on Douglas-fir radial growth and analysis of remotely-sensed imagery with climate and hydrology data from paired watershed experiments with old-growth and young planted forests, aimed at answering three questions:

1. How do tree growth rates, streamflow, remotely sensed canopy greenness, and wetness, and soil C and N differ among watersheds with contrasting ages and forest histories?
2. How does water use efficiency; that is, biomass increment per unit of ET, depend on forest history?
3. What factors best predict carbon-water tradeoffs in watersheds with differing forest histories?

In forested landscapes, the physiological responses of dominant tree species to environmental stressors (e.g., climate variability), is hypothesized to drive coupled variation in primary productivity and water use across multiple spatiotemporal scales (e.g., Correa-Diaz et al., 2023; Uscanga et al., 2023, 2024). For the particular case of Douglas-fir dominated forests of the PNW, we expect productivity at both the tree and watershed scale to be more sensitive to drought and carbon-water tradeoffs are expected to be steeper (i.e., higher water loss through ET per unit of carbon fixed) in young forest plantations than in old-growth forest. This general hypothesis is based on processes that can vary across forest structure and stand age gradients, as observed in: (a) well known physiological mechanisms linking canopy transpiration and energy budget leading to predictable patterns in ecosystem water use and carbon assimilation (Bernacchi & VanLoocke, 2015); (b) alterations of hydrologic processes caused by logging of old-growth forest more than 50 years ago, which continue to modify streamflow today due to impacts on transpiration, interception, snowmelt, and flow routing (Crampe et al., 2021); and (c) stronger microclimatic buffering effects on rising temperatures expected for old-growth forests compared to young forest plantations (Frey et al., 2016). The multiscale data integration and analyses devised to test this hypothesis may be broadly applicable, because first-order watersheds similar to those studied at H.J. Andrews, occupy 80%–90% of large river basins and are representative of forest history in the PNW.

2. Methods

2.1. Study Site

The study was conducted in three small (13–22 ha) watersheds (hereafter WS06, WS07, and WS08) at the H.J. Andrews Experimental Forest (hereafter "Andrews Forest") in the western Cascade Range of Oregon (44.23°N, 122.18°W) (Figure 1, Table 1). These watersheds are broadly representative of regional wildfire history and forest management since 1500 CE (Johnson & Swanson, 2009; Weisberg & Swanson, 2003).

Elevation ranges from 860 to 1,190 m and area-averaged slope gradients are >30%. The climate is Mediterranean with wet winters and dry summers. Mean daily temperature ranges from 1°C (December) to 17°C (July) at

Table 1
Characteristics of Study Watersheds in the H.J. Andrews Experimental Forest

Watershed	Area (ha)	Max elevation (m asl)	Soil type	LAI (m^2/m^2)	Basal area (m^2/ha)	Douglas-fir density (stems/ha)	Forest history
6	13	1,029	Andesitic deposits	3.18 ± 0.27	35 ± 9	699	100% clear-cut 1974, broadcast burn
7	15.4	1,102	Andesitic deposits	3.45 ± 0.78	23 ± 10	551	60% overstory harvest 1974; partial broadcast burn; remaining canopy removed 1984; 12% basal area thin 2001
8	21.4	1,182	Andesitic deposits	3.81 ± 0.80	86 ± 24	144	Stand-replacing wildfire, ~1,500, multiple moderate-severity wildfires 1800–1850

Note. Average ground-based leaf area index (LAI) was measured in June 2019 at 27 locations in each watershed (Figure 1). Basal area and stem density of Douglas-fir are from surveys in 2008 and 2009 (Harmon et al., 2023; Perry & Jones, 2017).

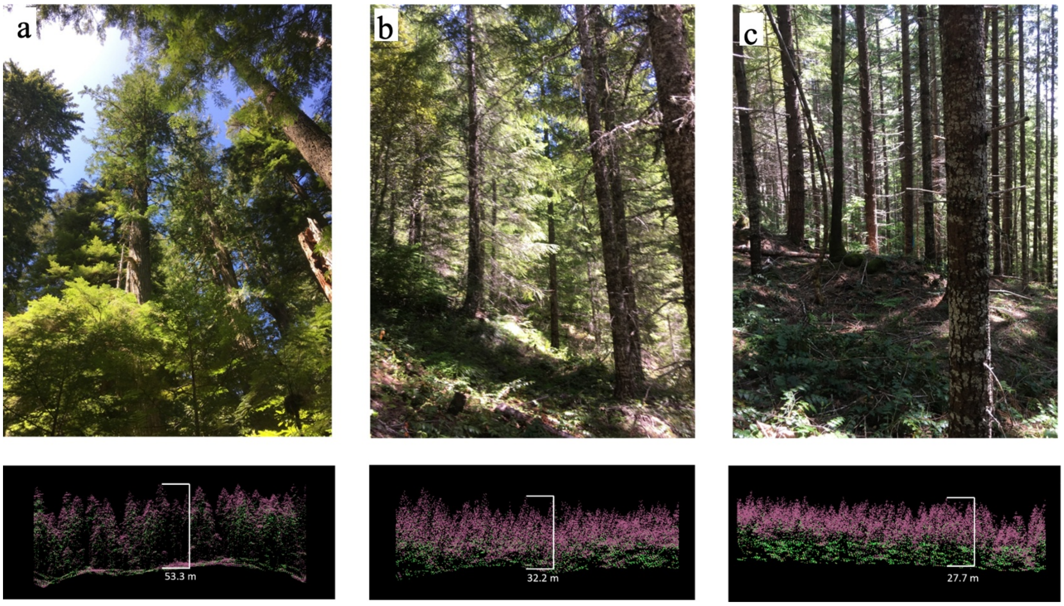

Figure 2. Photographs and lidar profiles from the center of (a) WS08 = mature/old-growth forest; (b) WS07—young forest planted after shelterwood cut, followed by removal of overstory and thinning, and (c) WS06 = young forest planted after clearcutting (Table 1). Canopy height was determined from 2008 lidar imagery using ArcMap version 10.8. Photos: M. Farinacci (2020).

1,300 m. Mean annual precipitation is 2300 mm, and >75% of precipitation falls between November and April. Actual ET (mean annual precipitation minus mean annual streamflow) is 45% of precipitation. Average snowpack water equivalent on April 30 exceeds 700 mm (30% of annual precipitation), and snow may persist from November through June. Soils are derived from andesitic bedrock; soil texture is loam to sandy gravelly loam with 5%–20% gravel content by volume (Dyrness & Hawk, 1972). Large portions of WS06, WS07, and WS08 are mapped as deep earthflow deposits (Swanson & James, 1975), so surface topography is not a reliable indicator of watershed boundaries. Mean water residence times are 1–3 years (McGuire et al., 2005; Segura, 2021).

The original vegetation was mature and old-growth forest established after stand-replacing fire circa 1500 CE and multiple episodes of moderate-severity wildfire in the first half of the 1800s (Teensma, 1987). Native forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). As of 1970, vegetation in WS06 and WS07 consisted largely of second-growth (125-year-old post-fire) Douglas-fir with scattered old-growth (approximately 450 years old) Douglas-fir in certain locations, while stands in WS08 were 33% old-growth Douglas-fir and 70% 125-year-old post-fire Douglas-fir; estimated basal areas in 1972 were 70 ± 10.5, 75 ± 4.8, and 83 ± 8.3 m^2/ha in WS06, WS07, and WS08, respectively (Dyrness & Hawk, 1972). Genetic variation of Douglas-fir is quite high within the Andrews Forest (R. K. Campbell, 1979; R. K. Campbell & Franklin, 1981).

WS06 was 100% clear-cut in 1974, 90% of logs were yarded uphill by a high-lead cable system, and the remaining 10% was yarded by tractor (Table 1). The site was broadcast burned after logging and planted with Douglas-fir (Experimental Watersheds and Gauging Stations, 2017). WS07 was shelterwood cut in 1974, when approximately 60% of basal area was removed and 12 to 16 trees per hectare were left as overstory. Logs were tractor logged in the upper portion of the watershed and cable logged in the lower portion. The cable-logged portion of WS07 was broadcast burned in 1975, and Douglas-fir seedlings were planted in 1976. The remainder of the overstory was removed from WS07 in 1984, and in 2001, the upper portion of WS07 was thinned to 4.5 m spacing, leaving 81 trees per hectare. At the time of this study (2019), WS06 consisted of approximately 45-year-old planted forest, WS07 consisted of 35 to 45-year-old planted and thinned forest, and WS08 was mature and old growth forest dominated by trees aged approximately 170 years with occasional trees aged approximately 500 years. Overstory canopy density exceeded 90%, with a leaf area index (LAI) >3 and obvious structural differences (e.g., tree density, canopy cover, and height) attributable to different histories (Figure 2).

2.2. Climate, Streamflow, and Vegetation Data

Mean daily air temperature and total precipitation were obtained from the CS2MET meteorological station (−122.249, 44.214) (Daly et al., 2019). Mean daily streamflow were obtained for 1963 to 2017 (Johnson et al., 2020). No streamflow data were collected at WS07 for 1988 through 1994. Monthly and annual unit-area streamflow (mm) were calculated for each watershed and adjusted to provide equal average values in the pre-treatment period (water years 1964–1973) when all watersheds had the same forest history and structure (Table S1 in Supporting Information S1, Dyrness & Hawk, 1972). Monthly and annual actual ET were calculated for each watershed as precipitation minus unit-area streamflow. Monthly ET values therefore also include changes in soil water storage; both are expected to be relevant to year to year variations in tree growth within a watershed.

Individual trees have been measured at 6-year intervals since 2002 in 250 m^2 plots ($n = 22$ for WS06, $n = 24$ for WS07) (Harmon et al., 2023) and at ∼5-year intervals since 1979 in 1,000 m^2 plots ($n = 22$ for WS08) (Franklin et al., 2023). Tree diameter distributions and basal area of all trees and Douglas-fir were estimated for the most recent available data (2008 and 2014 for WS06 and WS07, 2009 and 2015 for WS08) (Figure S1 in Supporting Information S1), and watershed basal area (Table 2) was used to scale tree-level measurements to the watershed scale.

2.3. Basal Area Increment of Live Trees, Soil C and N, Forest Structure

Individual trees were sampled following methods and sample sizes of prior studies (e.g., Camarero et al., 2018; Castruita-Esparza et al., 2019; Correa-Díaz et al., 2020; Giguère-Croteau et al., 2019; Maxwell et al., 2018; Quadri et al., 2021; Silva et al., 2016). Trees and soils were sampled along three, 100-m transects parallel to contour centered within each watershed (Figure 1c). Five living healthy dominant trees, identified using visual inspection of trunk and canopy, were sampled along each transect (5 trees per transect, 15 trees per watershed, 45 total). An increment core was collected and diameter was measured at each tree at 1.5 m above ground. Trees sampled in WS08 date from the 1850s, after moderate-severity fire(s) in a ∼300-yr-old stand that had regenerated after region-wide fires of ∼1500 CE. Hence, these trees originated from local seed sources and established gradually under partial shade. On average over eight centuries in the central western Cascades or Oregon, it took 43.5 years to reach establishment of 90% of the trees in post-fire stands (Tepley et al., 2014). In contrast, trees sampled in the stands in WS06 and WS07 grew from seedlings of cultivated stock and from abundant local seed sources. Sampled trees were in the fourth quartile of the distribution of trees in WS06 and WS07, and the third quartile in WS08 (Figure S1, Table S2 in Supporting Information S1).

Variations in annual tree growth for dominant species serve as proxies for NPP, which can be deduced from tree rings across a broad range ort forest ecosystems (Evans et al., 2022; Jevon et al., 2022; Silva & Anand, 2013; Xu et al., 2017). In our study, variation in tree growth patterns were determined using increment cores and standard dendrochronology procedures. Cores were oven-dried, mounted, sanded, polished, and digitally scanned to obtain ring widths using an open source software (image-J). Annual ring width index (RWI, unitless) and basal area increment (BAI, $cm^2\ yr^{-1}$) was determined for each tree and year using the dplR package (Bunn, 2008). The average and standard error of annual BAI was calculated for each year for all sampled trees in each watershed (Farinacci, 2020) and water use efficiency was defined as the ratio between BAI and ET. Standing biomass can be estimated from our measurements of basal area and canopy height using well-established allometric scaling relationships applicable to Douglas-fir trees and many other species, regardless of age or size (Grier & Logan, 1977; Halpern et al., 1996; Jenkins et al., 2003). However, data on canopy height derived from lidar (Figure 2) are collected much less frequently than annual BAI data, limiting our ability to approximate changes in ecosystem biomass over time within the scope of this study.

A large literature has established how annual BAI and soil C and N are related to whole ecosystem dynamics for young, mature, and old-growth Douglas-fir dominated forests in the PNW. These studies include work on live and dead biomass (Chen et al., 2004; Denison et al., 1972; Grier & Logan, 1977; Halpern et al., 1996), tree mortality (Bible, 2001), trends in live and dead biomass (Acker et al., 2002; Janisch & Harmon, 2002), decomposition (Harmon et al., 1986), and net ecosystem production (J. Campbell, 2004; Gholz, 1982) in young, mature, and old-growth forests. These studies, some of which are based on vegetation plots in the study sites, have established the basic components of relationships among annual growth, live and dead biomass, and above- and below-ground carbon. For example, it is known that rates of live biomass accumulation decline with stand age (Acker et al., 2002), but dead and down wood increases with stand age (Harmon, 2021), resulting in much greater carbon

Table 2
Correlation Matrix of All Annual Variables, 1984–2017, for Each Watershed

	RWI	BAI	NDVI	NDWI	SF	ET	T_{avg}
WS06							
RWI							
BAI	0.166						
NDVI	−0.117	0.415*					
NDWI	−0.123	0.479**	0.887***				
SF	0.126	−0.117	0.027	0.172			
ET	0.349*	0.519**	0.000	0.001	0.025		
T_{avg}	0.064	−0.170	−0.013	−0.151	−0.249	−0.219	
P_{tot}	0.351*	0.345*	0.016	0.102	0.606***	0.810***	−0.320
WS07							
RWI							
BAI	0.334						
NDVI	0.168	0.622***					
NDWI	0.167	0.667***	0.859***				
SF	0.056	−0.283	−0.191	0.001			
ET	0.175	0.370	0.111	0.214	0.314		
T_{avg}	−0.026	−0.242	−0.074	−0.245	−0.186	−0.271	
P_{tot}	0.169	0.248	0.046	0.189	0.550**	0.966***	−0.290
WS08							
RWI							
BAI	0.913***						
NDVI	0.166	0.208					
NDWI	0.042	0.103	0.786***				
SF	0.004	0.052	−0.061	0.125			
ET	0.325	0.310	−0.086	−0.206	0.348*		
T_{avg}	−0.090	−0.186	0.026	−0.205	−0.324	−0.233	
P_{tot}	0.246	0.256	−0.092	−0.099	0.709***	0.907***	−0.320

Note. Variables are ring width index (RWI, unitless), average tree-level basal area increment (BAI, mm^2), greenness (NDVI, unitless), wetness (NDWI, unitless), streamflow (SF, mm), evapotranspiration (ET, mm), mean daily temperature (T_{avg}, °C), and precipitation (P_{tot}, mm). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

storage in older stands and watersheds (e.g., Argerich et al., 2016; Harmon et al., 1990; Lajtha & Jones, 2018; B. S. Lee & Lajtha, 2016; Smithwick et al., 2002; Stephenson et al., 2014; Zald et al., 2016). However, most publications on forest carbon dynamics do not explore interannual changes and, to the best of our knowledge, none has examined how interannual carbon accumulation is related to water and energy balances at the watershed scale over multiple decades.

Our study therefore focuses on two key forest variables: tree growth and soil properties. We used BAI as the only annually resolved metric available that can serve as a proxy for above-ground production, allowing us to reconstruct productivity over centuries, and that can be related to long-term climate and streamflow data. Consistent with studies of soil dynamics in the PNW (Crow et al., 2009; Homann et al., 2004; Pierson, Evans, et al., 2021; Pierson, Peter-Contesse, et al., 2021), we use changes in soil C and N as proxies for changes in whole ecosystem dynamics beyond those recorded in BAI and aboveground biomass.

Soil samples were obtained using a soil auger to extract ~200 g of bulk soil at 0–20, 20–40, and 40–60 cm depths at three locations along each of three transects (9 locations, 3 depths, 27 samples per watershed, except at WS07, where $n = 25$) (Farinacci, 2020). Soil samples were oven-dried at 50°C for 72 hr, subsamples (30 g) of the <2 mm fraction were ground, and total C and N (percent) were determined using a Costech ECS-4010 elemental combustion analyzer. For the estimation of C and N stocks (total mass per area), we used ~75-g undeformed bulk density samples collected at 0–20 and 20–40 cm depth at three locations in each watershed using cylindrical metal cups designed to prevent compacting the soil. A hemispherical photo was obtained at each sampling location, and stand-level ecosystem structure and LAI was determined (Farinacci, 2020; Frazer et al., 1999) (Table 1, Figure 2).

2.4. Remote Sensing

Canopy profiles for the sampled area in the center of each watershed were generated from 2008 lidar data obtained from the National Oceanic and Atmospheric Association using the LAS Toolbar in ArcMap version 10.5 (Figure 2). Average canopy height was calculated for each watershed from bare earth digital elevation models and first return digital surface models using the Raster Calculator tool in ArcMap (Farinacci, 2020). Values of normalized difference vegetation index (NDVI), an indicator of forest productivity (Myneni et al., 1995) and normalized difference water index (NDWI), an indicator of canopy water status (Gao, 1996) were calculated for a 2.25-ha (1,500 × 1,500 m) area centered in each watershed (19.2% of WS06,16.2% of WS07%, and 11.6% of WS08) for each year, 1984 to 2017.

Surface reflectance imagery was acquired for the area of each watershed and processed through Google Earth Engine to calculate NDVI and NDWI for all images between 1984 and 2017 using 30-m resolution Landsat data (Farinacci, 2020). All available images for each year and pixel were collected and a cloud mask was used to remove any anonymously low NDVI and NDWI images, determined using a threshold analysis of significant deviations from surrounding pixels that form the contiguous canopy of each watershed (Uscanga et al., 2024). Spatial windows (5 × 5 of 30-m pixels) were selected as the area to be analyzed from each watershed. The spatial windows were placed in the center of the watershed, away from roads and parking lot clearings. Once the raw data were filtered to each spatial window, all data from Landsat 5 and Landsat 8 were homogenized to Landsat 7 values using the following equations (Su et al., 2017):

$$\mathrm{NDVI}_{\mathrm{Landsat5\_homogenized}} = \mathrm{NDVI}_{\mathrm{Landsat5}} \times 1.1307 - 0.0571$$

$$\mathrm{NDVI}_{\mathrm{Landsat8\_homogenized}} = \mathrm{NDVI}_{\mathrm{Landsat8}} \times 0.9938 - 0.0167$$

$$\mathrm{NDWI}_{\mathrm{Landsat5\_homogenized}} = \mathrm{NDWI}_{\mathrm{Landsat5}} \times 1.10375 - 0.0346$$

$$\mathrm{NDWI}_{\mathrm{Landsat8\_homogenized}} = \mathrm{NDWI}_{\mathrm{Landsat8}} \times 0.9748 - 0.0117$$

The final analysis was based on 997 quality-controlled Landsat images from which time series data were derived. Area-under-the-curve (AUC) calculations were performed on these time series to obtain integrated measures of productivity and water use over time. This method involves calculating the area between data points of NDVI and NDWI indices, and aggregating these areas to derive annual values within polygons of each watershed. This approach parallels techniques used in recent ecological monitoring and management studies, including: Araya et al. (2016) who used phenologic metrics derived from AUC calculations to assess available water and vegetation dynamics; Pastick et al. (2021) who applied AUC integration to estimate biomass accumulation of invasive species, aiding in their early detection in the western United States; and Thaler et al. (2023) who used AUC integration to train machine learning models that predict changes in permafrost distribution based on phenological patterns.

2.5. Statistical Analysis

Relationships among environmental variables (ET, streamflow, air temperature, and precipitation) and forest variables (tree BAI, canopy greenness and wetness, soil carbon and nitrogen concentrations and stocks) were assessed using bivariate correlations. Temporal trends in growth and climate were assessed using least-squares regressions. Mixed-effect models related annual water yield measured at streamflow gages (dependent variable) to annual precipitation and mean annual temperature, annual tree growth BAI, annual average canopy greenness and wetness from remotely sensed data, and forest history (independent variables) using nlme in R. Differences in C, N, and C:N (dependent variables) by watershed and soil depth (independent variables) was

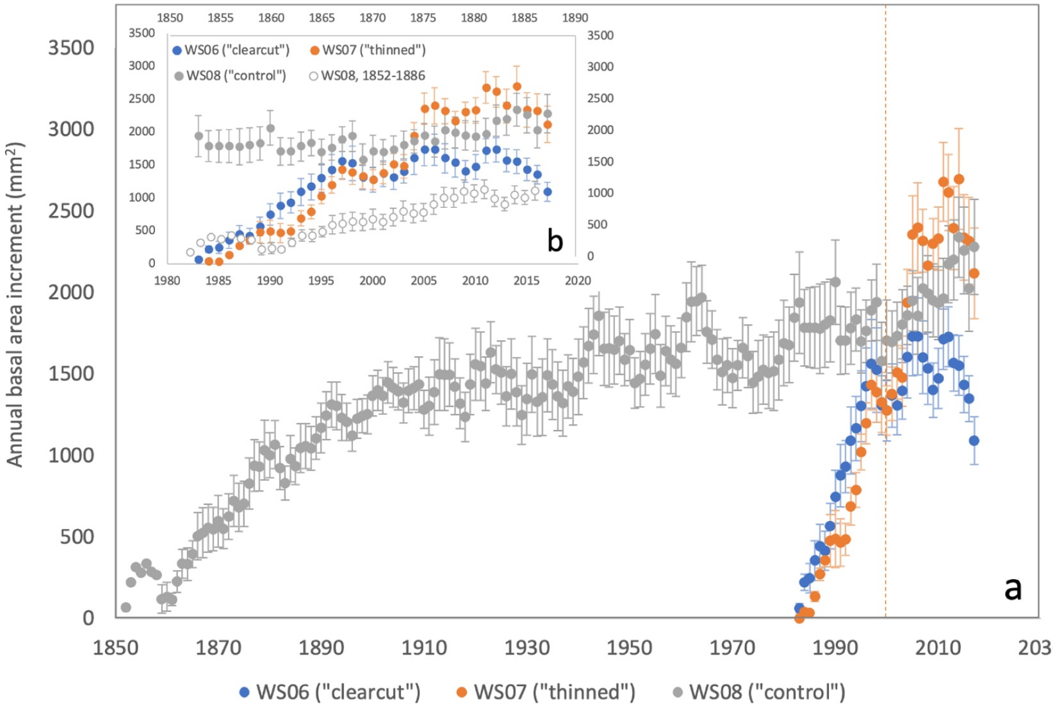

Figure 3. Average and standard error of annual basal area increment (BAI) of dominant Douglas-fir trees ($n = 15$ per watershed) for (a) 1852 to 2017 in WS06 (100% clear-cut in 1974 and planted), WS07 (50% shelterwood cut in 1974, partly planted, remaining overstory removed 1984, thinned in 2001), and WS08 (mature and old-growth forest regenerated after fires in the early 1800s). Inset (b) annual BAI for the first 25 years after the earliest tree establishment date, 1980 to 2017 in WS06, WS07, and WS08, compared to 1850 to 1887 in WS08. Earliest tree establishment dates were 1983 for WS06, 1984 for WS07, and 1852 for WS08.

evaluated using two-way analysis of variance. Soil C, N, and C:N data were log transformed prior to analysis. Means with significant differences were identified using Tukey post-hoc tests. All statistical analyses were performed in R using the following packages: dplR, treeClim, plyr, sjPlot, detrendeR, and agricolae (Farinacci, 2020).

3. Results

There were no significant trends in annual precipitation in the study site over the study period (1984–2017). Air temperature increased, especially in midwinter (January) and summer (July–September), and summer precipitation declined, consistent with regional trends (Farinacci, 2020; Washington State Climatologist, 2023).

Average tree-level BAI differed markedly between old-growth and young forests from 1850 to 2017 (Figure 3a). Tree BAI in the mature and old-growth watershed (WS08) increased from <5 cm^2/year in the 1850s and 1860s to ~15 cm^2/year in the early 1900s and reached >23 cm^2/year by the 2010s. After 2010, tree BAI declined ~30% in the young thinned forest (WS07) and ~37% in the young unthinned forest (WS06), but it continued to increase steadily in the mature/old-growth forest (WS08). From 2005 to 2015, the average annual tree-level BAI in the young thinned forest watershed (WS07, 24 ± 2 cm^2/year) was slightly greater than in the mature/old-growth watershed (WS08, 21 ± 2 cm^2/year), and least in the young unthinned forest watershed (WS06, 15 ± 2 cm^2/year) (Figures 3a and 3b). Trees in planted forest (WS06 and WS07) grew at ~15 cm^2/year in the 1980s and 2000s, whereas trees of similar age in naturally regenerating post-fire stands (WS08) grew at ~5–10 cm^2/year in the 1870s and 1880s (Figure 3b).

Streamflow and precipitation were strongly positively related (WS06 $r^2 = 0.601$, $P < 0.001$; WS07 $r^2 = 0.550$, $P < 0.001$; WS08 $r^2 = 0.706$, $P < 0.001$). Annual BAI and RWI were not related to annual temperature or annual precipitation, except for a weak relationship of BAI to annual precipitation at WS06 (Table 2). Temporal trends in RWI did not differ among watersheds (Figure S2a in Supporting Information S1) or as a function of cambial age

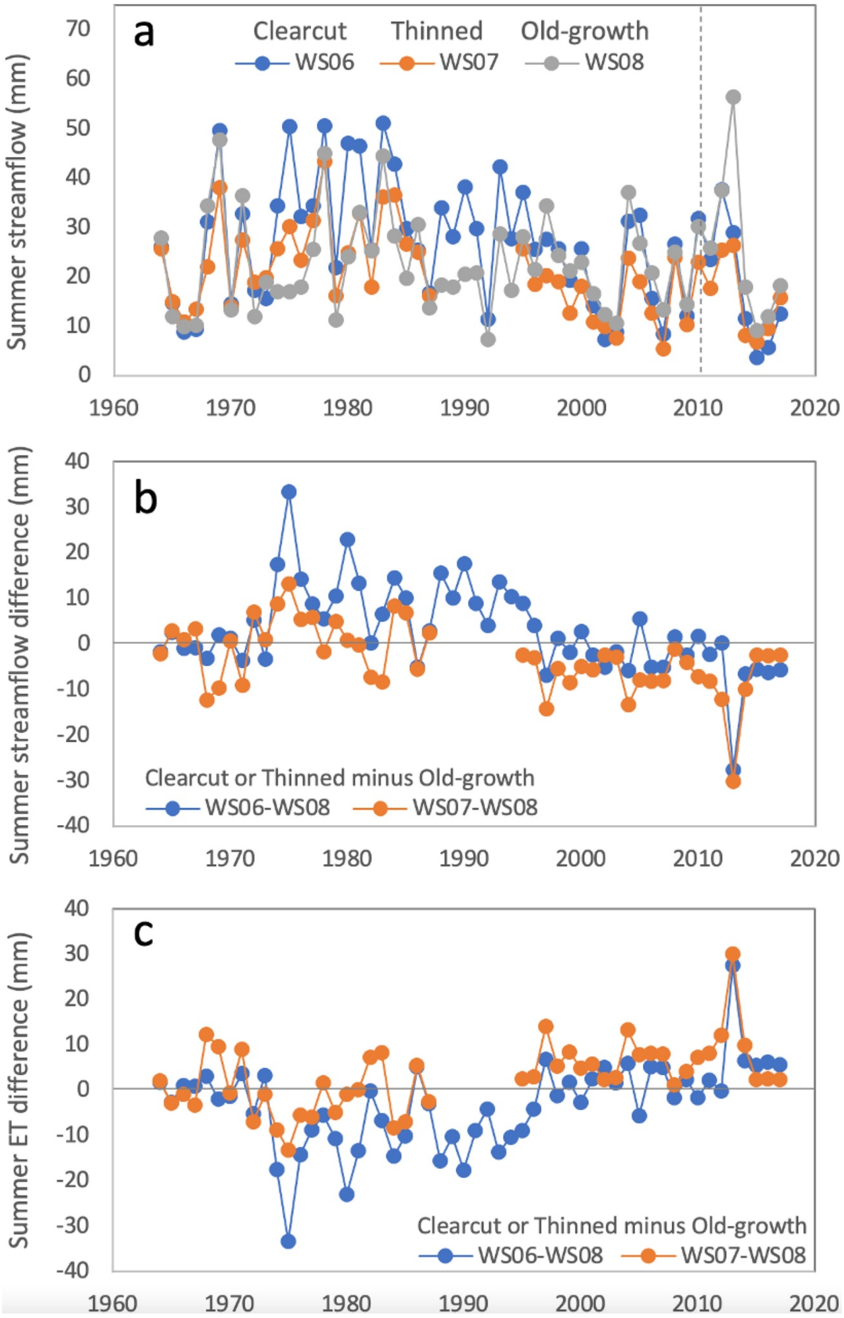

Figure 4. Watershed scale hydrological measurements: (a) summer streamflow, July-September, showing higher streamflow in the young forest watersheds (WS06, WS07) compared to the mature/old-growth forest watershed (WS08) in the mid-1970s to mid 1990s, when trees in WS06 and WS07 were aged 0–20 years, followed by lower streamflow in WS06 and WS08 than in WS08, especially after 2010; (b) summer streamflow differences (treated minus control) showing a major decline in ecosystem water supply over time in young forest (WS06, WS07) relative to old forest (WS08); and (c) summer evapotranspiration differences (treated minus control) showing a major increase in ecosystem water use over time in young forest (WS06, WS07) relative to old forest (WS08).

(Figure S2b in Supporting Information S1). Summer streamflow and summer ET were not related to BAI ($R^2 < 0.1$; data not shown).

Nevertheless, since 2010 marked declines in young trees but not in old-growth trees (Figure 3) coincide with changes in streamflow and ET (Figure 4). After 2010, summer streamflow was lower than in any prior period in

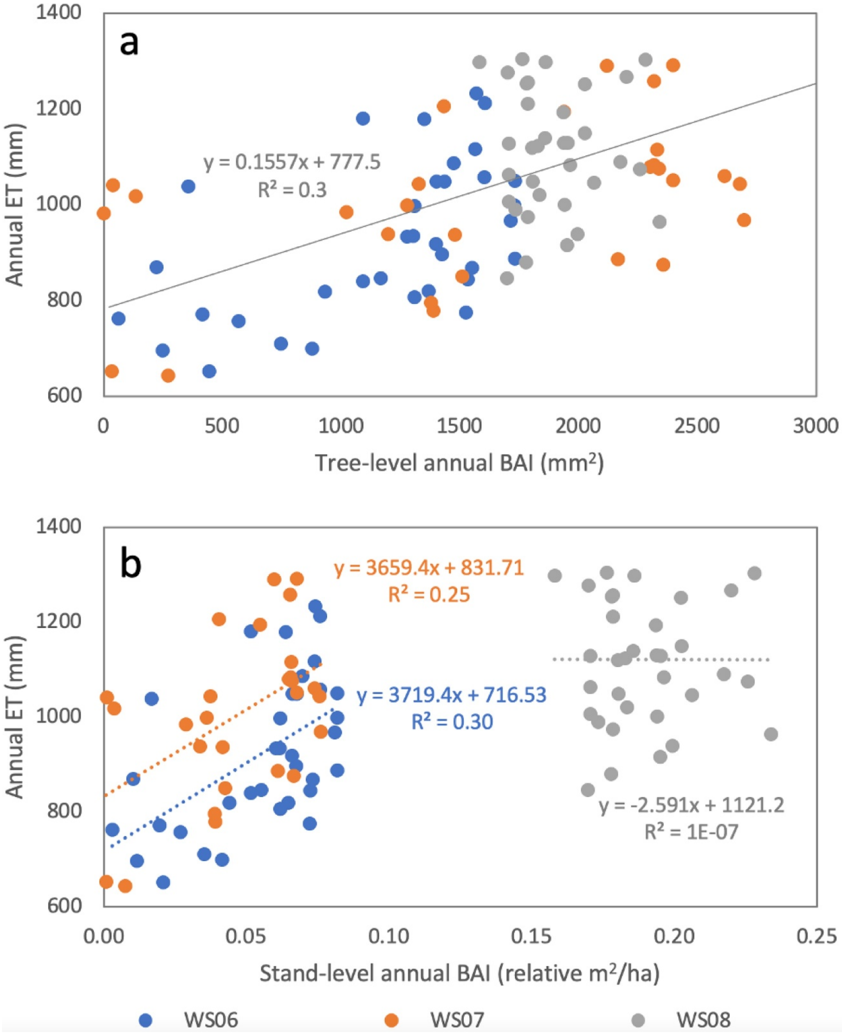

Figure 5. Relationship between annual evapotranspiration and tree basal area increment (BAI) of dominant Douglas-fir trees, 1983–2017. (a) Average annual tree-level BAI ($n = 15$ trees per watershed, Figure 3) versus annual evapotranspiration and (b) average annual stand-level BAI versus annual evapotranspiration. Relative BAI per hectare is determined by rescaling average annual tree-level values based on 2008 relative basal area (Table 1), WS08 = 1, WS06 = 0.47, WS07 = 0.28 (Figure 1).

the record (Figure 4a). Summer streamflow after 2010 was consistently lower (Figure 4b), and ET was consistently higher (Figure 4c) in the watersheds with young forest (WS06, WS07) than in the watershed with mature and old-growth forest (WS08). Summer (July-September) streamflow was higher in WS08 than in WS06 or WS07 from 2005 to 2017, and much higher in 2013, a year with an unusually wet September (Figure 4b). Overall, summer ET in the young forest watersheds (WS06, WS07) was about twice that in the mature/old growth forest watershed (WS08) (Figure 4c).

Average tree-level BAI was weakly positively related to annual ET across all watersheds for 1983 to 2017 (Figure 5a, $r^2 = 0.36$; $p < 0.01$), indicating that higher growth was associated with greater water use by trees. Stand-level BAI was strongly related to annual ET in the young forest (WS06, WS07), but not in the mature/old-growth forest (Figure 5b). Stand-level BAI was higher in the 35 to 45-yr-old planted and thinned watershed (WS07) than in the 45-yr-old planted forest that was not thinned (WS06), but this higher growth was associated with ~100 mm higher water use per year on average (Figure 5b). Stand-level BAI (scaled by watershed basal area) per unit of ET, a measure of water use efficiency, was almost five times greater in the mature/old growth watershed (WS08) than in the young forest watersheds (WS06, WS07).

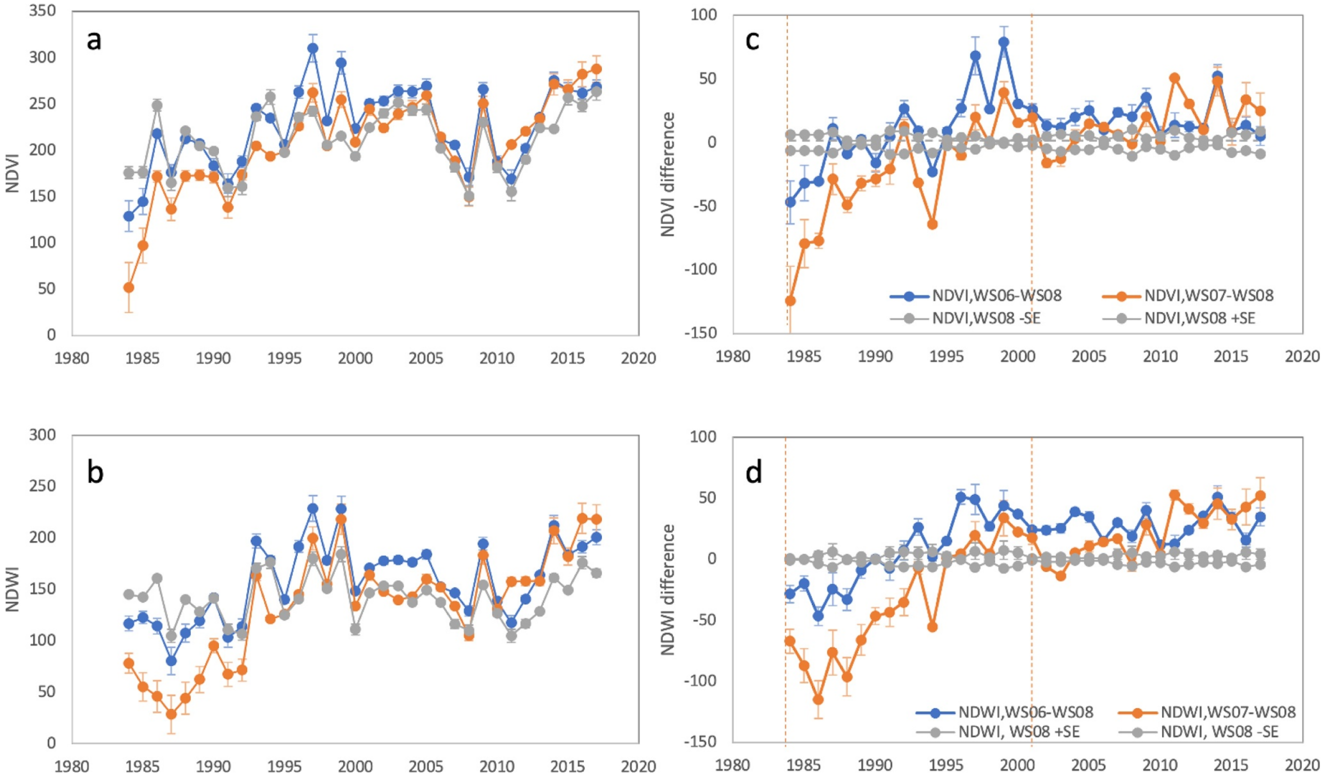

Figure 6. Remotely-sensed indices based on a 2.25-ha plot centered in each watershed for (a) canopy greenness (normalized difference vegetation index); (b) wetness (normalized difference water index); and differences in greenness (c) and wetness (d) between young unthinned forest (WS06, blue symbols) and young thinned forest (WS07, orange symbols) compared with mature/old-growth forest (WS08, gray symbols) over the period 1984 to 2017. Vertical dashed lines are dates of removal of remaining overstory (1984) and pre-commercial thin (2001) in WS07.

Temporal patterns of canopy greenness (NDVI) and wetness (NDWI) increased from 1985 to the mid 1990s and then were relatively flat; patterns were similar for WS06, WS07, and WS08 (Figures 6a and 6b). Greenness and wetness were lower in young planted forest (WS06, WS07) than in the old forest until planted stands reached canopy closure at ~20 years of age in the mid 1990s (Figures 6c and 6d). Greenness and wetness were higher in young forest than in old forest after the mid 1990s (Figures 6c and 6d), but BAI was higher in old forest than young forest in most of those years (Figure 3). Year-to-year changes in canopy greenness and wetness were not related to changes in BAI or summer moisture. For example, from 2008 to 2009, greenness and wetness increased, BAI changed very little, and summer ET increased slightly (Table 2, Figures 3b, 4a, 6a, and 6b). Ecosystem-scale greenness (NDVI) and wetness (NDWI) were positively related to BAI in young planted forests (WS06, WS07), but not in the mature/old-growth forest (WS08) (Table 2).

Precipitation, forest history (i.e., cutting, planting, and thinning), and BAI (average and standard errors) explained most variation in streamflow over the period 1984 to 2017 (Figure 7a). Average BAI was positively associated with precipitation amounts and thus with streamflow, whereas increasing variation in BAI measured as standard errors were negatively associated with variation in streamflow over time. Remotely- sensed greenness and wetness indices did not explain variation in streamflow because greenness and wetness indices become saturated at high leaf areas (Zhu & Liu, 2015) characteristic of these forest stands (Figures 2, 7b, and 7c). NDVI and NDWI was unrelated to BAI in the study sites except when trees were <15 years old (Figures 7b and 7c). Greenness and wetness also were unrelated to precipitation, temperature, or streamflow (Table 2). Hence, greenness and wetness indices did not capture differences in BAI or water use efficiency (BAI per unit of ET) among the study watersheds.

Soil C, N, and C:N did not vary significantly among watersheds at any depth, and bulk density did not vary significantly among watersheds at the 0–20 cm depth (Figure S3 in Supporting Information S1). C and N in the 0–20 cm layer were more variable, C at 40–60 cm was lower, and bulk density at 20–40 cm was lower at WS07 than at WS06 or WS08. Soil C was concentrated the 0–20 cm layer in WS07 (71% of total) and distributed more evenly with depth in WS06 and WS08.

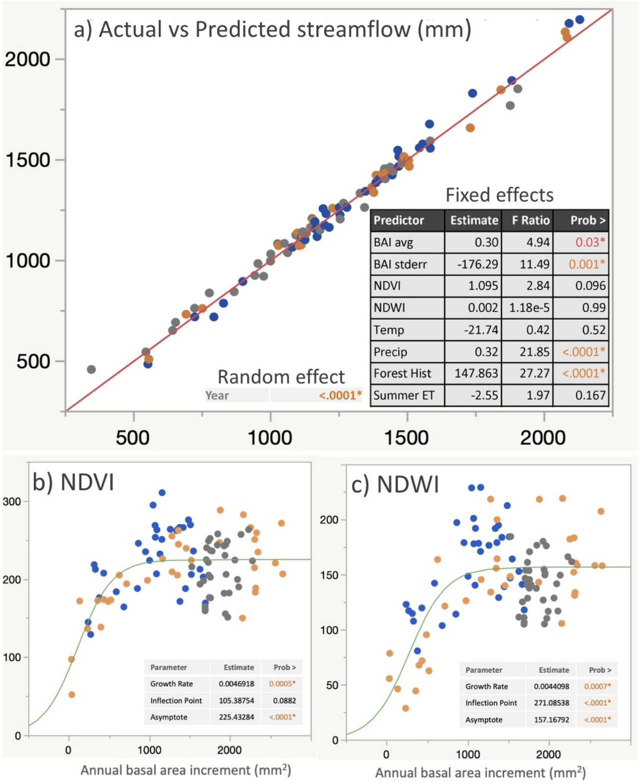

Figure 7. Mixed effects model (a) showing actual (*Y* axis) versus predicted (*X* axis) streamflow from 1984 to 2017. Coefficient estimates and F-ratios, the ratio of the between group variance to the within group variance represent significance probability effects for basal area increment (average and standard error), forest history, canopy greenness and wetness (normalized difference vegetation index (NDVI) and normalized difference water index (NDWI)), temperature and precipitation, as fixed effects, and year as random effect. Logistic functions relating canopy greenness (b) and wetness (c) with BAI with growth rate, inflection point, and asymptote. Asymptotes are interpreted as saturation thresholds beyond which NDVI and NDWI indices did not capture observed changes in tree growth, watershed productivity, or evapotranspiration (Figures 4 and 5). Blue symbols represent young planted, unthinned Douglas-fir forest (WS06), orange symbols represent young planted, thinned forest (WS07), gray symbols represent mature/old-growth forest (WS08).

4. Discussion

This study showed that tree growth rates, streamflow, and remotely sensed canopy greenness and wetness differed, but soil C and N did not differ, among watersheds with contrasting forest disturbance histories. Supporting our hypothesis, productivity and water use were coupled at multiple scales, with growth at both the tree and watershed level being more sensitive to drought and carbon-water tradeoffs being steeper in young forests than in old-growth forest. Tree growth rates, expressed as average BAI was higher in 20 to 40-yr-old planted, recently thinned Douglas-fir (WS07), and lower in 30 to 40-yr-old unthinned Douglas-fir (WS06), than in mature/old Douglas-fir (WS08) (Figure 3). Summer streamflow was lower and summer ET was higher in young forest (WS06, WS07) than in mature/old-growth forest (WS08) after young forest reached canopy closure (Figure 4). Tree BAI in young forests (WS06, WS07) declined to levels below that of mature/old Douglas-fir (WS08) during summer drought in 2015–2017. NDVI and NDWI were higher in young than old forest (Figure 6) and not related to tree growth rates (Figures 7b and 7c).

Water use efficiency differed based on forest history. Tree-level BAI was positively related to ET (1984–2017) in all three watersheds (Figure 5a), but stand-level growth was positively related to water use only in young forest (Figure 5b). Stand-level water use efficiency (i.e., BAI per unit of ET) was much higher in the mature/old-growth forest watershed (WS08) than in young planted forest (WS06, WS07) (Figures 4 and 5). Remotely-sensed greenness and wetness indices did not explain variation in streamflow (Figures 7b and 7c). Yet, consistent with previous work on tree ring variance as "early warning signs or regime shifts in coupled human-environment systems" (Bauch et al., 2016) BAI (average and standard errors) were significant predictors of watershed-scale streamflow, albeit with different coefficient signs (positive for BAI average and negative for BAI standard error; Figure 7a). This result emphasizes the importance of within watershed variation in productivity in interpreting the effects of precipitation and forest history on tree growth rates, which explained most variation in streamflow over the period 1984 to 2017.

Scaling of carbon-water tradeoffs from the tree to the watershed was possible because of long-term vegetation, streamflow, and climate studies. We sampled the most representative cohort within each watershed, including larger Douglas-fir trees within the mature/old-growth than the young forest (DBH in WS08 >2× that of WS06 and WS07, Figure S1 in Supporting Information S1). This selection criterion is conservative because growth rates of montane forest species, including many dominant pines and firs (i.e., *Pinus* spp. and *Abies* spp.) vary predictably with cambial age and tree size in many different ecosystems (e.g., Correa-Diaz et al., 2023; Quadri et al., 2021; Silva, 2017; Silva et al., 2016). At H.J. Andrews, long-term streamflow and climate measurements permitted calculation of differences in water use and water use efficiency among watersheds. These findings are consistent with regional and local studies of carbon in PNW forests. For example, Gray et al. (2016) found significant though modest C accumulation in forests aged 200–400 years, based on measurements of change in live and dead wood biomass from 8,767 inventory plots on 9.1 million ha of forest lands. In the study watersheds, tree biomass is 5–10 times higher (dead and down wood, stumps/snags, and forest floor litter are 2–3 times higher) in mature/old-growth forest watershed (WS08) compared to harvested and replanted forests (WS06, WS07) (Lajtha & Jones, 2018).

Our tree-level results are consistent with published studies showing that old trees have higher tree-level growth and are more drought resistant than young trees (Anderson-Teixeira et al., 2022; Au et al., 2022; Stephenson et al., 2014). Findings of this study also are consistent with faster growth (e.g., Manrique-Alba et al., 2020) and less drought-related tree mortality (C. Restaino et al., 2019) in thinned than unthinned forests. The temporarily higher growth of trees in the thinned forest (WS07) (2005–2014, Figure 3) is consistent with research showing that Douglas-fir growth response to thinning is parabolic, starting low immediately following thinning, reaching a peak or stable level for a period of time, and then declining as pre-thinning competition is re-established (Briggs & Kantavichai, 2018). Overall, our findings indicate that mature/old-growth forest watersheds have higher stand-level BAI and higher water use efficiency than young forest watersheds. The study watersheds are typical of first-order watersheds, which occupy most of large river basins and are representative of regional forest disturbance history. By scaling results from the tree to the watershed, this study contributes to the debate about carbon-water tradeoffs in young versus mature/old-growth forests. At the watershed scale, although younger forests may exhibit rapid growth and carbon uptake, the substantial carbon reserves of old-growth forests, coupled with continued basal growth of old trees and their greater resistance to drought, confirm expectations of increasing carbon sequestration in old trees despite age-related declines in forest productivity (Silva, 2017).

The lower BAI per unit of ET in the young forest compared to mature/old-growth forest is consistent with other studies showing reductions in streamflow in rapidly growing young Douglas-fir forest compared to mature/old-growth forest (Crampe et al., 2021; Perry & Jones, 2017; Segura et al., 2020). In our study, carbon accumulation was directly related to ET in the young forest watersheds (WS06, WS07), demonstrating a strong carbon-water tradeoff, but carbon accumulation was unrelated to water use in the mature/old-growth forest watershed (WS08) (Figure 5b). Tree growth in young forests also declined during a recent summer drought but continued to increase in the mature/old-growth forest. The greater sensitivity of young forest to summer drought is consistent with research showing that recent increases in temperature and vapor pressure deficit and reductions in summer soil moisture likely have reduced Douglas-fir growth in the PNW (Jarecke et al., 2023; Jiang et al., 2019; E. H. Lee et al., 2022; C. M. Restaino et al., 2016).

The findings of this study related to NDVI and NDWI reveal potential limitations of large-scale remotely sensed studies in detecting carbon-water tradeoffs. Our results indicate that while these indices can identify broad-scale patterns of vegetation and moisture, they may not capture trends in BAI, a key indicator of carbon accumulation in live trees. Although NDVI and NDWI have been successfully used to link productivity and water use in other ecosystems (Correa-Díaz et al., 2020), these indices did not vary with tree growth in the dense Douglas-fir forests that cover the study watersheds. Remotely sensed analyses missed key differences in carbon sequestration among forests with different resource use and histories of disturbance, emphasizing the need for ground-based measurements to complement remotely-sensed estimates of carbon stocks. For example, ground-based measurements conducted in this study, are consistent with physiological mechanisms that link canopy transpiration and C assimilation (Bernacchi & VanLoocke, 2015), reflecting the effects of logging on hydrological processes (Crampe et al., 2021), and a stronger microclimatic buffering effect of old-growth forests compared to younger forests (Frey et al., 2016).

The lack of significant differences in soil C and N between logged and undisturbed watersheds is consistent with long-term detrital input and removal treatment (DIRT) experiments (Lajtha et al., 2018). Across all DIRT experiments, soil C pools responded only slightly, or not at all, to chronic doubling of aboveground litter inputs, presumably because litter additions stimulate microbial decomposition of new inputs and old soil organic matter. In our study, clearcutting of prior mature/old-growth forest followed by broadcast burning disturbed soils and reduced litter inputs temporarily in WS06, whereas three logging entries (shelterwood cut including tractor logging and limited broadcast burning, removal of the remaining overstory, and thinning) disturbed soils and increased litter and fine wood inputs in WS07. Soil disturbance and litter additions may account for the higher variability of soil C and N, the slightly higher C:N ratio, and lower bulk density of soil in WS07 compared to WS06 and WS08 (Figure S3 in Supporting Information S1). Overall, these findings illustrate the resilience of soils to infrequent forest disturbances.

Finally, the studied watersheds are broadly representative of forest history in the PNW, including regional wildfire history and forest management since 1500 CE (Johnson & Swanson, 2009; Weisberg & Swanson, 2003). Extrapolating these results to other regions would require a nuanced understanding of forest history and additional factors influencing carbon and water cycling across spatial and temporal scales. Such extrapolation could provide valuable insights and test emerging hypotheses and predictions of changes in ecosystem structure and function under climate change (e.g., Hunter et al., 2023; Maxwell & Silva, 2020; Silva & Lambers, 2020) in the PNW and beyond.

5. Conclusion

This study showed that young forests have lower water use efficiency and are more sensitive to drought than mature/old-growth forest, based on tree growth rates and long-term streamflow, climate, and vegetation studies in paired watersheds at the H.J. Andrews Experimental Forest in Oregon, USA. Young forests displayed strong carbon-water tradeoffs, and growth declined during periods of summer drought, whereas carbon accumulation in aboveground biomass and ET were not strongly related, and tree growth is less sensitive to drought in mature/old-growth forest. Trees in young forests grew rapidly after logging of mature/old-growth forest, but tree growth rates peaked at ~30 years and declined sharply in response to drought. Thinning temporarily increased tree growth rates in young forest above those of old-growth trees, but ET also increased, reducing water use efficiency and streamflow. Tree growth in young forests was sensitive to fluctuations in climate and declined during a recent summer drought. In contrast, tree growth continued to increase steadily in mature/old-growth forest despite summer drought, and unit area summer streamflow (July to September) remained two times higher than in the young forest watersheds.

Overall, our findings indicate that old-growth forest watersheds store and accumulate more carbon, are more drought resistant, and better sustain water availability compared to young forests. Testing hypotheses that relate carbon-water tradeoffs from the tree to the watershed scale and from seasons to centuries was possible because of long-term vegetation, streamflow, and climate studies. By nesting studies of individual trees within watershed studies with long-term vegetation, climate, and streamflow data, this analysis provided new insights and transfer functions that may be useful to quantify and predict carbon-water tradeoffs that are not apparent in studies based simply on individual trees or remotely sensed vegetation indices. Our results contribute to the ongoing debate regarding the carbon sequestration capabilities of young versus mature/old-growth forests. They highlight the crucial role of old-growth forests in carbon storage, emphasizing their resilience to drought and their continued growth and carbon uptake even at advanced ages. These findings are potentially broadly applicable because first-order watersheds like the study watersheds represent most of the total area in large river basins. Moreover, these watersheds are broadly representative of regional wildfire history and forest management since 1500 CE. Long-term experiments hold exceptional potential to uncover the influence of climate fluctuations and human disturbances on ecosystem carbon and water balances, both historically and into the future.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Long-term climate, streamflow, and vegetation datasets for the study watersheds can be obtained at the H.J. Andrews Forest data repository: http://andlter.forestry.oregonstate.edu/data/catalog/datacatalog.aspx. Subsets of data from that repository were selected to generate figures and tables for this study, including: daily temperature and precipitation https://doi.org/10.6073/pasta/c021a2ebf1f91adf0ba3b5e53189c84f; mean daily streamflow for 1963 to 2017 https://doi.org/10.6073/pasta/0066d6b04e736af5f234d95d97ee84f3; individual tree data measured at 5- or 6-year intervals in 250 m^2 plots https://doi.org/10.6073/pasta/4b7bc8c4f8e8a2b7bba96ada2f9cd643 and in 1000 m^2 plots https://doi.org/10.6073/pasta/5835a1fadb7fd65842f90256edae999c. Additionally, new tree ring and soil C and N data used in the main text figures and supplementary materials are enclosed in this manuscript and available at https://scholarsbank.uoregon.edu/xmlui/handle/1794/25891.

Acknowledgments
This study was supported by funding from the NSF Long-term Ecological Research (LTER) program to the Andrews Forest LTER (NSF 1440409 and 2025755), Convergence Accelerator and Rules of Life programs (NSF 1939511 and 2319597), and U.S. Forest Service Pacific Northwest Research Station support of hydrology and climate records at the H.J. Andrews Experimental Forest. Mark Schulze provided valuable input on manuscript drafts. Carolyn Fish and Nick Kohler contributed advice on remote sensing. Schyler Reis assisted in field data collection and data interpretation.

References

Abatzoglou, J. T., Rupp, D. E., & Mote, P. W. (2014). Seasonal climate variability and change in the Pacific Northwest of the United States. *Journal of Climate*, *27*(5), 2125–2142. https://doi.org/10.1175/jcli-d-13-00218.1

Acker, S. A., Halpern, C. B., Harmon, M. E., & Dyrness, C. T. (2002). Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. *Tree Physiology*, *22*(2–3), 213–217. https://doi.org/10.1093/treephys/22.2-3.213

Anderson-Teixeira, K. J., Herrmann, V., Rollinson, C. R., Gonzalez, B., Gonzalez-Akre, E. B., Pederson, N., et al. (2022). Joint effects of climate, tree size, and year on annual tree growth derived from tree-ring records of ten globally distributed forests. *Global Change Biology*, *28*(1), 245–266. https://doi.org/10.1111/gcb.15934

Araya, S., Lyle, G., Lewis, M., & Ostendorf, B. (2016). Phenologic metrics derived from MODIS NDVI as indicators for plant available water-holding capacity. *Ecological Indicators*, *60*, 1263–1272. https://doi.org/10.1016/j.ecolind.2015.09.012

Argerich, A., Haggerty, R., Johnson, S. L., Wondzell, S. M., Dosch, N., Corson-Rikert, H., et al. (2016). Comprehensive multiyear carbon budget of a temperate headwater stream. *Journal of Geophysical Research: Biogeosciences*, *121*(5), 1–10. https://doi.org/10.1002/2015JG003050

Au, T. F., Maxwell, J. T., Robeson, S. M., Li, J., Siani, S. M., Novick, K. A., et al. (2022). Younger trees in the upper canopy are more sensitive but also more resilient to drought. *Nature Climate Change*, *12*(12), 1168–1174. https://doi.org/10.1038/s41558-022-01528-w

Baldocchi, D., Chu, H., & Reichstein, M. (2018). Inter-annual variability of net and gross ecosystem carbon fluxes: A review. *Agricultural and Forest Meteorology*, *249*, 520–533. https://doi.org/10.1016/j.agrformet.2017.05.015

Baldocchi, D., & Penuelas, J. (2019). The physics and ecology of mining carbon dioxide from the atmosphere by ecosystems. *Global Change Biology*, *25*(4), 1191–1197. https://doi.org/10.1111/gcb.14559

Bauch, C., Sigdel, R., Pharaon, J., & Anand, M. (2016). Early warning signals of regime shifts in coupled human–environment systems. *Proceedings of the National Academy of Sciences*, *113*(51), 14560–14567. https://doi.org/10.1073/pnas.1604978113

Bernacchi, C. J., & VanLoocke, A. (2015). Terrestrial ecosystems in a changing environment: A dominant role for water. *Annual Review of Plant Biology*, *66*(1), 599–622. https://doi.org/10.1146/annurev-arplant-043014-114834

Bible, K. J. (2001). *Long-term patterns of Douglas-fir and western hemlock mortality in the western Cascade Mountains of Washington and Oregon, Ph.D. dissertation* (p. 85). University of Washington.

Briggs, D. G., & Kantavichai, R. (2018). Effects of thinning on ring mass growth along stem of Douglas fir in four Coastal Pacific Northwest sites. *Forest Science*, *64*(2), 139–148. https://doi.org/10.1093/forsci/fxx003

Bunn, A. G. (2008). A dendrochronology program library in R (DplR). *Dendrochronologia*, *26*(2), 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Camarero, J. J., Sánchez-Salguero, R., Sangüesa-Barreda, G., & Matías, L. (2018). Tree species from contrasting hydrological Niches show divergent growth and water-use efficiency. *Dendrochronologia*, *52*, 87–95. https://doi.org/10.1016/j.dendro.2018.10.003

Campbell, J. (2004). *Carbon fluxes across three climatically-distinct forest chronosequences in Oregon, Ph.D. dissertation* (p. 133). Oregon State University.

Campbell, R. K. (1979). Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology*, *60*(5), 1036–1050. https://doi.org/10.2307/1936871

Campbell, R. K., & Franklin, J. F. (1981). A comparison of habitat type and elevation for seed-zone classification of Douglas-fir in western Oregon. *Forest Science*, *27*(1), 49–59.

Castruita-Esparza, L. U., Silva, L. C., Gómez-Guerrero, A., Villanueva-Díaz, J., Correa-Díaz, A., & Horwath, W. R. (2019). Coping with extreme events: Growth and water-use efficiency of trees in western Mexico during the driest and wettest periods of the past one hundred sixty years. *Journal of Geophysical Research: Biogeosciences*, *124*(11), 3419–3431. https://doi.org/10.1029/2019jg005294

Chafe, O. E., Broz, A. P., Levenson, E. S., Farinacci, M. D., Anderson, R. O., & Silva, L. C. R. (2024). The spatiotemporal domains of natural climate solutions research and strategies for implementation in the Pacific Northwest, USA. *Frontier in Climate*, *6*, 1273632. https://doi.org/10.3389/fclim.2024.1273632

Chen, J., Song, B., Rudnicki, M., Moeur, M., Bible, K., North, M., et al. (2004). Spatial relationship of biomass and species distribution in an old-growth Pseudotsuga-Tsuga forest. *Forest Science*, *50*(3), 364–375. https://doi.org/10.1093/forestscience/50.3.364

Cohen, W. B., Harmon, M. E., Wallin, D. O., & Fiorella, M. (1996). Two decades of carbon flux from forests of the Pacific Northwest: Estimates from a new modeling strategy. *BioScience*, *46*(11), 836–844. https://doi.org/10.2307/1312969

Correa-Díaz, A., Silva, L. C. R., Horwath, W. R., Gómez-Guerrero, A., Vargas-Hernández, J., Villanueva-Díaz, J., et al. (2020). From trees to ecosystems: Spatiotemporal scaling of climatic impacts on montane landscapes using dendrochronological, isotopic and remotely-sensed data. *Global Biogeochemical Cycles*, *34*(3), e2019GB006325. https://doi.org/10.1029/2019GB006325

Correa-Díaz, A., Villanueva-Díaz, J., Gómez-Guerrero, A., Martínez-Bautista, H., Castruita-Esparza, L. U., Horwath, W. R., & Silva, L. C. R. (2023). A comprehensive resilience assessment of Mexican tree species and their relationship with drought events over the last century. *Global Change Biology*, *29*(13), 3652–3666. https://doi.org/10.1111/gcb.16705

Crampe, E. A., Segura, C., & Jones, J. A. (2021). Fifty years of runoff response to conversion of old-growth forest to planted forest in the H. J. Andrews forest, Oregon, USA. *Hydrological Processes*, *35*(5), e14168. https://doi.org/10.1002/hyp.14168

Crow, S. E., Lajtha, K., Bowden, R. D., Yano, Y., Brant, J. B., Caldwell, B. A., & Sulzman, E. W. (2009). Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. *Forest Ecology and Management*, *258*(10), 2224–2232. https://doi.org/10.1016/j.foreco.2009.01.014

Daly, C., Schulze, M., & McKee, W. (2019). Meteorological data from benchmark stations at the HJ Andrews experimental forest, 1957 to present. Long-term ecological research [Dataset]. *Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/c021a2ebf1f91adf0ba3b5e53189c84f

Deak, A. L., Lucash, M. S., Coughlan, M. R., Weiss, S., & Silva, L. C. R. (2024). Prescribed fire placement matters more than increasing frequency and extent in a simulated Pacific Northwest landscape. *Ecosphere*, *15*(4), e4827. https://doi.org/10.1002/ecs2.4827

Denison, W. C., Tracy, D. M., Rhoades, F. M., & Sherwood, M. (1972). Direct, nondestructive measurement of biomass and structure in living, old-growth Douglas-fir. In *Research on coniferous forest ecosystems: First year progress in the coniferous forest biome, US/IBP: Proceedings of a symposium, 1972 March 23–24, Bellingham, WA. Portland, OR* (pp. 147–158). U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Dyrness, C. T., & Hawk, G. (1972). *Vegetation and soils of the Hi-15 watersheds, H.J. Andrews experimental forest* (p. 28). University of Washington; Coniferous For. Biome Internal Report 43.

Estes, L., Elsen, P. R., Treuer, T., Ahmed, L., Caylor, K., Chang, J., et al. (2018). The spatial and temporal domains of modern ecology. *Nature Ecology & Evolution*, *2*(5), 819–826. https://doi.org/10.1038/s41559-018-0524-4

Evans, M. E. K., DeRose, R. J., Klesse, S., Girardin, M. P., Heilman, K. A., Alexander, M. R., et al. (2022). Adding tree rings to North America's national forest inventories: An essential tool to guide Drawdown of atmospheric CO_2. *BioScience*, *72*(3), 233–246. https://doi.org/10.1093/biosci/biab119

Experimental Watersheds and Gauging Stations. (2017). H. J. Andrews experimental forest. Retrieved from https://andrewsforest.oregonstate.edu/research/infrastructure/watersheds

Farinacci, M. (2020). *Impacts of management on forest response to climate variability in Oregon's Cascades. MS thesis*. University of Oregon. Retrieved from https://scholarsbank.uoregon.edu/xmlui/handle/1794/25891

Franklin, J., Bell, D., Remillard, S., & Powers, M. (2023). Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present. Long-Term Ecological Research [Dataset]. *Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/5835a1fadb7fd65842f90256edae999c

Frazer, G. W., Canham, C. D., & Lertzman, K. P. (1999). *Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999*. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies.

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gao, B.-C. (1996). NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment*, *58*(3), 257–266. https://doi.org/10.1016/s0034-4257(96)00067-3

Gholz, H. L. (1982). Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, *63*(2), 469–481. https://doi.org/10.2307/1938964

Giguère-Croteau, C., Boucher, É., Bergeron, Y., Girardin, M. P., Drobyshev, I., Silva, L. C. R., et al. (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*(7), 2749–2754. https://doi.org/10.1073/pnas.1816686116

Gray, A. N., Whittier, T. R., & Harmon, M. E. (2016). Carbon stocks and accumulation rates in Pacific Northwest forests: Role of stand age, plant community, and productivity. *Ecosphere*, *7*(1), e01224. https://doi.org/10.1002/ecs2.1224

Green, J. K., Zhang, Y., Luo, X., & Keenan, T. F. (2024). Systematic underestimation of canopy conductance sensitivity to drought by Earth System Models. *AGU Advances*, *5*(1), e2023AV001026. https://doi.org/10.1029/2023av001026

Grier, C. C., & Logan, R. S. (1977). Old-growth Pseudotsuga menziesii communities of a western Oregon watershed: Biomass distribution and production budgets. *Ecological Monographs*, *47*(4), 373–400. https://doi.org/10.2307/1942174

Gronsdahl, S., Moore, R. D., Rosenfeld, J., McCleary, R., & Winkler, R. (2019). Effects of forestry on summertime low flows and physical fish habitat in snowmelt-dominant headwater catchments of the Pacific Northwest. *Hydrological Processes*, *33*(25), 3152–3168. https://doi.org/10.1002/HYP.13580

Halpern, C. B., Miller, E. A., & Geyer, M. A. (1996). Equations for predicting above-ground biomass of plant species in early successional forests of the western Cascade Range, Oregon. *Northwest Science*, *70*(4), 306–320.

Harmon, M., O'Connell, K., & Bell, D. (2023). Plant biomass dynamics following logging, burning, and thinning in Watersheds 6 and 7, Andrews Experimental Forest, 1979 to present. Long-Term Ecological Research [Dataset]. *Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/4b7bc8c4f8e8a2b7bba96ada2f9cd643

Harmon, M. E. (2021). The role of woody detritus in biogeochemical cycles: Past, present, and future. *Biogeochemistry*, *154*(2), 349–369. https://doi.org/10.1007/s10533-020-00751-x

Harmon, M. E., Ferrell, W. K., & Franklin, J. F. (1990). Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, *247*(4943), 699–702. https://doi.org/10.1126/science.247.4943.699

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., et al. (1986). Ecology of coarse woody debris in temperate ecosystems. In A. MacFadyen & E. D. Ford (Eds.), *Advances in ecological research* (Vol. 15, pp. 133–302). Academic Press, Inc. https://doi.org/10.1016/s0065-2504(08)60121-x

Homann, P. S., Remillard, S. M., Harmon, M. E., & Bormann, B. T. (2004). Carbon storage in coarse and fine fractions of Pacific Northwest old-growth forest soils. *Soil Science Society of America Journal*, *68*(6), 2023–2030. https://doi.org/10.2136/sssaj2004.2023

Hunter, B. D., Roering, J. J., Almond, P. C., Chadwick, O. A., Polizzotto, M. L., & Silva, L. C. (2023). Pedogenic pathways and deep weathering controls on soil organic carbon in Pacific Northwest forest soils. *Geoderma*, *436*, 116531. https://doi.org/10.1016/j.geoderma.2023.116531

Iroumé, A., Jones, J., & Bathurst, J. C. (2021). Forest operations, tree species composition and decline in rainfall explain runoff changes in the Nacimiento experimental catchments, south central Chile. *Hydrological Processes*, *35*(6), e14257. https://doi.org/10.1002/hyp.14257

Jackson, R. B., Jobbágy, E. G., Avissar, R., Roy, S. B., Barrett, D. J., Cook, C. W., et al. (2005). Trading water for carbon with biological carbon sequestration. *Science*, *310*(5756), 1944–1947. https://doi.org/10.1126/science.1119282

Janisch, J. E., & Harmon, M. E. (2002). Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. *Tree Physiology*, *22*(2–3), 77–89. https://doi.org/10.1093/treephys/22.2-3.77

Jarecke, K. M., Hawkins, L. R., Bladon, K. D., & Wondzell, S. M. (2023). Carbon uptake by Douglas-fir is more sensitive to increased temperature and vapor pressure deficit than reduced rainfall in the western Cascade Mountains, Oregon, USA. *Agricultural and Forest Meteorology*, *329*, 109267. https://doi.org/10.1016/j.agrformet.2022.109267

Jenkins, J. C., Chojnacky, D. C., Heath, L. S., & Birdsey, R. A. (2003). National-scale biomass estimators for United States tree species. *Forest Science*, *49*(1), 12–35. https://doi.org/10.1093/forestscience/49.1.12

Jevon, F. V., Polussa, A., Lang, A. K., William Munger, J., Wood, S. A., Wieder, W. R., & Bradford, M. A. (2022). Patterns and controls of aboveground litter inputs to temperate forests. *Biogeochemistry*, *161*(3), 335–352. https://doi.org/10.1007/s10533-022-00988-8

Jiang, Y., Kim, J. B., Trugman, A. T., Kim, Y., & Still, C. J. (2019). Linking tree physiological constraints with predictions of carbon and water fluxes at an old-growth coniferous forest. *Ecosphere*, *10*(4), e02692. https://doi.org/10.1002/ecs2.2692

Johnson, K. N., & Swanson, F. J. (2009). Historical context of old-growth forests in the Pacific Northwest—Policy, practices, and competing worldviews. In T. A. Spies & S. L. Duncan (Eds.), *Old growth in a new world: A Pacific northwest icon reexamined, chapter 2* (pp. 12–28). Island Press.

Johnson, S., Wondzell, S., & Rothacher, J. (2020). Stream discharge in gaged watersheds at the HJ Andrews experimental forest, 1949 to present. Long-term ecological research [Dataset]. *Forest Science Data Bank, Corvallis, OR*. https://doi.org/10.6073/pasta/0066d6b04e736af5f234d95d97ee84f3

Jones, J. A., & Hammond, J. C. (2020). River management response to multi-decade changes in timing of reservoir inflows, Columbia River Basin, USA. *Hydrological Processes*, *34*(25), 4814–4830. https://doi.org/10.1002/hyp.13910

Lajtha, K., Bowden, R. D., Crow, S., Fekete, I., Kotroczó, Z., Plante, A., et al. (2018). The detrital input and removal treatment (DIRT) network: Insights into soil carbon stabilization. *Science of the Total Environment*, *640*, 1112–1120. https://doi.org/10.1016/j.scitotenv.2018.05.388

Lajtha, K., & Jones, J. (2018). Forest harvest legacies control dissolved organic carbon export in small watersheds, western Oregon. *Biogeochemistry*, *140*(3), 299–315. https://doi.org/10.1007/s10533-018-0493-3

Lara, A., Jones, J., Little, C., & Vergara, N. (2021). Streamflow response to native forest restoration in former Eucalyptus plantations in south central Chile. *Hydrological Processes*, *35*(8), e14270. https://doi.org/10.1002/hyp.14270

Lee, B. S., & Lajtha, K. (2016). Hydrologic and forest management controls on dissolved organic matter characteristics in headwater streams of old-growth forests in the Oregon Cascades. *Forest Ecology and Management*, *380*(15), 11–22. https://doi.org/10.1016/j.foreco.2016.08.029

Lee, E. H., Beedlow, P. A., Brooks, J. R., Tingey, D. T., Wickham, C., & Rugh, W. (2022). Physiological responses of Douglas-fir to climate and forest disturbances as detected by cellulosic carbon and oxygen isotope ratios. *Tree Physiology*, *42*(1), 5–25. https://doi.org/10.1093/treephys/tpab122

Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., et al. (2023). *IPCC sixth assessment report (AR6): Summary for policymakers*. Intergovernmental Panel on Climate Change.

Lefsky, M. A., Turner, D. P., Guzy, M., & Cohen, W. B. (2005). Combining lidar estimates of aboveground biomass and Landsat estimates of stand age for spatially extensive validation of modeled forest productivity. *Remote Sensing of Environment*, *95*(4), 549–558. https://doi.org/10.1016/j.rse.2004.12.022

Liles, G. C., Maxwell, T. M., Silva, L. C. R., Zhang, J. W., & Horwath, W. R. (2019). Two decades of experimental manipulation reveal potential for enhanced biomass accumulation and water use efficiency in ponderosa pine plantations across climate gradients. *Journal of Geophysical Research: Biogeosciences*, *124*(7), 2321–2334. https://doi.org/10.1029/2019JG005183

Manrique-Alba, À., Beguería, S., Molina, A. J., González-Sanchis, M., Tomàs-Burguera, M., del Campo, A. D., et al. (2020). Long-term thinning effects on tree growth, drought response and water use efficiency at two Aleppo pine plantations in Spain. *Science of the Total Environment*, *728*, 138536. https://doi.org/10.1016/j.scitotenv.2020.138536

Markoff, M. S., & Cullen, A. C. (2008). Impact of climate change on Pacific Northwest hydropower. *Climatic Change*, *87*(3–4), 451–469. https://doi.org/10.1007/s10584-007-9306-8

Maxwell, T. M., & Silva, L. C. (2020). A state factor model for ecosystem carbon–water relations. *Trends in Plant Science*, *25*(7), 652–660. https://doi.org/10.1016/j.tplants.2020.02.007

Maxwell, T. M., Silva, L. C. R., & Horwath, W. R. (2018). Integrating effects of species composition and soil properties to predict shifts in montane forest carbon–water relations. *Proceedings of the National Academy of Sciences*, *115*(18), 201718864. https://doi.org/10.1073/PNAS.1718864115

McGuire, K. J., McDonnell, J. J., Weiler, M., Kendall, C., McGlynn, B. L., Welker, J. M., & Seibert, J. (2005). The role of topography on catchment-scale water residence time. *Water Resources Research*, *41*(5), W05002. https://doi.org/10.1029/2004WR003657

Myneni, R. B., Hall, F. G., Sellers, P. J., & Marshak, A. L. (1995). The interpretation of spectral vegetation indexes. *IEEE Transactions on Geoscience and Remote Sensing*, *33*(2), 481–486. https://doi.org/10.1109/tgrs.1995.8746029

Novick, K. A., Keenan, T. F., Anderegg, W. R. L., Normile, C. P., Runkle, B. R. K., Oldfield, E. E., et al. (2024). We need a solid scientific basis for nature-based climate solutions in the United States. *Proceedings of the National Academy of Sciences*, *121*(14), e2318505121. https://doi.org/10.1073/pnas.2318505121

Pastick, N. J., Wylie, B. K., Rigge, M. B., Dahal, D., Boyte, S. P., Jones, M. O., et al. (2021). Rapid monitoring of the abundance and spread of exotic annual grasses in the western United States using remote sensing and machine learning. *AGU Advances*, *2*, e2020AV000298. https://doi.org/10.1029/2020AV000298

Perry, T. D., & Jones, J. A. (2017). Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA: Summer streamflow deficits from regenerating Douglas-fir forest. *Ecohydrology*, *10*(2), e1790. https://doi.org/10.1002/eco.1790

Pierson, D., Evans, L., Kayhani, K., Bowden, R. D., Nadelhoffer, K., Simpson, M., & Lajtha, K. (2021). Mineral stabilization of soil carbon is suppressed by live roots, outweighing influences from litter quality or quantity. *Biogeochemistry*, *154*(3), 433–449. https://doi.org/10.1007/s10533-021-00804-9

Pierson, D., Peter-Contesse, H., Bowden, R. D., Nadelhoffer, K., Kayhani, K., Evans, L., & Lajtha, K. (2021). Competing processes drive the resistance of soil carbon to alterations in organic inputs. *Frontiers in Environmental Science*, *9*, 527803. https://doi.org/10.3389/fenvs.2021.527803

Pugh, T. A., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., & Calle, L. (2019). Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences*, *116*(10), 4382–4387. https://doi.org/10.1073/pnas.1810512116

Quadri, P., Silva, L. C. R., & Zavaleta, E. S. (2021). Climate-induced reversal of tree growth patterns at a tropical treeline. *Science Advances*, *7*(22), eabb7572. https://doi.org/10.1126/sciadv.abb7572

Restaino, C., Young, D. J. N., Estes, B., Gross, S., Wuenschel, A., Meyer, M., & Safford, H. (2019). Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecological Applications*, *29*(4), e01902. https://doi.org/10.1002/eap.1902

Restaino, C. M., Peterson, D. L., & Littell, J. (2016). Increased water deficit decreases Douglas fir growth throughout western US forests. *Proceedings of the National Academy of Sciences*, *113*(34), 9557–9562. https://doi.org/10.1073/pnas.1602384113

Segura, C. (2021). Snow drought reduces water transit times in headwater streams. *Hydrological Processes*, *35*(12), e14437. https://doi.org/10.1002/hyp.14437

Segura, C., Bladon, K. D., Hatten, J. A., Jones, J. A., Hale, V. C., & Ice, G. G. (2020). Long-term effects of forest harvesting on summer low flow deficits in the Coast Range of Oregon. *Journal of Hydrology*, *585*, 124749. https://doi.org/10.1016/j.jhydrol.2020.124749

Shukla, P. R., Skea, J., Slade, R., Al Khourdajie, A., Vyas, P., Luz, S., et al. (2022). IPCC mitigation of climate change working group III contribution to the sixth assessment. Retrieved from www.ipcc.ch

Silva, L. C. R. (2017). Carbon sequestration beyond tree longevity. *Science*, *355*(6330), 1141. https://doi.org/10.1126/science.aan0109

Silva, L. C. R. (2022). Expanding the scope of biogeochemical research to accelerate atmospheric carbon capture. *Biogeochemistry*, *161*(1), 19–40. https://doi.org/10.1007/s10533-022-00957-1

Silva, L. C. R., & Anand, M. (2013). Probing for the influence of atmospheric CO_2 and climate change on forest ecosystems across biomes. *Global Ecology and Biogeography*, *22*(1), 83–92. https://doi.org/10.1111/j.1466-8238.2012.00783.x

Silva, L. C. R., & Lambers, H. (2020). Soil-plant-atmosphere interactions: Structure, function, and predictive scaling for climate change mitigation. *Plant and Soil*, *461*(1–2), 5–27. https://doi.org/10.1007/s11104-020-04427-1

Silva, L. C. R., Sun, G., Zhu-Barker, X., Liang, Q., Wu, N., & Horwath, W. R. (2016). Tree growth acceleration and expansion of Alpine forests: The synergistic effect of atmospheric and edaphic change. *Science Advances*, *2*(8), e1501302. https://doi.org/10.1126/sciadv.1501302

Silva, L. C. R., Wood, M. C., Johnson, B. R., Coughlan, M. R., Brinton, H., McGuire, K., & Bridgham, S. D. (2022). A generalizable framework for enhanced natural climate solutions. *Plant and Soil*, *479*(1–2), 3–24. https://doi.org/10.1007/s11104-022-05472-8

Smithwick, E. A. H., Harmon, M. E., Remillard, S. M., Acker, S. A., & Franklin, J. F. (2002). Potential upper bounds of carbon stores in forests of the Pacific Northwest. *Ecological Applications*, *12*(5), 1303–1317. https://doi.org/10.1890/1051-0761(2002)012[1303:pubocs]2.0.co;2

Spies, T. A., Long, J. W., Charnley, S., Hessburg, P. F., Marcot, B. G., Reeves, G. H., et al. (2019). Twenty-five years of the Northwest forest plan: What have we learned? *Frontiers in Ecology and the Environment*, *17*(Issue 9), 511–520. https://doi.org/10.1002/fee.2101

Stephenson, N. L., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., Beckman, N. G., et al. (2014). Rate of tree carbon accumulation increases continuously with tree size. *Nature*, *507*(7490), 90–93. https://doi.org/10.1038/nature12914

Su, Y., Bales, R. C., Ma, Q., Nydick, K., Ray, R. L., Li, W., & Guo, Q. (2017). Emerging stress and relative resiliency of giant sequoia groves experiencing multiyear dry periods in a warming climate: Emerging stress of giant sequoia groves. *Journal of Geophysical Research: Biogeosciences*, *122*(11), 3063–3075. https://doi.org/10.1002/2017JG004005

Swanson, F. J., & James, M. E. (1975). Geology and geomorphology of the H.J. Andrews experimental forest, western Cascades, Oregon. In *Research Paper PNW-188*.

Teensma, P. D. A. (1987). *Fire history and fire regimes of the central western Cascades of Oregon, Ph.D. dissertation* (p. 188). University of Oregon.

Tepley, A. J., Swanson, F. J., & Spies, T. A. (2014). Post-fire tree establishment and early cohort development in conifer forests of the western Cascades of Oregon, USA. *Ecosphere*, *5*(7), 1–23. https://doi.org/10.1890/es14-00112.1

Thaler, E. A., Uhleman, S., Rowland, J. C., Schwenk, J., Wang, C., Dafflon, B., & Bennett, K. E. (2023). High-resolution maps of near-surface permafrost for three watersheds on the Seward Peninsula, Alaska derived from machine learning. *Earth and Space Science*, *10*(12), e2023EA003015. https://doi.org/10.1029/2023EA003015

Uscanga, A., Bartlein, P. J., & Silva, L. C. R. (2023). Local and regional effects of land-use intensity on aboveground biomass and tree diversity in tropical montane cloud forests. *Ecosystems*, *26*(8), 1734–1752. https://doi.org/10.1007/s10021-023-00861-1

Uscanga, A., Schuler, S., & Silva, L. C. R. (2024). Incorporating small-scale disturbances in models of forest structure and aboveground biomass of tropical mountains. *Ecosphere*, *15*(2), e4744. https://doi.org/10.1002/ecs2.4744

Washington State Climatologist. (2023). PNW temperature, precipitation, and SWE trend analysis tool. Retrieved from https://climate.washington.edu/climate-data/trendanalysisapp/

Weisberg, P. J., & Swanson, F. J. (2003). Regional synchroneity in fire regimes of western Oregon and Washington, USA. *Forest Ecology and Management*, *172*(1), 17–28. https://doi.org/10.1016/s0378-1127(01)00805-2

Xiao, J., Chevallier, F., Gomez, C., Guanter, L., Hicke, J. A., Huete, A. R., et al. (2019). Remote sensing of the terrestrial carbon cycle: A review of advances over 50 years. *Remote Sensing of Environment*, *233*, 111383. https://doi.org/10.1016/j.rse.2019.111383

Xu, K., Wang, X., Liang, P., An, H., Sun, H., Han, W., & Li, Q. (2017). Tree-ring widths are good proxies of annual variation in forest productivity in temperate forests. *Scientific Reports*, *7*(1), 1945. https://doi.org/10.1038/s41598-017-02022-6

Zald, H. S. J., & Dunn, C. J. (2018). Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. *Ecological Applications*, *28*(4), 1068–1080. https://doi.org/10.1002/eap.1710

Zald, H. S. J., Spies, T. A., Seidl, R., Pabst, R. J., Olsen, K. A., & Steel, E. A. (2016). Complex mountain terrain and disturbance history drive variation in forest aboveground live carbon density in the western Oregon Cascades, USA. *Forest Ecology and Management*, *366*, 193–207. https://doi.org/10.1016/j.foreco.2016.01.036

Zhang, Y., Li, C., Chiew, F. H., Post, D. A., Zhang, X., Ma, N., et al. (2023). Southern Hemisphere dominates recent decline in global water availability. *Science*, *382*(6670), 579–584. https://doi.org/10.1126/science.adh0716

Zhu, X., & Liu, D. (2015). Improving forest aboveground biomass estimation using seasonal Landsat NDVI time-series. *ISPRS Journal of Photogrammetry and Remote Sensing*, *102*, 222–231. https://doi.org/10.1016/j.isprsjprs.2014.08.014